

REVISION OF THE HYBODONT SELACHIAN GENUS *LISSODUS* BROUGH (1935)

REVISION DER HYBODONTEN SELACHIER-GATTUNG *LISSODUS* BROUGH (1935)

BY

CHRISTOPHER J. DUFFIN, Morden^{*)}

with 7 plates, 27 figures and 1 table in the text

Zusammenfassung

Lissodus (Unterkarbon bis Oberkreide) ist eine Gattung der hybodontiformen Selachier, die durch niedrig - kronige, mit einem labialen Fortsatz versehene Zähne charakterisiert ist. Das einzig bekannte zusammenhängende Material gehört der Typus-Art der Gattung (*Lissodus africanus*) aus der unteren Trias Südafrikas an. Das Gebiß dieser Art zeigt eine anaulacorhize Gefäßversorgung der Wurzel und die Zähne sind wechselweise angelegt. Allem Anschein nach existierten diese beiden Merkmale zu einem gewissen Grad auch bei allen anderen *Lissodus*-Arten. Der Name *Lonchidion* ist als jüngeres ungültiges Synonym von *Lissodus*-Arten. Der Name *Lonchidion* ist als jüngeres ungültiges Synonym von *Lissodus* anzusehen, aber '*Lonchidion*' rhizion, aus der englischen Unterkreide, ist kein echter *Lissodus*-Zahn. Die folgenden Arten sind in die Gattung *Lissodus* einzubeziehen: *Lissodus zideki* (Unterperm, U.S.A.); *L. angulatus* (Untertrias, Spitzbergen); *L. humblei* (Obertrias, U.S.A.); *L. nodosus* (Obertrias, Deutschland); *L. minimus* (Obertrias, Nordwesteuropa); *L. leiodus* (Mitteljura, England); *L. heterodon*, *L. brevis*, *L. crenulatus*, *L. pustulatus*, *L. striatus* and *L. levis* (alle aus der englischen Unterkreide); *L. anitae*, *L. babulskii* und *L. selachos* (alle aus der Oberkreide der U.S.A.). Als neue Arten sind in der Arbeit beschrieben: *L. wirksworthensis* n. sp. (Unterkarbon, England); *L. pattersoni* n. sp. und *L. wardi* n. sp. (Mitteljura, England); *L. weltoni* n. sp. (Oberkreide, U.S.A.). *Lissodus* war benthisch und durophag. Der *Lissodus*-Stamm war anscheinend marinen Ursprungs, ist aber während der Trias- und der Kreide-Periode in das Süßwasser eingedrungen, vielleicht als Erfolg der Konkurrenz irgendwelcher Aktinopterygier.

Schlüsselwörter: Selachier - Zähne - Evolution - Taxonomie - Zoogeographic.

Abstract

Lissodus is a genus of hybodontiform shark possessing low-crowned teeth bearing a labial peg, and ranging from Lower Carboniferous to Upper Cretaceous strata. *Lissodus africanus* (lower Triassic, South Africa), the type species, provides the only articulated material known. The dentition of this species shows anaulacorhize vascularisation of the root, and alternation of teeth in adjacent files; both of these characters are believed to be present to some extent in all other *Lissodus* species. *Lonchidion* is a junior synonym of *Lissodus*. '*Lonchidion*' rhizion (Lower Cretaceous, Britain) is not a *Lissodus* tooth. The following species are incorporated into the genus *Lissodus*: *Lissodus zideki* (Early Permian, U.S.A.); *L. angulatus* (Lower Triassic, Spitsbergen); *L. humblei* (Upper Triassic, U.S.A.); *L. nodosus* (Upper Triassic, Germany); *L. minimus* (Upper Triassic, north west Europe); *L. leiodus* (Middle Jurassic, Britain); *L. heterodon*, *L. brevis*, *L. crenulatus*, *L. pustulatus*, *L. striatus* and *L. levis* from the Lower Cretaceous of Britain; *L. anitae*, *L. babulskii* and *L. selachos* from the Upper Cretaceous of the U.S.A. The following new species are described: *L. wirksworthensis* n. sp. (Lower Carboniferous, Britain), *L. pattersoni* n. sp. and *L. wardi* n. sp. (Middle Jurassic, Britain), and *L. weltoni* n. sp. (Upper Cretaceous, U.S.A.). *Lissodus* was a benthonic shark of durophagous habit. Although

^{*)} Address of the author: Dr. C. J. DUFFIN, 113. Shaldon Drive, Morden Surrey SM4 4BQ, England

apparently a marine stock, it invaded freshwater during the Triassic and Cretaceous, possibly in response to competition from various marine actinopterygians.

Key words: Selachian - teeth - evolution - taxonomy - biogeography.

Contents

Zusammenfassung	105
Abstract	105
1. Introduction	107
2. Definition of descriptive terms	107
3. A review of the species previously ascribed to <i>Lonchidion</i>	108
<i>Lissodus selachos</i> (ESTES)	108
<i>Lissodus breve</i> (PATTERSON)	109
<i>Lissodus crenulatus</i> (PATTERSON)	110
<i>Lissodus pustulatus</i> (PATTERSON)	111
<i>Lissodus striatus</i> (PATTERSON)	111
<i>Lissodus heterodon</i> (PATTERSON)	112
Comments on " <i>Lonchidion rhizion</i> "	112
<i>Lissodus babulskii</i> (CAPPETTA & CASE)	113
<i>Lissodus anitae</i> (THURMOND)	113
<i>Lissodus humblei</i> (MURRY)	114
4. The record of <i>Lissodus africanus</i> (BROOM)	115
Description of the teeth	116
5. A comparison of the teeth of ' <i>Lonchidion</i> ' and <i>Lissodus africanus</i>	117
6. Other published selachian species referable to <i>Lissodus</i>	117
A note on Carboniferous teeth of <i>Lissodus</i>	117
<i>Lissodus zideki</i> (JOHNSON)	118
<i>Lissodus angulatus</i> (STENSIÖ)	119
<i>Lissodus nodosus</i> (SEILACHER)	119
<i>Lissodus minimus</i> (AGASSIZ)	122
<i>Lissodus leiodus</i> (WOODWARD)	125
<i>Lissodus levis</i> (WOODWARD)	127
7. Description of new material	129
<i>Lissodus wirksworthensis</i> n. sp.	129
<i>Lissodus pattersoni</i> n. sp.	133
<i>Lissodus wardi</i> n. sp.	134
<i>Lissodus weltoni</i> n. sp.	136
8. A note on tooth histology	138
9. Dorsal fin spines	138
10. Cephalic spines	140
11. Summary of taxonomy	142
12. Palaeoecological significance	143
13. Evolution	144
14. Conclusions	148
Literature	148

Abbreviations

- BM(NH). Department of Palaeontology, British Museum (Natural History), London.
BGM. Bath Geology Museum, 18 Queen Square, Bath, Avon, England.
BRSMG. Department of Geology, Bristol City Museum and Art Gallery, Queens Road, Bristol, England.
SAM. South African Museum, P. O. Box 61, Cape Town, South Africa.
SMNS. Staatliches Museum für Naturkunde in Stuttgart, Rosenstein 1, Stuttgart, West Germany.
SMU-SMP. Shuler Museum of Palaeontology, Southern Methodist University, Dallas, Texas, U.S.A.
U.C. University of California at Berkeley, California, U.S.A.

I. Introduction

ESTES (1964) first erected the genus *Lonchidion* for a series of selachian teeth from the Type Lance Formation (Late Cretaceous) of eastern Wyoming, U. S. A. PATTERSON (1966) later described teeth belonging to the genus from the English Wealden (Lower Cretaceous), from which a later record was made by FREEMAN (1975: 309), and the Purbeck (Lower Cretaceous). Further species were then described from the Upper Carnian (Upper Triassic) of Texas (MURRY 1981), the Upper Campanian of New Jersey (CAPPETTA & CASE 1975), the Albian of Texas (SLAUGHTER 1971: 132; THURMOND 1970, 1972, 1974; MEYER 1970), and HERMAN (1973, 1977) tentatively recorded the genus from the Belgian Campanian.

ESTES (1964) and PATTERSON (1966) have remarked upon the similarity of certain hybodont teeth to those described as *Lonchidion*. I have examined material from most of the above species and compared it to as many hybodont species as possible, from Lower Carboniferous to Upper Cretaceous deposits. From this comparison emerges the conclusion that the teeth of *Lonchidion* and *Lissodus* BROUGH (from the Lower Triassic of South Africa) are congeneric (DUFFIN 1981 a, 1981 b: 296; MAISEY 1982: 29), and that the latter name takes precedence (DUFFIN 1981 b, MURRY 1981). The teeth of further species, some new and some previously described, are here allocated to the genus *Lissodus*, giving it a stratigraphical range of Lower Carboniferous to Upper Cretaceous.

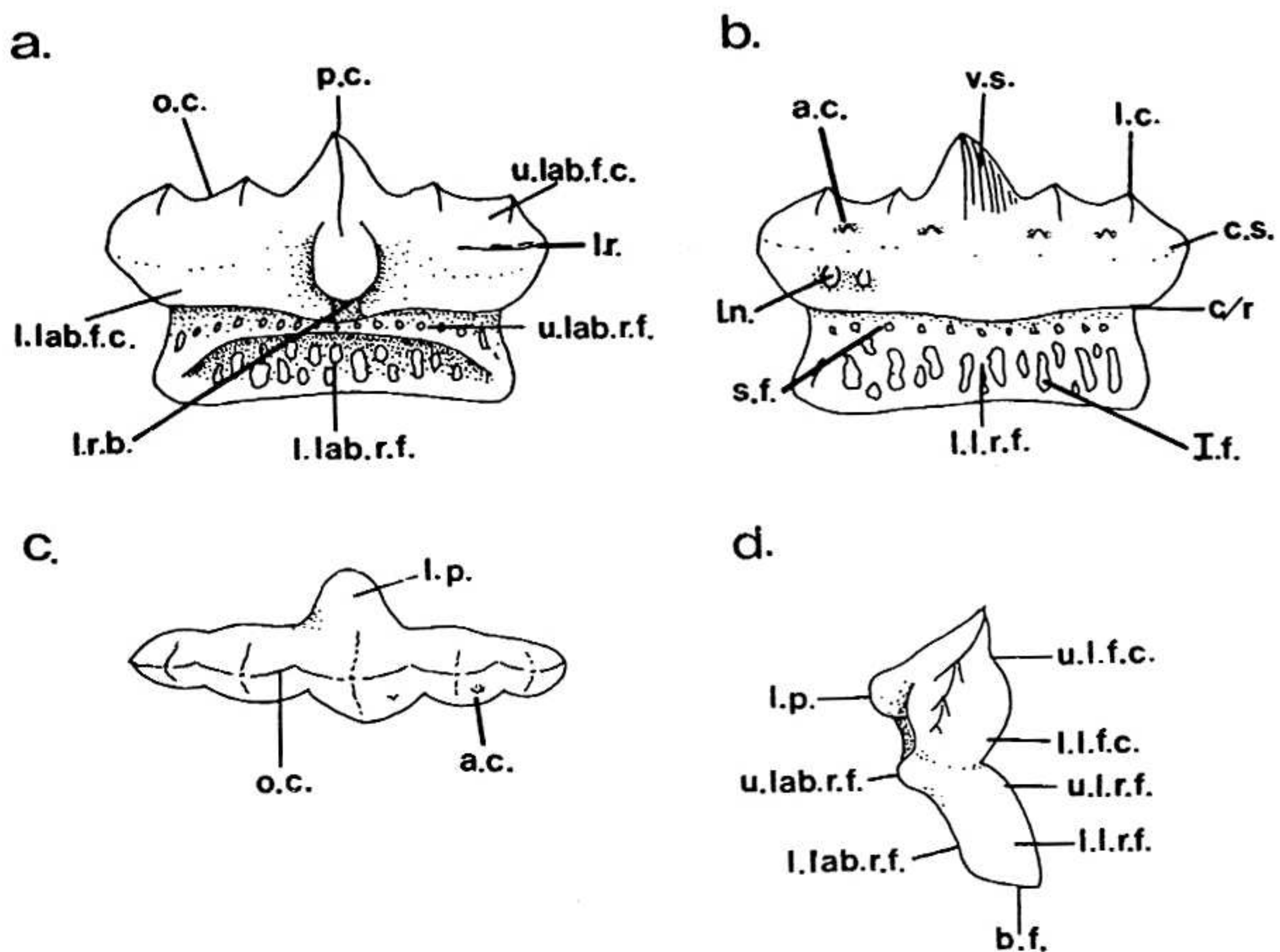
It should be noted that the definition of hybodont genera on the basis of isolated teeth has long been problematical. Much confusion has existed in the literature on points of both morphology and histology. Recent work (eg. JOHNSON 1981, RIEPPEL 1981, MAISEY 1982) has begun to identify and resolve these problems, but much further work remains. The formal definition of hybodont genera other than *Lissodus* is outside the scope of this paper. I have preferred the use of morphological criteria in the definition of *Lissodus* below because in most cases the study material for individual species is limited and the cutting of thin sections has been either difficult or ill advised.

2. Definition of Descriptive Terms

A key to the descriptive terms used in this paper is given in text-fig. 1.

In a generalised tooth of *Lissodus*, the **principal cusp** (p. c. text-fig. 1 a) is the highest on the crown, and is always located in a central position (occasionally called the central cusp). The **lateral cusplets** (l. c., text-fig. 1 b) are lower than the principal cusp, sub-equal to each other in size, and flank the principal cusp on either side. **Vertical striations** (v. s., text-fig. 1 b) are ridges in the enameloid which ascend the crown. The **occlusal crest** (o. c., text-fig. 1 a, 1 c) is a ridge or keel of enameloid passing mesiodistally from end to end of the crown, linking the cusp apices. The crown is divisible into two distinct areas on both labial and lingual faces. The **upper labial face of the crown** and the **upper lingual face of the crown** (u. lab. f. c. and u. l. f. c. respectively, text-fig. 1 a, 1 d) slope toward the occlusal crest. The **lower labial face of the crown** (l. lab. f. c., text-fig. 1 a) and the **lower lingual face of the crown** (l. l. f. c., text-fig. 1 d) slope toward the **crown/root junction** (c/r., text-fig. 1 b). The lower face of the crown may bear **labial or lingual nodes** (l. n., text-fig. 1 b). The point at which these upper and lower crown faces meet defines the **labial and lingual crown shoulder** (c. s., text-fig. 1 b). This feature is usually located just below the middle of the height of the crown in labial and lingual views. A series of **longitudinal ridges** (l. r., text-fig. 1 a) in the enameloid may be present along the crown shoulder on either or both lingual and labial crown faces. The labial face of the crown possesses a swelling at the level of the crown shoulder; this is termed the **labial peg** (l. p., text-fig. 1 c, 1 d). It may be directly supported from below by a **labial root buttress** (l. r. b., text-fig. 1 a). **Accessory cusplets** (a. c., text-fig. 1 b, c) are very small cusplets which are not located along the occlusal crest; they are present on the upper labial and lingual crown faces of some species.

The **crown/root junction** is defined as the line of junction between the enamelled crown and the root. The root itself is divisible into three main faces; the **basal face** (b. f., text-fig. 1 d) is usually flat and forms the root undersurface; the labial and lingual faces of the root are each further divisible. On each of these two root faces there is an upper and a lower face. The **lower labial root face** (l. lab. r. f., text-fig. 1 a) is always located in a central position and is presumed to include the 'root sulcus' of JOHNSON (1981, fig. 1). It is easily distinguished from the **upper labial root face** (u. lab. r. f., text-fig. 1 a) in that it is usually concave and slopes toward the labial face/basal face junction. The upper labial root face is shallow and projects labially from the crown/root junction. The entire



Text-fig. 1. A generalised tooth of *Lissodus* to indicate descriptive nomenclature. a, labial view; b, lingual view; c, occlusal view; d, lateral view. Abbreviations: p.c., principal cusp; o.c., occlusal crest; u.lab.f.c., upper labial face of the crown; l.lab.f.c., lower labial face of the crown; u.l.f.c., upper lingual face of the crown; l.l.f.c., lower lingual face of the crown; u.lab.r.f., upper labial root face; l.lab.r.f., lower labial root face; v.s., vertical striations; l.c., lateral cusplet; c.s., crown shoulder; c/r, crown/root junction; l.l.r.f., lower lingual root face; u.l.r.f., upper lingual root face; l.p., labial peg; b.f., basal face of root; lr., longitudinal ridges (occasionally present); ln., lingual node (occasionally present); l.r.b., labial root buttress (occasionally present); a.c., accessory cusplet (occasionally present).

lingual face of the root is convex and slopes lingually in a curve to its junction with the basal face. In certain teeth, an **upper lingual root face** (u.l.r.f., text-fig. 1 d) can be distinguished as a shallow, minimally convex shelf along the top of the lingual face of the root, arising from the crown/root junction. By comparison, the **lower lingual root face** (l.l.r.f., text-fig. 1 d) is deep and descends in a more vertical plane to the basal face.

I follow JOHNSON (1981, fig. 1) in calling the simple, subcircular foramina on the upper labial root face (oral margin of root sulcus according to JOHNSON 1981, fig. 1) specialised (s.f., text-fig. 1 b) (JOHNSON 1981: 4, PATTERSON 1966: 321). Irregular foramina (l.f., text-fig. 1 b) are elongate in outline, entering the root at an angle.

3. A review of the species previously ascribed *Lonchidion*

Lissodus selachos (ESTES)

Plate 1, figs. 1 a-d

1964 *Lonchidion selachos* ESTES, p.7, text-figs. 1-4.

Holotype: complete tooth, UC catalogue number 53897.

Other material: complete and broken teeth, cephalic spines and dorsal fin spines, UC catalogue number 53898 to 53906 inclusive; 62854, ten teeth from U.C. locality V 5817; 119288, complete tooth from U.C. locality V 5817 (pl. 1, figs. 1 a-d); many unnumbered specimens. BM (NH) P. 47560 -47567 (7 isolated crowns, 1 complete tooth) from V-5711.

Age: Type Lance Formation, Maestrichtian, Upper Cretaceous.

Localities: UC locality numbers V-5003, V-5620, V-5622, V-5711, V-5713, V-5815, V-5818, V-5918.

Diagnosis: Teeth of *Lissodus* measuring up to 4.5 mm in length. The labial peg is moderately developed. The occlusal crest is well developed, may be crenulated, and bears a number of small or incipient lateral cusplets both mesially and distally. Accessory cusplets are lacking. The coronal profile is low, and the crown smooth. Small lingual nodes may be developed at the crown shoulder. Vertical striations are absent, although some teeth may possess a longitudinal ridge lingually. The central principal cusp is low. A few specialised foramina are present on the upper labial root face, and occasionally on the upper lingual root face. Other foramina are irregular. The labial peg bears a small cusplet and occasionally an incipient vertical striation on its crest.

Comments: Many of the teeth of this species show evidence of heavy antemortem wear on the crest of the central principal cusp and labial peg. Lateral cusplets do not tend to be well developed and often appear incipient, giving rise to a crenulate occlusal crest. While virtually all the crowns lack ornament, P. 47067 bears occasional very small nodes on the lingual crown shoulder, and P. 47066 appears to bear an indistinct longitudinal ridge in this position. Lateral teeth (eg. P. 47065) appear to possess a long, shallow crown, while mesials are deeper and more robust in appearance.

Discussion: ESTES (1964) referred two distinct tooth types to this, the type species of his genus *Lonchidion*. Teeth ascribed by ESTES to a symphyseal position are of neoselachian organisation (DUFFIN 1981 a: 296). The crown is short, comprising a high principal cusp flanked by up to three lateral cusplets on each side. The root is lingually extended and the basal face is V-shaped (ESTES 1964, figs. 2 a-c). This appears to be an autopomorphic character of the Neoselachii (DUFFIN 1980 a, 1981 a, THIES 1983). The vascularisation of the root follows the squatinoid type of CASIER (1947), whereas in the "lateral" teeth it is hybodontoid. PATTERSON (1966: 331) states that "it is possible that in *Lonchidion* the anterior teeth could, by the Upper Cretaceous, have evolved a squatinoid root, in parallel with the heterodontids", but that it "seems equally possible that the teeth ascribed by ESTES belong to a squatinoid or orectolobid, perhaps related to his species *Squatirhina americana* or a related form". In his generic diagnosis, however, PATTERSON retains ESTES suggestion in stating "tricuspid anterior teeth present in some forms" (PATTERSON 1966: 312). Further, BIRKENMAJER & JERZMAŃSKA (1979) accept the validity of specialised anterior teeth with squatinoid roots in *L. selachos* without discussion.

It is not necessary to postulate such a heterodont dentition for the teeth described by ESTES. HERMAN (1977: 40) erects the species *Mesiteia estesi* HERMAN for the supposed symphyseal teeth (Family Orectolobidae). CASE (1979: 225) originally considered that they should be placed in the orectolobid genus *Chiloscyllium*, but in a footnote to the same paper further suggests that they should be considered as *Brachaelurus estesi*.

LUPTON, GABRIEL & WEST (1980: 118) further record a single dorsal fin spine which "compares well" with those described for *L. selachos* by ESTES (1964) from Chris's Bonebed high in the Hell Creek Formation (Maestrichtian, Upper Cretaceous) from an isolated hill in McCone County, Montana, U.S.A. The dorsal fin spines of *Lissodus* spp. are discussed below (p. 138).

Lissodus breve (PATTERSON)

Text-figures 2 a-d

1966 *Lonchidion breve breve* PATTERSON, p. 313, pl. 5 fig. 3, text-figs. 14-16, 29 e.

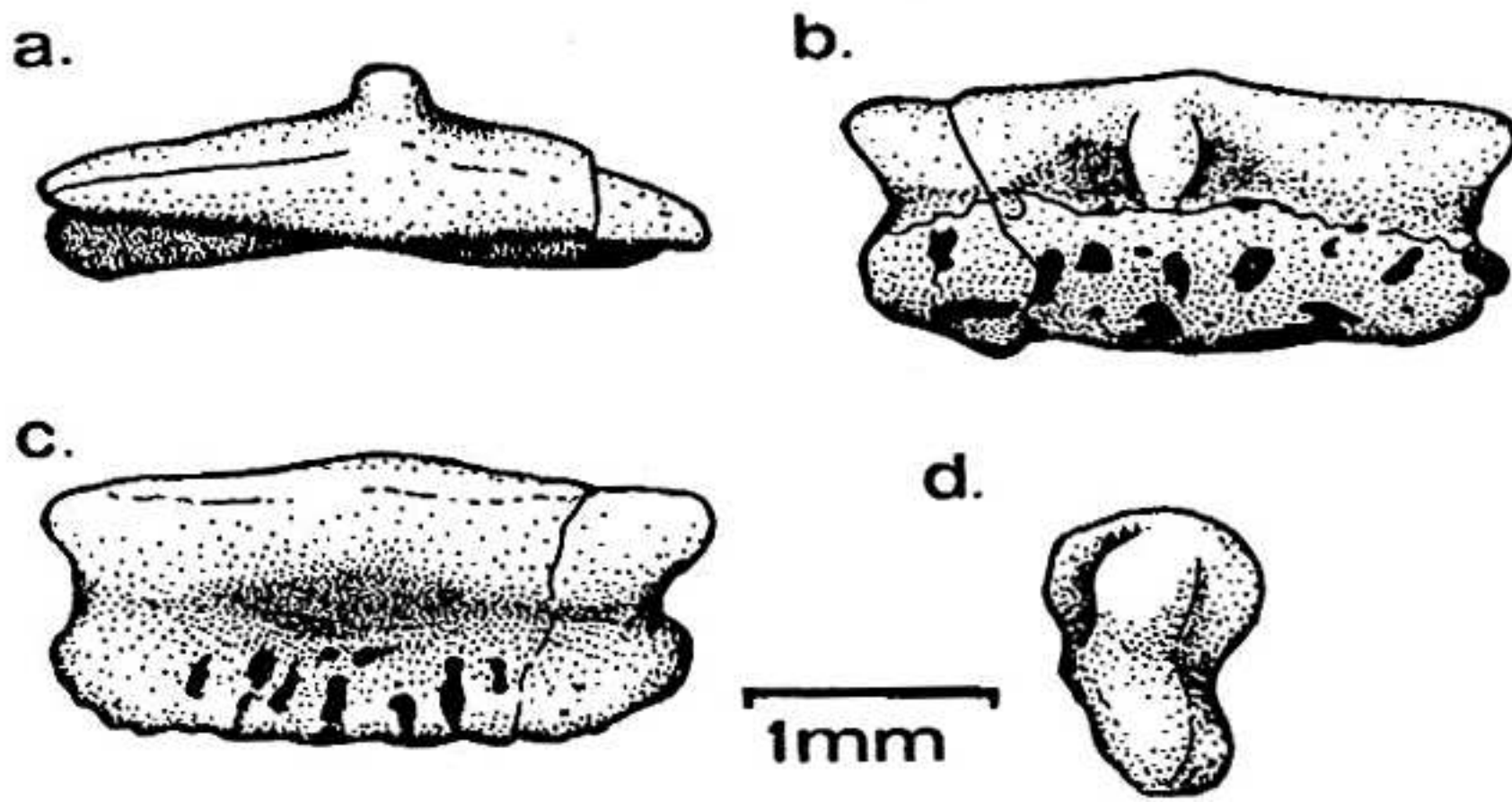
Holotype: P. 47024 (BM(NH)), a complete tooth (text-figs. 2 a-d), from the Paddockhurst bone bed of Paddockhurst Park, Sussex, England.

Other material: about 120 teeth.

Horizons and localities: Ashdown Beds (Cliff End bone bed); Wadhurst Clay (Telham bone bed) of Stone, Kent, and Hastings, Sussex; Ashurst Wood, Sussex; Grinstead Clay (Paddockhurst bone bed); Weald Clay, Henfield; Atherfield Clay (*Perna* Bed) of Sandown Bay.

Age: "Wealden", Neocomian, Lower Cretaceous.

Diagnosis: Teeth measuring up to 3.5 mm long with a smooth, unornamented crown. The labial peg is moderate to strong and the coronal profile low. The principal cusp is low; there are no lateral or accessory cusplets. There are no specialised foramina in the root.



Text-fig. 2. Holotype of *Lissodus breve* (PATTERSON 1966). BM(NH) P 47024. The tooth comes from the Grinstead Clay (Wealden, Lower Cretaceous) of Paddockhurst Park, Sussex. a, occlusal view; b, labial view; c, lingual view; d, lateral view. Note the smooth crown, strong labial peg and low coronal profile.

Remarks: PATTERSON (1966) originally divided *L. breve* into three subspecies, *L. breve breve*, *L. breve crenulatum* and *L. breve pustulatum*, since the specimens "intergrade both morphologically and stratigraphically", (PATTERSON 1966: 313). From my own examination of the material, I consider that the types described by PATTERSON deserve distinction at the species level. Accordingly, I here elevate each of the subspecies described by PATTERSON to the status of species.

MEYER (1970: 30, fig. 8) records teeth with close affinity to *L. breve* from Upper Cenomanian to Middle Campanian marine deposits of east Texas.

Lissodus crenulatus (PATTERSON)

Text-figures 3 a-c, pl. 1, figs. 2 a-b

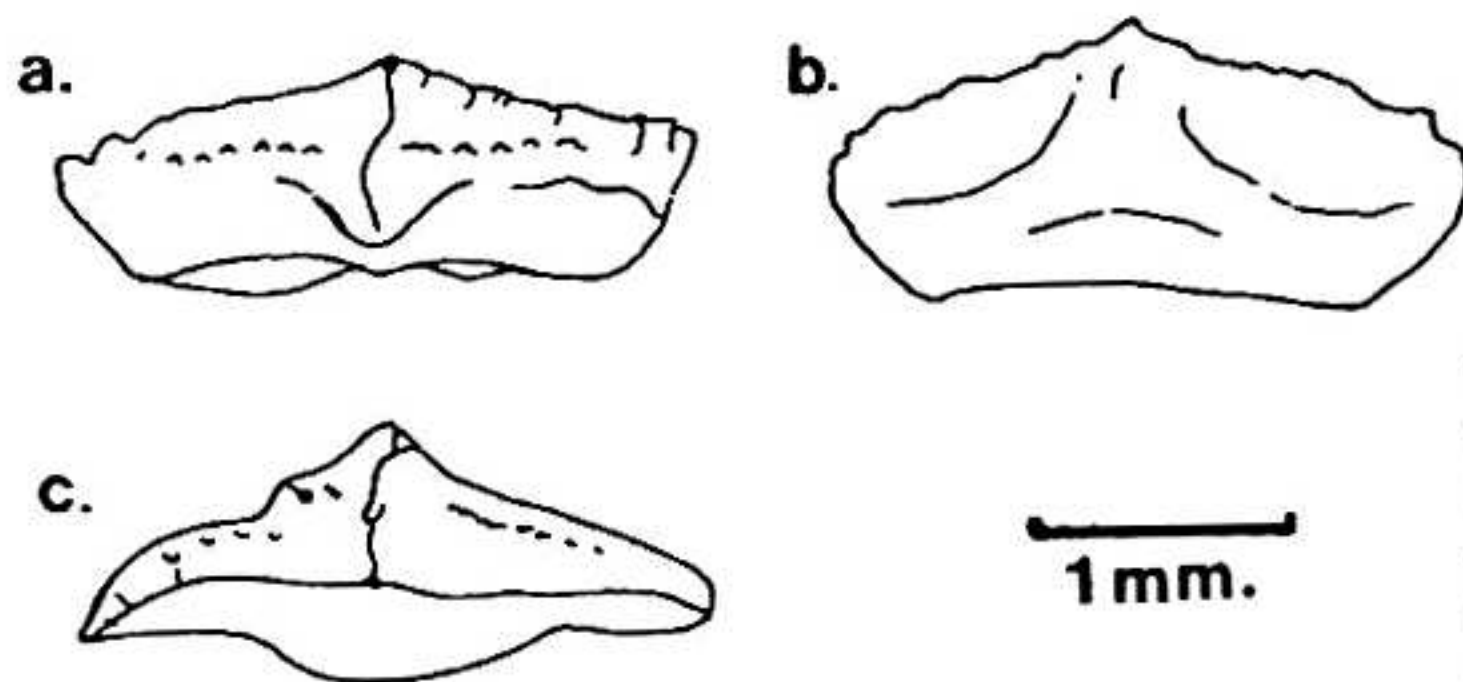
1966 *Lonchidion breve crenulatum* PATTERSON, p. 316, text-figs. 17, 18.

Holotype: P. 47060 (BM(NH)), an isolated crown (text-figs. 3 a-c), from the Paddockhurst bone bed of Paddockhurst Park, Sussex, England.

Other material: 25 isolated crowns from the Wadhurst Clay of Ashurst Wood, Sussex and the Paddockhurst bone bed of the Grinstead Clay at Paddockhurst, Sussex; approximately 50 isolated crowns from Chilton Chine (SZ 409829) on the Isle of Wight. The latter specimens were collected by Mr. E. F. FREEMAN, P. 60729 (BM(NH)), being figured in pl. 1, fig. 2 a, P. 60767 (BM(NH)) in pl. 1, fig. 2 b.

Age: "Wealden", Neocomian, Lower Cretaceous.

Diagnosis: The occlusal crest is weakly, irregularly and finely crenulate. The coronal profile is low. Sparse vertical striations are present on both labial and lingual faces of the crown. The labial peg is weak to moderate and may bear a vertical ridge and cusplet. The root is unknown. The teeth measure up to 3.5 mm long.



Text-fig. 3. Holotype of *Lissodus crenulatus* (PATTERSON, 1966) from the Paddockhurst bone-bed (Wealden, Lower Cretaceous) of Paddockhurst Park, Sussex. BM(NH) P. 47060. After PATTERSON (1966 fig. 17B). a, labial view; b, lingual view; c, occlusal view. Note the fairly strong labial peg, cusped occlusal crest and weak vertical striations.

Lissodus pustulatus (PATTERSON)

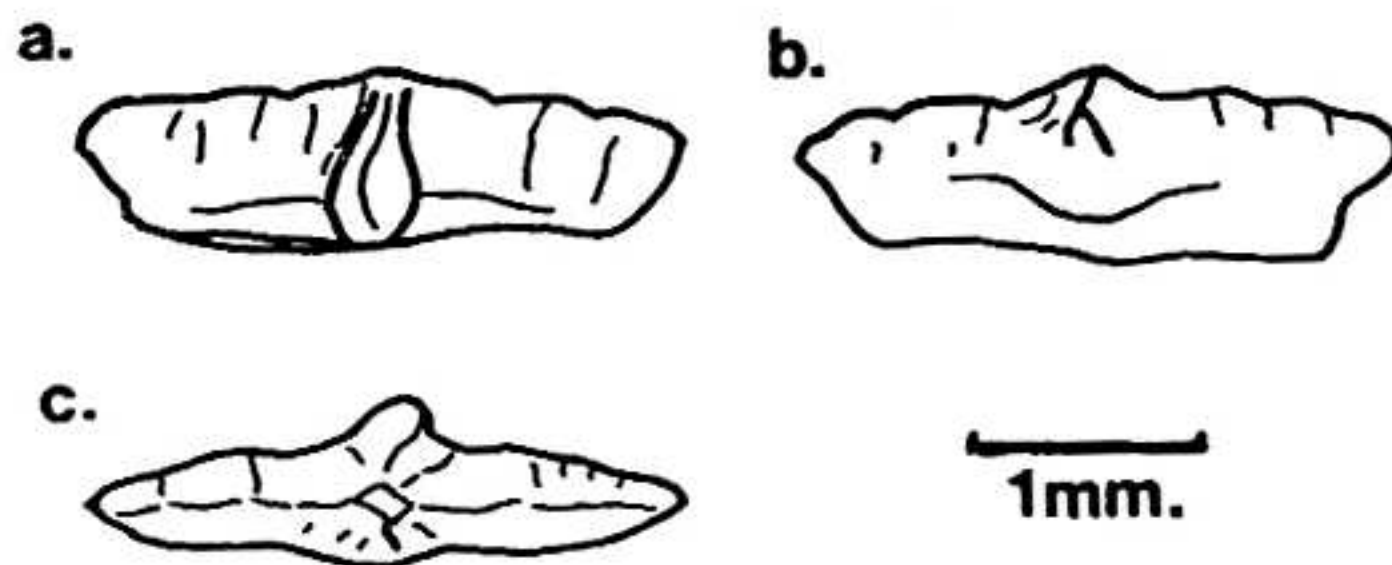
Text-figures 4 a-c, 5 a-d, pl. 1, figs. 2 c-g

1966 *Lonchidion breve pustulatum* PATTERSON, p. 317, text-fig. 19.

Holotype: P. 47085 (BM(NH)), an isolated crown from the *Perna* Bed of Sandown Bay, Isle of Wight, England (text-figs. 4 a-c).

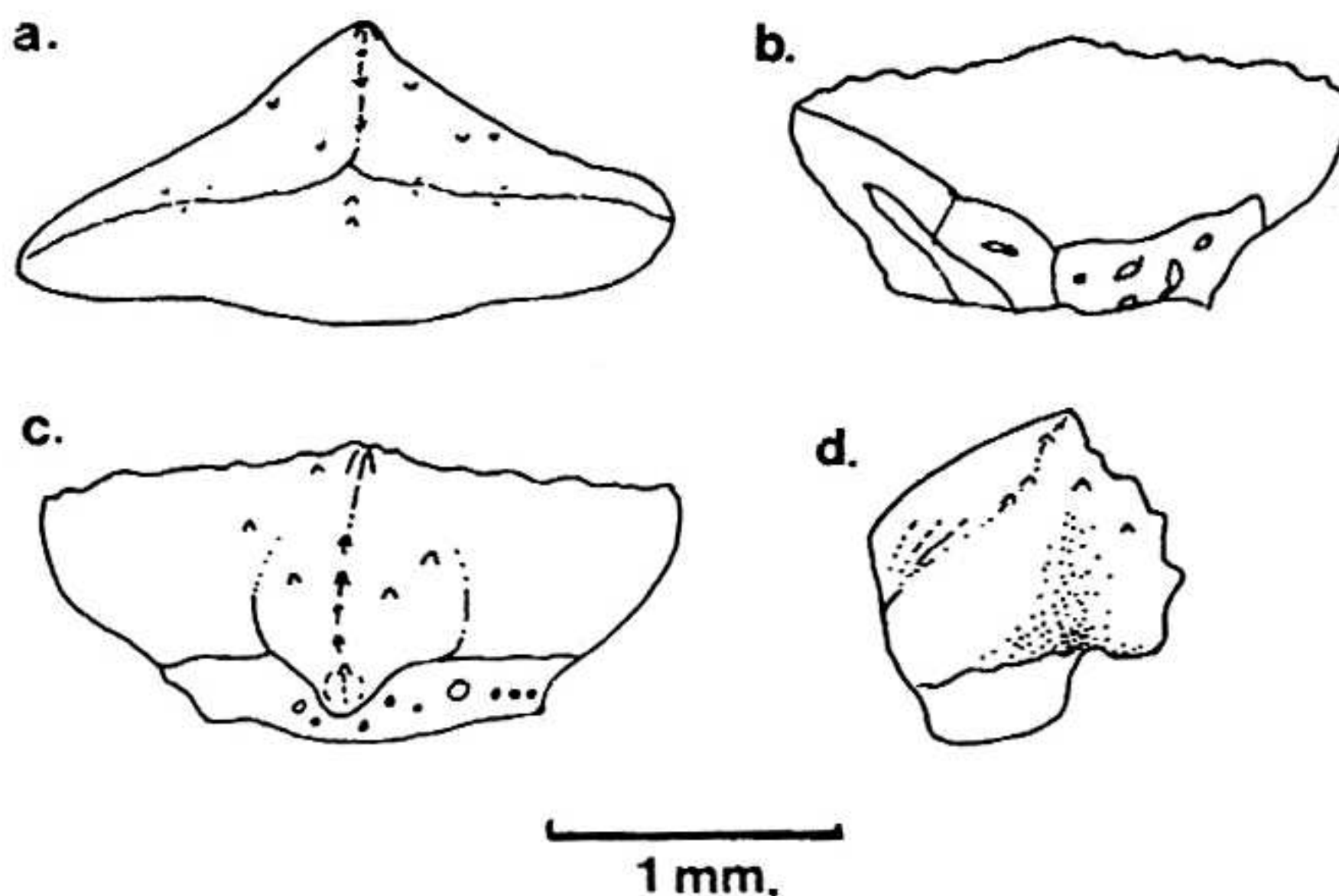
Other material: 14 isolated crowns from the same locality and horizon as the holotype; several hundred isolated crowns, some with root remnants, from the Wealden of Chilton Chine, Isle of Wight, collected by Mr. E. F. FREEMAN, including P. 60728 (BM(NH)) (text-figs. 5 a-d), P. 60768 (BM(NH)) (pl. 1, figs. 2 c-d), and P. 60769 (pl. 1, fig. 2 c-g).

Age: "Wealden", Neocomian, Lower Cretaceous.



Text-fig. 4. Holotype of *Lissodus pustulatus* (PATTERSON 1966) from the *Perna* Bed, Atherfield Clay (Wealden, Lower Cretaceous), after PATTERSON (1966, fig. 19B). BM(NH) P. 47085. a, labial view; b, lingual view; c, occlusal view. Note the weakly crenulate occlusal crest and smooth crown bearing accessory cusps, mostly on the labial face.

Diagnosis: The principal cusp is low and the occlusal crest is irregularly and finely crenulate. The labial peg is moderate. The labial face of the crown bears minute accessory cusps, but no striations. Accessory cusps are rarely developed on the lingual face of the crown. The accessory cusps may be organised into longitudinal rows, restricted to the surface of the labial peg, or indiscriminately distributed over the labial face of the crown. The teeth range from 1.8-3.6 mm in length.



Text-fig. 5. Tooth of *Lissodus pustulatus* (PATTERSON 1966), with fragmentary root, from the Wealden (Lower Cretaceous) of Chilton Chine, Isle of Wight. BM(NH) 60728. a, occlusal view; b, lingual view; c, labial view; d, lateral view. Note that, unlike in the holotype, the accessory cusps are concentrated along the top of the labial peg in this specimen.

Lissodus striatus (PATTERSON)

Plate 1, figs. 3 a-d

1966 *Lonchidion striatum* PATTERSON, p. 320, text-figs. 21, 22.

Holotype: P. 47103 (BM(NH)), a complete tooth from the Weald Clay of Henfield, Sussex, England.

Other material: over 100 teeth from the same locality and formation. P. 60726 (BM(NH)) (pl. 1, figs. 3 a-c); P.60727 (BM(NH)) (pl. 1, fig. 3 d).

Age: "Wealden", Neocomian, Lower Cretaceous.

Diagnosis: The teeth range from 1.1 to 4.2 mm in length. The crown is elongate with a strong occlusal crest possessing weak and irregular lateral cusplets. The principal cusp is very low. Strong vertical striations, occasionally bifurcating basally, ascend the crown from the crown shoulder and attain the occlusal crest. The labial peg is small and weak. Specialised foramina are present on the upper labial face of the root, and occasionally on the upper lingual face of the root. The remaining vascular foramina are irregular.

Lissodus heterodon (PATTERSON)

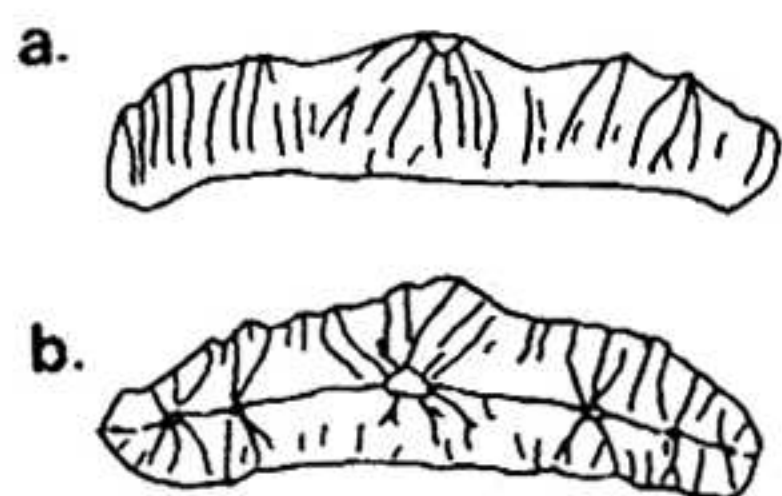
Text-figures 6 a-b

1966 *Lonchidion heterodon* PATTERSON, p. 326. text-fig. 25.

Holotype: P. 47188 (BM(NH)), an isolated crown from the Upper Purbeck (Ryazanian, Lower Cretaceous) of Friar Waddon, Dorset, England (text-figs. 6 a-b).

Other material: 12 isolated crowns from the type locality, and the Cliff End bone bed (Ashdown Beds, Wealden) of Cliff End, Sussex, and the Wadhurst Clay of Hastings, Sussex.

Age: "limestone above the Broken Shell Limestone in the Upper Purbeck" (PATTERSON 1966: 287), Ryazanian, Lower Cretaceous (cf. RAWSON et alia 1978), to "Wealden", Neocomian, Lower Cretaceous.



Text-fig. 6. Holotype of *Lissodus heterodon* (PATTERSON 1966) from the Upper Purbeck (Ryazanian, Lower Cretaceous) of Friar Waddon, Dorset, England, after PATTERSON (1966, fig. 25). BM(NH) P. 47188. a, labial view; b, occlusal view. Note the well developed lateral cusplets along the occlusal crest, the weak labial peg and the coarse, downwardly diverging vertical striations arising from the occlusal crest.

Diagnosis: The teeth range in length from 2.5 to 4 mm. The crown is shallower than it is broad, and is elongate. The principal cusp is moderately high (higher than in *L. striatus*), and there is up to three pairs of lateral cusplets. Vertical striations diverge downwards from the strong occlusal crest, being few and weak in anterior and posterior teeth, but numerous and strong in large lateral teeth. The striations do not reach the base of the crown. The labial peg is strong in anterior and posterior teeth, but weak in lateral teeth. The root is unknown.

Comments on "*Lonchidion rhizion*"

PATTERSON (1966: 322) erected the species *Lonchidion rhizion* PATTERSON for 35 specimens from the Cliff End bone bed of Cliff End, and further bone beds of Wealden (Neocomian, Lower Cretaceous) age in Sussex and Kent. The specimens are all less than 2 mm long. PATTERSON concluded that the lingual face of the crown possesses a pair of depressions, there is a very strong labial peg, and that the root is very small or absent altogether. There is no ornament on the specimens.

HERMAN (1977: 42) expresses doubt as to whether the specimens are oral teeth. He states that if the specimens do, indeed, belong to a shark, then they are more likely to be dermal denticles.

THURMOND (1972: 218) suggests that the specimens may belong to a primitive skate (and cf. MURRY 1981: 606).

A stereoscan study of the specimens (BM(NH) P. 47164; pl. 2, figs. 1 a-d) reveals that they lack enameloid. Other teeth from the same deposits and supposedly belonging to the same genus in this and other faunas in the Wealden of south east England all possess enameloid. It is unlikely that the enameloid has been removed by postmortem abrasion, and therefore that "*L. rhizion*" represents a species of extreme allochthony within a fauna of otherwise minimally allochthonous teeth. It is also unlikely that the teeth belong to a species which lacks enameloid, but belongs to a long lineage of forms, all of which possess enameloid. It has been suggested (DUFFIN & WARD 1983 a) that some shark teeth lack enameloid, and that enameloid may have evolved several times within the Selachii (DUFFIN & WARD 1983 a: 107), but this refers to much older (Lower Carboniferous) teeth, which are distinct from all other genera on other grounds.

It is concluded here that the specimens comprising "*L. rhizion*" are not teeth (see JOHNSON 1981: 7). Their precise origin and affinities remain obscure. Since *Lonchidion* can be synonymised with *Lissodus*, and the dermal denticles are known to be of hybodontoid morphotype (REIF 1978, BROUGH 1935, and see below p. 116), it is most unlikely that the specimens allocated to "*L. rhizion*" are dermal denticles of *Lissodus*.

Lissodus babulskii (CAPPETTA & CASE)

Plate 2, figs. 2 a-c

1975 *Lonchidion babulskii* CAPPETTA & CASE, p. 7, pl. 1, figs. 7-12.

Holotype: WBR 11 (Laboratoire de Paléontologie, Université de Montpellier, France), an isolated crown.

Other material: 500 isolated teeth (Montpelier); P. 60770 (BM(NH)) (pl. 2, figs. 2 a-c); P. 58105-58122, P. 57732-57735.

Localities: Hop Brook and Willow Brook, Monmouth County, New Jersey, U.S.A.

Age: Mount Laurel Formation, Upper Campanian, Upper Cretaceous.

Diagnosis: Teeth measuring up to 7 mm long bearing a moderate labial peg. The principal cusp is low and lateral cusplets rarely developed. The crown possesses no ornament, but is elongate and very narrow at the base. A vertical striation may surmount the labial peg. The root is unknown.

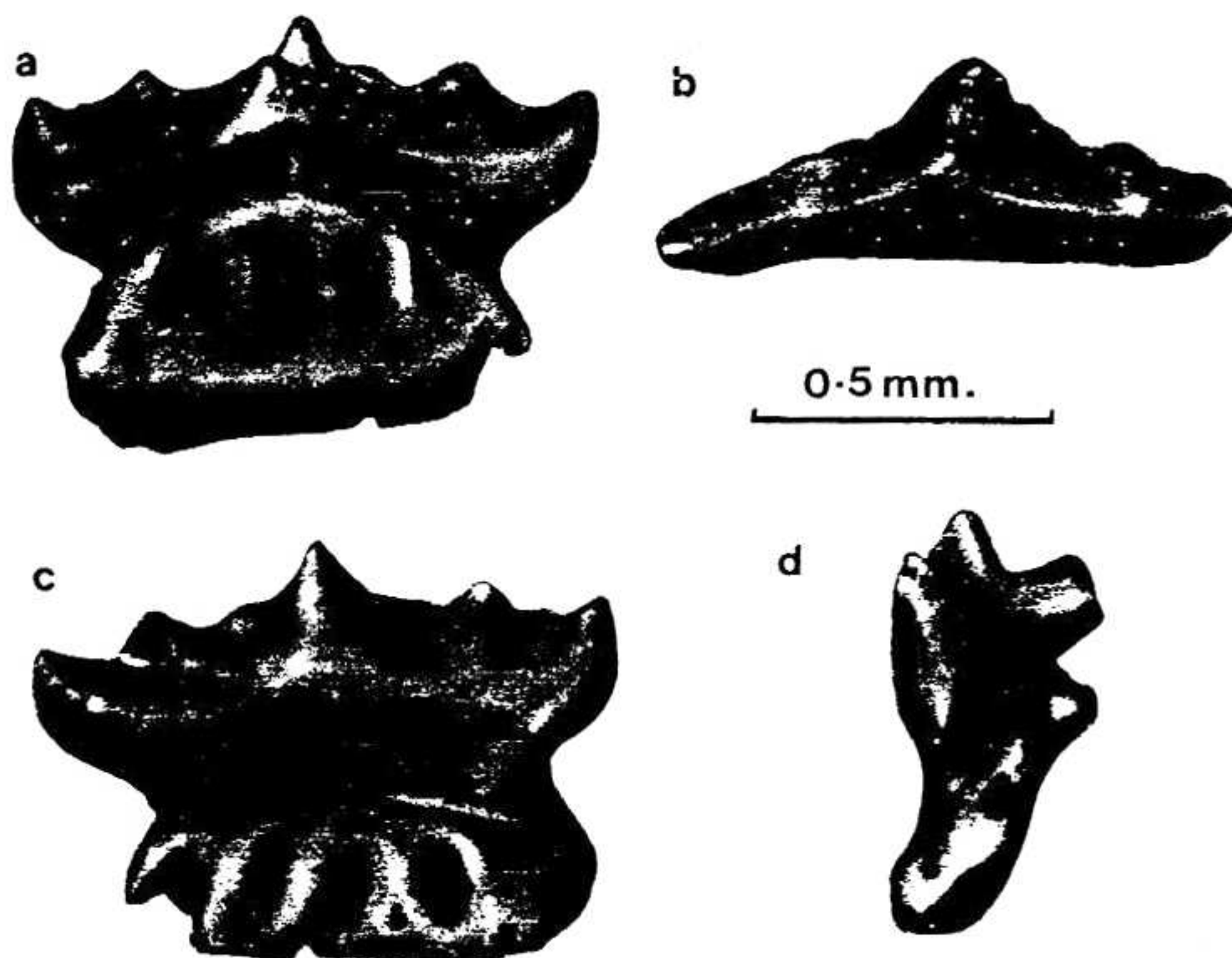
Lissodus anitae (THURMOND)

Text-figures 7 a-d, pl. 6, figs. 2 a-e

1972 *Lonchidion anitae* THURMOND, p. 217, fig. 9.

Holotype: SMU-SMP Catalogue number 62144, a complete isolated tooth (text-figs. 7 a-d).

Other material: five isolated crowns, SMU-SMP 62145-62149, (62146, pl. 6, figs. 2 a-e).



Textfig. 7. Holotype of *Lissodus anitae* (THURMOND 1972) from the Paluxy Formation (Albian, Lower Cretaceous) of Butler Farm, Wise County, Texas. SMU-SMP 62144. a, labial view; b, occlusal view; c, lingual view; d, lateral view. Note the strong labial peg and well developed lateral cusplets along the strong occlusal crest. The crown/root junction is incised and the vascularisation visible. Diagram by Ms. PAT GASSER.

Age: Butler Farm local fauna, Middle Member, Middle Paluxy Formation, Trinity Group, Albian, Lower Cretaceous (SLAUGHTER 1971: 132, THURMOND 1970, 1974).

Locality: Butler Farm, Wise County, Texas, U.S.A.

Diagnosis: The teeth range in length from 1.01 to 1.65 mm. The occlusal crest is well developed. The principal cusp is moderately high. Up to three pairs of lateral cusplets are present. The crown is otherwise unornamented, and the labial peg strong. There are no specialised foramina in the root.

Lissodus humblei (MURRY)

Text-figures 8 a-e

1981 *Lonchidion humblei* MURRY: MURRY, Journ. Paleont., 55 (3), 603, pl. 1.

Holotype: SMU-SMP catalogue number 67951, a complete isolated tooth (MURRY 1981, pl. 1 figs. 1A, 1B) (text-fig. 8a).

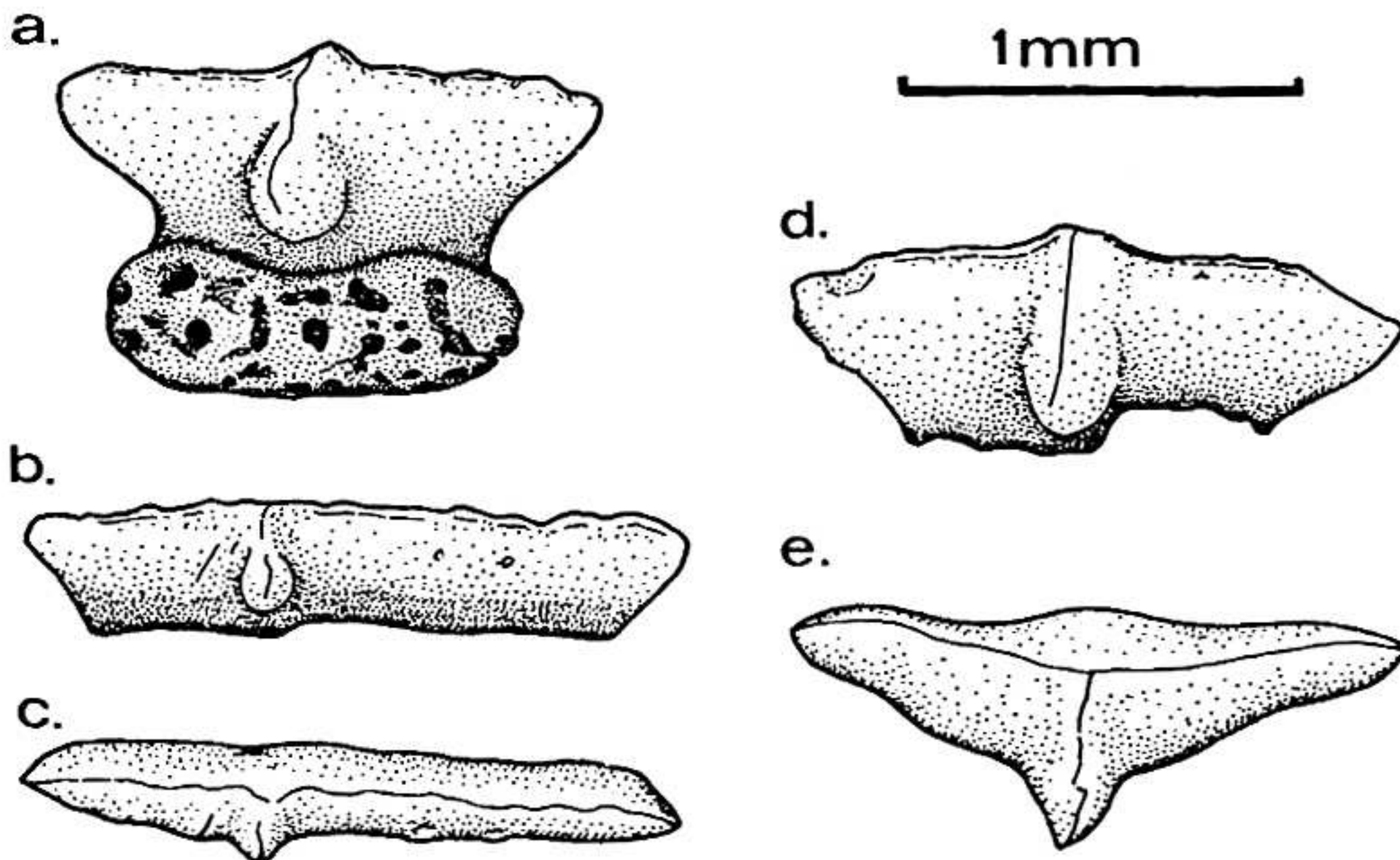
Other material: five incomplete teeth (SMU-SMP 66559, 66690, 67952-67954), twenty three dorsal fin spine fragments (SMU-SMP 67462-67484), one cephalic spine fragment (SMU-SMP 67955).

Locality: "Near the headwaters of Home Creek", S. E. Crosby County, Texas, U.S.A.

Age: Tecovas Formation, Dockum Group, ?Upper Carnian, Upper Triassic.

Diagnosis: Teeth ranging from 1.0 to 1.56 mm in length. The labial peg is moderately developed, "does not overhang the root" (MURRY 1981: 605), and is surmounted by a moderate vertical ridge. The occlusal crest is well developed and the coronal profile is low; the central principal cusp and lateral cusplets are very low. Accessory cusplets may be developed on the labial face of the crown in some specimens. The crown is smooth and lacks ornament. The root is less than half the total tooth height. Specialised foramina are not developed on the root.

Remarks: The teeth of *L. humblei* figured by MURRY show little heterodonty. The tooth crowns are mostly conservative, although there is a tendency for longer, narrower crowns to develop labial accessory cusplets and a less pronounced labial peg. MURRY (1981: 603) cites the presence of accessory cusplets in the diagnosis, but states that *L. humblei* lacks such features in the text (MURRY 1981: 605).



Text-fig. 8. Teeth of *Lissodus humblei* (MURRY 1981) from the Tecovas Formation (Dockum Group, ? Upper Carnian, Upper Triassic) of Crosby County, Texas. a, SMU-SMP 67591 (Holotype) in labial view (after MURRY 1981, pl. 1, fig. 1A); b, SMU-SMP 67592, a lateral tooth in labial view (after MURRY 1981, pl. 1, fig. 4A); c, SMU-SMP 67592 in occlusal view (after MURRY 1981, pl. 1, fig. 4B); d, SMU-SMP 66593, a mesial tooth in labial view (after MURRY 1981, pl. 1, fig. 2A); e, SMU-SMP 66593 in occlusal view (after MURRY 1981, pl. 1, fig. 2B). Note the low coronal profile, crenulate occlusal crest and presence of accessory cusplets in lateral teeth.

The root is preserved only in the holotype. Here, the vascular foramina have no preferred orientation on the labial root face (MURRY 1981, pl. 1, fig. 1A).

4. The record of *Lissodus Africanus* (BROOM)

Lissodus africanus (BROOM)

Text-figure 9; pl. 3, fig. 1; pl. 4, figs. 1, 2

- 1909 *Hybodus africanus* BROOM, p. 252, pl. 1, figs. 1, 2.
1931 *Acrodus africanus* - BROUGH, p. 237.
1935 *Lissodus africanus* - BROUGH, p. 36, pl. s I, II, III fig. 2.
1975 *Hybodus africanus* - JUBB & GARDINER, p. 410, fig. 15

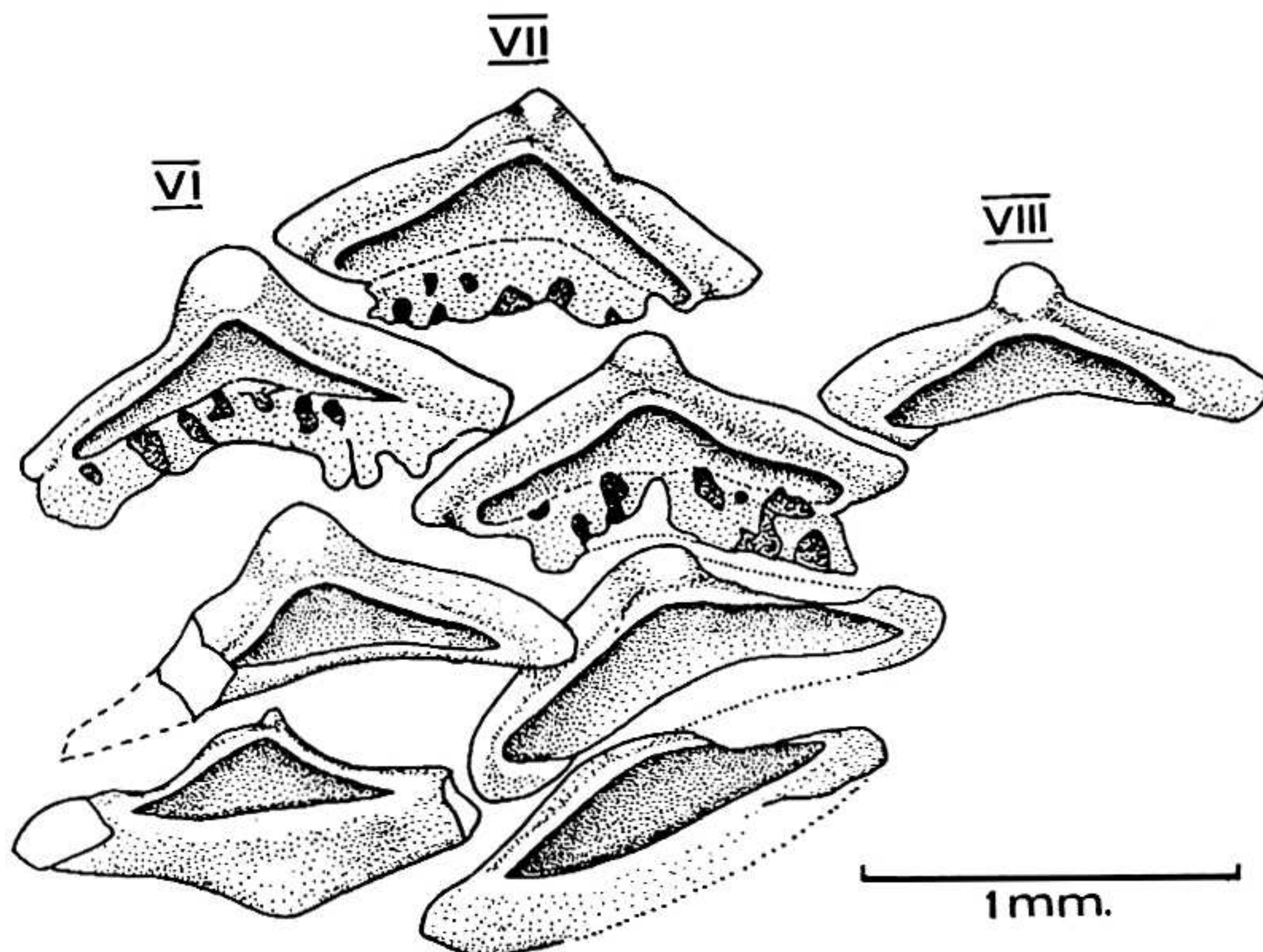
Holotype: SAM 1082 (pl. 3, fig. 1).

Other material: seven specimens, (BM(NH)) P. 16035-16038, P. 16039 (pl. 4, fig. 1), 17530, 17531 (pl. 4, fig. 2), comprising isolated fin spines and body fragments; 7 specimens (not seen) SAM 1183, 1185, 1186, 1084 (comprising dorsal fin spine and body fragments), 2776, 6020, 6039 JUBB & GARDINER 1975: 410; VAN DEN HEEVER, written communication).

Age: Lower *Cynognathus* zone, Upper Beaufort Series (Karoo System), Scythian, Lower Triassic.

Locality: Becker's Kraal, District Rouxville, Orange Free State, South Africa.

Diagnosis: (compiled from BROUGH 1935 and personal examination). Both jaws are fairly deep and relatively solid. The lower jaw is deep posteriorly, tapering rapidly anteriorly, and rounded toward the symphysis. The upper jaw is deep along much of its length. Cephalic spines are present behind the orbit in the male. The notochord persists. The neural arches, transverse processes and haemal arches are calcified. The neural spines are moderately long, tapering to a point dorsally in examples from the anterior region of the vertebral column. The transverse



Text-fig. 9. Detail of part of the dentition from the left upper jaw of *Lissodus africanus* (BROOM). BM(NH) P. 17531, lateral part of the dentition. Note the imbrication of successive tooth files, the strong labial peg, concentration of the root toward the labial part of crown undersurface, and the nature of the root vascularisation.

processes are slender and triangular in shape. Moderately long and delicate ribs are located behind the pectoral girdle. The pectoral girdle comprises two stout, elongate and narrow scapulo-coracoid bars which are not fused ventrally. Each scapula is attached to the base of the first dorsal fin spine. The pectoral fins are fairly large. Claspers are present in the male. The dorsal fins are supported by costate, stout fin spines of hybodontiform organisation, each possessing a double row of denticles on the posterolateral margins. The first dorsal fin spine is the shorter and stouter, lying at 45° to the body in lateral view, with the basal plate not being surmounted by radials. The second dorsal fin spine is straighter (70° to the body in lateral view) with a similar triangular basal plate attached to the spine base, and a row of several delicate radials further supporting the fin.

Description of the teeth: The teeth of *Lissodus africanus* are described here on the basis of P. 17531 (pl. 4, fig. 2) and P. 16039 (pl. 4, fig. 1), and with reference to BROUGH (1935). P. 17531 preserves the greater part of the upper dentition of the left side (text-fig. 9), plus two more anterior teeth. The latter are preserved in lateral and occluso-lateral views, and the former all in oblique basal view (text-fig. 9). P. 16039 preserves three teeth from the right side of the lower dentition in lingual view.

The teeth average 1.2 mm in length. The larger and better preserved teeth are toward the centre of the tooth row exposed in P. 17531. BROUGH (1935) cites an average length for teeth in the specimens which he examined of 0.7 mm. The teeth under consideration here vary from the average 1.2 mm by only 0.1 mm.

The crown is smooth, showing the occasional development of very fine vertical striations. The base of the low central principal cusp is diamond-shaped in occlusal view, and expanded labially. The labial face of the crown is deeper than the lingual face. Lateral and accessory cusplets are not developed. On the labial side the crown shoulder is weak. The lower labial face of the crown is much shallower than the corresponding lingual face. The mesial and distal extremities of the crown are relatively deep, with margins which steeply undercut the crown toward the crown/root junction in labial and lingual view. The lingual crown shoulder is pronounced, giving way basally to a broad lower lingual face which deeply undercuts the crown and leads to the crown/root junction. The labial peg is moderately developed. The crown/root junction is deeply incised around the whole tooth.

The root is long and narrow, and its attachment to the crown concentrated labially (text-fig. 9). The attachment of the root to the crown undersurface is an elongate triangle in outline, an extension being developed labially toward the undersurface of the labial peg. The lingual margin of the root forms the long straight edge of the triangle. Traces of the root itself remain in some of the teeth in P. 17531 (text-fig. 9). These traces comprise lingual faces of the root in internal view in every case. From these fragments, it can be seen that the root is of hybodontiform organisation, conforming to the anaulacorhizoid vascularisation condition of CASIER (1947). The foramina exposed appear to be irregular in virtually every case. Some foramina close to the crown/root junction may be specialised, but unfortunately no trace of the upper labial root face remains to make a further judgement on this feature. The root projects somewhat lingually from the crown undersurface. The labial and basal faces of the root were probably destroyed during the mechanical preparation of the specimen in the past. It can be seen that the undersurface of the crown is occupied by a longitudinal pulp cavity.

As can be seen from BROUGH (1935, pl. 2, figs. 1-4), the teeth are organised such that there is regular alternation in adjacent tooth files (text-fig. 9). At least ten tooth positions occur in a single longitudinal tooth row along one side of the jaw exposed in P. 17531, and there are eleven tooth positions in a single tooth row in P. 16039. In P. 17531 there are four successional tooth rows exposed. BROUGH (1935) remarks that there are four successional rows of eight teeth in each jaw in the material which was available to him. He also notices that the mesial teeth in both jaws have a more prominent central principal cusp than more distal teeth, cusp depression occurring progressively. This implies a linear gradient monognathic heterodonty (DUFFIN & WARD 1983a) which, because of the state of preservation of the material, cannot be verified from the specimens held by the British Museum (Natural History).

The largest teeth occur in central jaw positions (ie. a medial tooth suite, JOHNSON 1981), the mesial teeth being short and high-crowned, and the distal teeth being smaller, weaker and low-crowned, with virtually no cusp development. There is no evidence from the specimens or the account by BROUGH for dignathic, gynandric or ontogenetic heterodonty.

The dermal skeleton comprises almost entirely simple, stud-like denticles with upright crowns. A few examples with inclined crowns were noticed in the lower flank regions of some specimens. The scales are non-growing and conform to the hybodontoid morphotype (REIF 1978).

5. A comparison of the teeth of *Lonchidion* and *Lissodus africanus*

It can be seen on comparing the above descriptions and figures that the teeth of *Lonchidion* spp. and *Lissodus africanus* are very similar morphologically. The shared characters shall be considered individually:

Crown: In *L. africanus* and all species referred to *Lonchidion* by previous authors, the low central principal cusp is quadrate in occlusal view, being expanded labially to form a distinct labial peg (medio-internal process of PATTERSON 1966) which is not supported beneath by any development of the root. The labial face of the crown is consistently deeper than the lingual face. Lateral cusplets may be present or absent in *Lonchidion* spp., and are absent in *Lissodus africanus*. The mesial and distal extremities of the crown are steeply angled toward the incised crown/root junction in labial and lingual views in all species. Beneath the crown shoulder, the lower lingual face deeply undercuts the crown, leading to the crown/root junction. The lower labial face of the crown is always the shallower. Vertical striations may or may not be developed.

Root: Further examination of the undersides of tooth crowns of *Lonchidion* spp. indicates that a longitudinal pulp cavity is consistently present, and that the area of root attachment is triangular in outline and concentrated labially, as in *Lissodus africanus*. In all of the species described above, where the root is known, it is of hybodontoid organisation. Vascularisation is anaulacorhizoid (CASIER 1947). Individual foramina are usually large and irregular. Simple, smaller, specialised foramina may be present on the upper labial root face in teeth of *Lonchidion*, but have not been directly and confidently observed in *Lissodus africanus*. From the figures of the teeth of *Lissodus* above it can be seen that vascular foramina are often organised into rough longitudinal rows, although this is not always true for the lower labial and lingual root faces.

Tooth succession: *Lissodus africanus* shows overlap of teeth in adjacent files, a condition unknown in any other hybodontiform genus. Noting strong occlusal wear facets on many crowns, PATTERSON (1966) concludes that *Lonchidion* teeth from the Wealden of England are adapted to durophagy. He further notes that the labial peg produces a pressure scar on the centre of the lingual face of the preceding tooth, and concludes that overlap between successive files of teeth must have been present. He states that this is "an advanced character recalling the rays, which does not normally occur in hybodonts" (PATTERSON 1966: 319). Pressure scars are quite common on the lingual faces of other species of *Lissodus* described below, and suggests that alternation of teeth in the dentition was a common feature within the genus.

It is concluded from the evidence of these shared characters that those teeth described as *Lonchidion* by previous authors are generically identical to those of *Lissodus*. Accordingly, it is recommended that all valid species previously described as *Lonchidion* be referred to *Lissodus*, which name should be retained because of priority.

6. Other published Selachian species referable to *Lissodus*

A note on Carboniferous teeth of *Lissodus*

TWAY & ZIDEK (1983: 419, fig. 77 a–e) briefly describe and figure teeth of *Lissodus* from the Iowa Point Shale (Shawnee Group, Late Pennsylvanian, Upper Carboniferous) in Shawnee County, Kansas, USA. The specimens are moderately large (3.8 mm mesiodistally) and comprise isolated crowns. The crown/root junction possesses the triangular shape in basal view so characteristic of *Lissodus* teeth (TWAY & ZIDEK 1983, fig. 77 e) (text-fig. 10 c). The overall tooth shape is very reminiscent of *Lissodus*, but certain details of the crown are unique. The presumed lingual margin of the crown is virtually straight; in most species of *Lissodus* it possesses a bulge toward the base of the central principal cusp. The presumed labial peg is robust. There is a single principal cusp which is situated labial to the crown centre in occlusal view. The occlusal crest is well defined, bears, incipient lateral cusplets (TWAY & ZIDEK 1983, figs. 77 a, d) (text-fig. 10 d, e), but is situated on the lingual side of the crown laterally, and then curves labial to the central principal cusp (TWAY & ZIDEK 1983, figs. 77 a, d) (text-figs. 10 a, b, e). In most species of *Lissodus*, the occlusal crest is situated in the mesiodistal midline of the crown and does not curve appreciably to the central cusp. Indeed, in the specimen figured by TWAY & ZIDEK (1983, fig. 77) the principal cusp surmounts the labial peg, and is itself directed labially. The principal cusp in other species of *Lissodus* are upright. The late Pennsylvanian teeth appear to have been arranged alternately, as in *Lissodus*; pressure scars are present on either

side of the labial peg (TWAY & ZIDEK 1983, fig. 77 e)(textfig. 10 c), accommodating the lateral blades of teeth in adjacent files. Thus, these teeth appear to belong to a distinct new species of *Lissodus*, whose adaptations for durophagous diet include a labially-directed central principal cusp.

ZANGERL (1979, 1981) describes the teeth of *Dabasacanthus inskasi* from the Mazon Creek fauna (Carbondale Formation, Westphalian Upper C or Lower D of Will County, Illinois, U.S.A.) and notes that they closely resemble those of *L. breve*. His outline drawings of the teeth (ZANGERL 1981, fig. 61 C) suggest that they are *Lissodus* teeth, and that *Dabasacanthus* is therefore a junior synonym. This suggestion needs to be corroborated by further examination of the American material, however.

Lissodus zideki (JOHNSON)

1981 *Polyacrodus zideki* JOHNSON, p. 9, figs. 2, 47-74, 162-173.

Holotype: SMU-SMP, 64410 (JOHNSON 1981, figs. 51-57), a complete, isolated tooth.

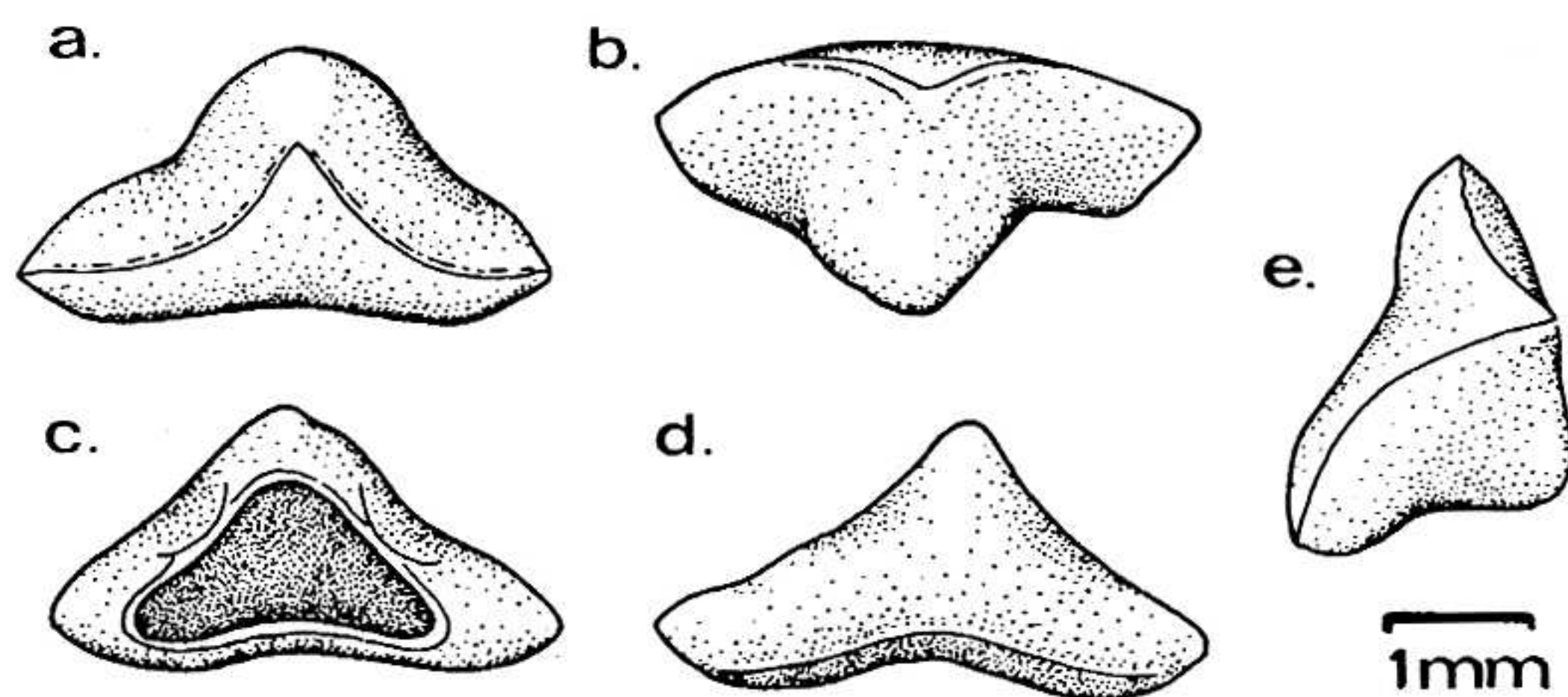
Other material: SMU-SMP 64435-64442, 64444-64461, 64463-64475, 64476-64482, 64681-64689, and referred teeth 64462, 64483-64516.

Localities: A number of local faunas, referred to as the Waggoner Ranch Collection, from Texas, U.S.A. See JOHNSON (1979, 1981). Age: Upper Admiral to Middle Lueders Formations, Wichita-Albany Group. Early Permian.

Diagnosis: Teeth of *Lissodus* showing moderate heterodonty. Mesial teeth are small (up to 1.5 mm long mesiodistally), whilst lateral teeth are larger (up to 2 mm long). The crown is highest in mesial teeth (JOHNSON 1981, fig. 67), and becomes flatter laterally (JOHNSON 1981, fig. 62). The labial peg is well developed in mesial teeth (JOHNSON 1981, figs. 66, 68), but tends to be weaker in lateral teeth (JOHNSON 1981, fig. 60). A lingual peg may or may not be developed at the base of the moderate principal central cusp (JOHNSON 1981, figs. 56, 71). Incipient lateral cusplets are developed in some mesial teeth. The occlusal crest is strong. Labial nodes may be present (JOHNSON 1981: 10). The root: crown junction is deeply incised in mesial teeth, and only moderately incised in laterals. Specialised foramina are present.

Remarks: The strong development of the labial peg in mesial teeth, together with the deeply incised (especially mesially and distally) crown/root junction, combined with overall tooth morphology, suggest that the teeth of this species belong to *Lissodus*. The lateral teeth show coronal elongation and flattening, accompanied by changes in the root morphology (see JOHNSON 1981: 9-10). JOHNSON (1981: 10) shows that tooth histology is "the typical pattern of *Polyacrodus*" (see below p. 138 for discussion of tooth histology).

L. zideki is one of several hybodont species described by JOHNSON from the Permian of the U.S.A. It should be noted here that certain other species described by him show development of a labial peg: ?*Acrodus olsoni* (JOHNSON 1981, figs. 8, 12-14, 23), ?*Acrodus sweetlacruzensis* (JOHNSON 1981, figs. 27, 33) and *Polyacrodus wichitaensis* (JOHNSON 1981, fig. 140). Johnson has based generic identifications mainly upon histology; a crown morphology reminiscent of *Lissodus africanus* and "*Lonchidion*" spp. is present only in *A. olsoni* and ?*A. sweetlacruzensis*. Based upon morphology, I tend toward the opinion that both these species may belong to *Lissodus*.



Text-fig. 10. Tooth of *Lissodus* sp., from the Iowa Point Shale, Stoner Limestone (Lansing Group), Lower Pennsylvanian of Madison County, Iowa, U.S.A. Diagram after TWAY & ZIDEK (1983, figs. 77 a-e). Note the angled principal cusp.

Lissodus angulatus (STENSIÖ)

Text-figures 11 a-c

1921 *Polyacrodus angulatus* STENSIÖ, p. 31, text-fig. 13, pl. 1 fig. 27.

1979 *Polyacrodus angulatus* - JERZMAŃSKA, p. 25, figs. 14-17.

Holotype: reported by STENSIÖ (1921: 31) to be in the collection of SALOMON at Heidelberg. Specimen as yet untraced. An isolated crown from Fish Horizon 1 (*Posidonomya* Bed), ?*Otoceras/Ophiceras* zone, Griesbachian, Scythian, Lower Triassic of Spitsbergen.

Other material: four isolated crowns from the type locality; about 200 teeth, some with roots (text-fig. 10) from the fine-grained conglomerates of the Brevassfjellet *Myalina* Beds, *Candidus* zone, Urnetoppen Member, Vardebukta Formation, Lower Dienerian, Lower Scythian, Lower Triassic of the south-eastern slope of Hyrnefjellet, inner Hornsund, south Spitsbergen (BIRKENMAJER & TRAMMER 1975, BIRKENMAJER & JERZMAŃSKA 1979: 8, figs. 1, 2). The material is held in the Paleozoology Department, Institute of Zoology, Wrocław University, Poland.

Age: Scythian, Lower Triassic.

Diagnosis: Teeth measuring up to 7 mm in length, with a moderate central principal cusp. The lateral cusplets are usually absent, but may show incipient development. The labial peg is moderate. The crown may be smooth or ornamented by fine vertical striations, those on the principal cusp bifurcating basally. A longitudinal ridge may be developed along the labial crown shoulder (BIRKENMAJER & JERZMAŃSKA 1979, fig. 16 c). The vertical striations may or may not attain the occlusal crest. Where known, the root is lingually-directed. Specialised foramina are present along the upper labial root face. All other foramina are irregular, but may be organised into longitudinal rows on both lower labial and lower lingual root faces. Mesial teeth are probably moderately long and symmetrical, while laterals are probably long and narrow with a prominent labial peg.

Remarks: After a thorough description of the teeth of this species, BIRKENMAJER & JERZMAŃSKA (1979: 28) note their close similarity to teeth of *L. breve*, but refrain from allocating them to *Lissodus* since details of the histology are lacking. The crown and root morphology are unmistakably that of *Lissodus* and the species should be placed in that genus.

The material originally described by STENSIÖ (1921) comprises poorly preserved isolated crowns which I have been unable to trace. The figures and description by STENSIÖ suggest that his specimens belong to *Lissodus*, but the confident assignation of the Hornsund material to *L. angulatus* needs confirmation.

BIRKENMAJER & JERZMAŃSKA (1979, fig. 17) indicate the importance of the labial peg in inter-tooth articulation between members of the same tooth family, as in other species of *Lissodus*.

Lissodus nodosus (SEILACHER)

Plate 5, figs. 1 a-i, 2 a-i; pl. 6, figs. 1 a-f

1888 *Acrodus* sp. - THÜRACH, p. 130, 134.

1910 *Acrodus* sp. - LANG, p. 19.

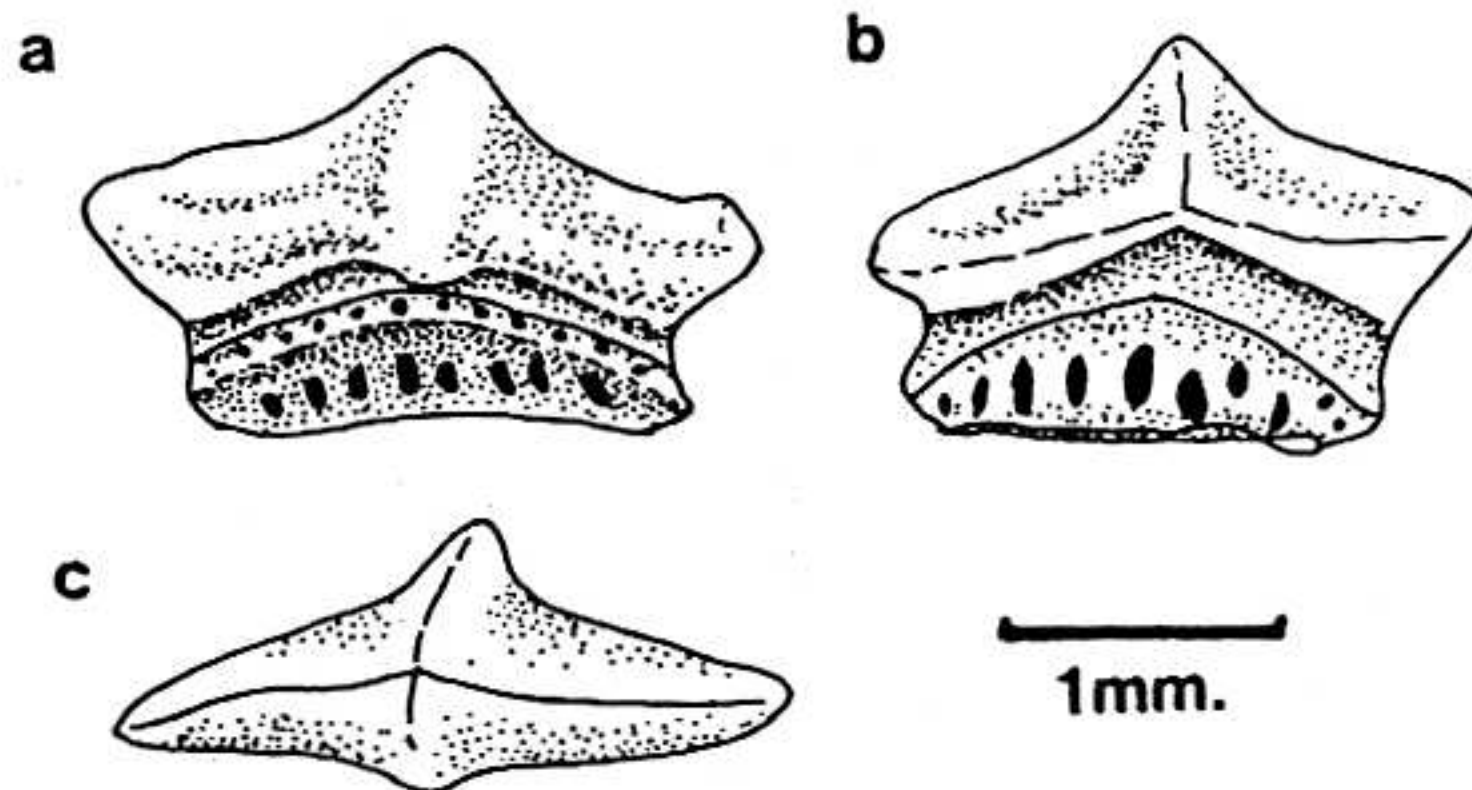
1928 *Acrodus lateralis* - OERTLE, p. 344, pl. 41 fig. 4.

1938 *Acrodus* sp. - REIFF, p. 114, 131, 136.

1943 *Palaeobates nodosus* SEILACHER, p. 274, figs. 18-23.

1943 *Palaeobates spinosus* SEILACHER, p. 278, figs. 24-29.

Text-fig. 11. Tooth of *Lissodus angulatus* (STENSIÖ 1921) from the Vardebukta Formation (Lower Dienerian, Lower Scythian, Lower Triassic) of Hyrnefjellet, southern Spitsbergen. Sp/22, Palaeozoology Department, Institute of Zoology, Wrocław University, Poland. After BIRKENMAJER & JERZMAŃSKA (1979, fig. 14). a, labial view; b, lingual view; c, occlusal view. Note the smooth crown, moderate labial peg and modified hybodontoid root vascularisation. There is a longitudinal row of specialised foramina on the upper labial root face, and similar rows of larger, simple foramina along the lower labial and lingual root faces. The specimen is probably an anterior tooth (BIRKENMAJER & JERZMAŃSKA 1979: 28).



Holotype: SMNS 52341, an isolated crown from a bone bed in the Vitriolschiefer of the lower Lettenkohle (SEILACHER 1943: 257) of Heldenmühle near Crailsheim, southern Germany. The specimen was previously figured by SEILACHER (1943, fig. 18).

Age: Upper Muschelkalk to Lower Bunte Mergel, middle to late Triassic.

Other material: several hundreds of specimens, mostly isolated crowns, from the Upper Muschelkalk and Keuper (Anisian to Norian, Upper Triassic) of south west Germany. For stratigraphic and locality details see SEILACHER (1943: 277–280). The specimens are held in the SMNS. Figured specimens are SMNS 50.206 (pl. 6, figs. 1 c–f), 50.209 (pl. 6, figs. 1 g–h), 50.210 (pl. 6, figs. 1 a–b), 50.211 (pl. 5, figs. 1 a–b, 2 i), 50.212 (pl. 5, figs. 1 c–d), 50.213 (pl. 5, fig. 1 e), 50.214 (pl. 5, figs. 1 f–i), 50.215 (pl. 5, fig. 2 a), 50.216 (pl. 5, figs. 2 b–c), 50.217 (pl. 5, figs. 2 f–g), and 50.218 (pl. 5, fig. 2 h).

Diagnosis: Species of *Lissodus* showing considerable heterodonty. Mesial teeth measure up to 1 mm in length, possess a deep crown, strong labial peg, lack vertical striations and lateral cusplets, but may possess small lingual nodes. The root attachment is triangular in outline, but the root itself is virtually unknown. Lateral teeth measure up to 5 mm in length, possess well developed labial nodes along the crown shoulder and basally bifurcating vertical ridges arising from the strong occlusal crest. The labial peg is gradually suppressed with increasing tooth size. The impression is obtained that the roots of lateral teeth are far more robust than those of the mesial suite, the root attachment being considerably larger. Vascular foramina show little or no longitudinal alignment, but may be crudely aligned vertically. No specialised foramina are present. Intermediate teeth may possess lateral cusplets and a low principal central cusp, all of which are suppressed in lateral teeth.

Description: The teeth here referred to *Lissodus* were originally allocated to two species, *Palaeobates nodosus* and *P. spinosus* by SEILACHER (1943). The two species were defined largely upon their stratigraphical range and geographic location. *P. nodosus* was restricted to the Upper Muschelkalk and overlying Lettenkohle of Westheim, Heldenmühle and Steppach; *P. spinosus* was found in the Gipskeuper, Schilfsandstein and Bunter Marls, particularly of Eisbach. Morphologically, the two groups of teeth are indistinguishable. There are two main tooth forms in the Ludwigsburg SEILACHER collection of *L. nodosus*: a tooth shape conforming to the general characters of *Lonchidion* as defined by previous authors; a larger tooth form more closely resembling the teeth of *Acrodus* in overall appearance. It is assumed that the former group comprises anteromesial teeth for reasons given below (p. 22), and that the larger teeth are laterals.

The mesial teeth (pl. 5, figs. 1 a–i, 2 a–i) are small, measuring 1 mm long on average. The crown is relatively deep (pl. 5, figs. 1 a–c), corresponding to approximately half the total crown length. The labial peg is strongly developed (pl. 5, figs. 1 e, f) and has produced corresponding pressure scars on the lingual face of adjacent teeth (pl. 5, fig. 1 a, 2 b). The occlusal surface of the crown is mostly narrow, and functional wear tends to be concentrated in the central area, around the position of the labial peg (pl. 5, fig. 2 a). The mesial and distal margins of the crown are deep and steeply inclined toward the crown/root junction in lingual view (pl. 5, figs. 1 a–c, h, g, 2 b, d). The crown may be considerably arched in labial view (pl. 5, figs. 1 g, h). There is little or no vertical or longitudinal ornament on the crown. Small nodes may be developed on the labial crown shoulder in a few of the larger crowns belonging to this morphotype (pl. 5, fig. 2 h). Lateral cusplets are lacking.

The crown/root junction is incised around the whole tooth (pl. 5, figs. 1 a, c, h, g, 2 b, d). The lingual face of the crown tends to be straight in smaller specimens, with the development of a fairly broad undercutting lower lingual face becoming more pronounced in larger specimens (pl. 5, fig. 1 i). The undercut toward the crown/root junction on the labial side is consistently deep. Short basal extensions of the crown may be present on both labial and lingual sides, before the root begins (pl. 5, figs. 1 a–d, g–h, 2 b, d).

The root attachment to the undersurface of the crown is triangular in shape (pl. 5, figs. 2 c). The long edge of the triangle is formed by the lingual face of the root, and the apex by the labial expansion of the root toward the labial peg. The root is incompletely known in teeth of this morphotype. From the crown undersurface, the vascularisation appears to be anaulacorhizoid. A central longitudinal canal is situated high up the root at the crown/root junction, protected labially and lingually by the downward-projecting flanges of the crown base.

The lateral teeth are larger and measure up to 5 mm long. The crown varies from being elongate with a weakly developed labial peg (pl. 6, figs. 1 a, b, g, h), through longer teeth with a gradual suppression of the labial peg in favour of a general central expansion of the whole crown (pl. 6, figs. 1 e, f), to very long teeth with only slight expansion in the centre, but with virtually no labial peg (pl. 6, figs. 1 c, d). In all teeth belonging to this morphotype, nodes are developed along the length of the labial shoulder of the crown, the largest nodes being situated centrally (pl. 6, Fig. 1 a). Coarse vertical ridges arise from the occlusal crest, bifurcating and often breaking as they travel toward the labial and lingual crown shoulders (pl. 6, figs. 1 e, h). The ridges tend to radiate from the

position of an extremely low central cusp. The lateral margins of the crown vary between high and steep to low and rounded.

The crown/root junction is incised around the tooth (pl. 6, fig. 1 a), with a well developed lower lingual face undercutting the crown. As is the case in the mesial teeth, the root is concentrated toward the labial underside of the crown (pl. 6, figs. 1 b, d), and in smaller teeth retains the triangular outline at its point of attachment with the crown. This feature becomes less obvious in larger specimens, in which the root attachment to the crown becomes much longer and expanded.

The root is simple in form. The basal face is long, fairly narrow, flat, and tends toward rectangular in outline. Small, simple, irregular foramina occasionally pierce its surface. The labial face of the root is concave to almost flat in some specimens. The upper labial face of the root is well developed. The vascular foramina on the lower labial root face are large, irregular, and vertically elongate in some specimens. There may be some vertical alignment of these foramina. The lingual root face is markedly convex, especially immediately beneath the crown/root junction. The upper lingual root face is almost horizontal, whilst the lower lingual root face is almost vertical. The irregular vascular foramina are more numerous on the lower part of the lingual face of the root. Again, they may show vertical alignment into rough rows. The whole root projects lingually from the crown underside.

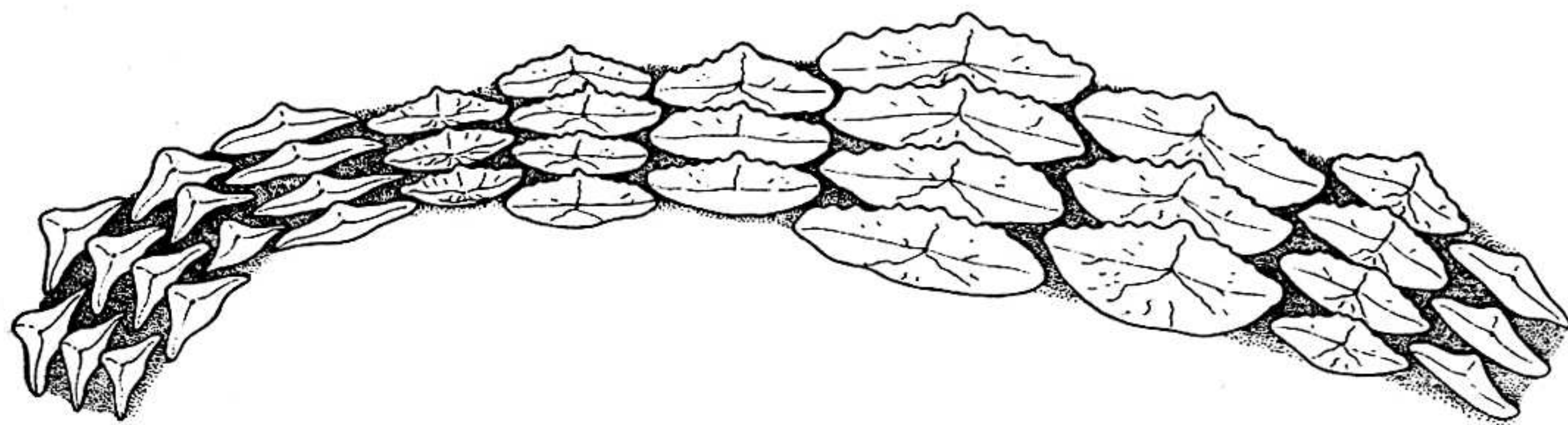
Intermediate tooth types (pl. 5, fig. 1 h, 2 f-i), with regard to both size and morphology, often preserve the root, which is identical to that of the mesial teeth, so far as can be determined. The crown is often quite arched in labial view, and lateral cusplets may be developed (pl. 5, fig. 1 h). The central principal cusp is moderate and may be flanked by up to three low lateral cusplets on each side (SEILACHER 1943 fig. 27 a, b). Labial nodes may (pl. 5, fig. 2 h) or may not be developed.

Discussion: From the above descriptions it is obvious that the three tooth forms described by SEILACHER do indeed show morphological transition; small, "Lonchidion-like" mesials vary through larger, cuspidate intermediates to "Acrodus-like" laterals. The labial peg is lost with increasing tooth size, and there is a concomitant increase in development of the labial nodes. The root is long and narrow in the mesial teeth, and becomes more robust in the larger laterals. The vascularisation of the root is consistently hybodontoid and anaulacorhize. The presence of a longitudinal central canal high up inside the tooth at the level of the crown/root junction is a further unifying feature.

These variations in tooth form must be of functional significance. In the mesial teeth, the labial peg is important in holding adjacent tooth files in functional and rigid juxtaposition. The pronounced development of the pressure scar on the lingual face of corresponding teeth (pl. 5, fig. 1 a, 2 b) indicates the importance of the labial peg in this rôle. In the mesial teeth, however, the root is less robust than in the larger laterals. In the larger teeth, the labial peg is suppressed, and finally lost in some specimens, while the root increases in importance. The root is required to be robust in large crushing teeth, as in the dentitions of *Acrodus*, *Asteracanthus*, *Palaeobates*, *Hylaeobatis* and *Ptychodus*. These genera are not necessarily sharks in a single, continuously evolving lineage, but furnish examples which do show overall similarity in that a robust root is developed directly beneath the crown, showing some lingual exaggeration, in order to counter the high pressures produced on the crown during occlusion. In these genera, and in the larger teeth of *L. nodosus*, the root forms the major anchoring and articulatory feature. The increase in importance of the labial nodes may have fulfilled the need for a more delicate positional influence for determining precise crown to crown relationships within successive tooth files, as might be required with increasing importance of the root in tooth articulation. A diagrammatic reconstruction of the dentition of *L. nodosus* is given in text-fig. 12.

Thus, it would seem that in the smaller mesial teeth, articulation was provided primarily by the labial peg, the importance of which gradually decreased with increasing tooth size and functional grinding capacity, in favour of a more robust root which could 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. The closest parallel amongst other shark dentitions would appear to be along the tooth family of recent and fossil species of *Heterodontus* (REIF 1976: 43).

SEILACHER (1943: 280) suggests that teeth here interpreted as mesials are actually extreme laterals of *L. nodosus*. It should be noted, however, that in shark dentitions smaller teeth are usually mesial in position, and larger teeth are laterals. This is particularly true for durophagous dentitions (eg. *Heterodontus*, *Acrodus*, although small extreme laterals are present in *Acrodus*, for example *A. nobilis* AGASSIZ, SMITH WOODWARD 1889, pl. 14, fig. 1). Furthermore,



Text-fig. 12. A reconstruction of the dentition of *Lissodus nodosus* (SEILACHER) from the Norian (Upper Triassic) of southern Germany. The diagram is based on the occlusal views of teeth in the SEILACHER collection, SMNS.

it appears that in other selachian lineages, mesial and symphyseal tooth morphotypes show primitive characters. For example, upright, multicuspoid crowns are typical of certain squaliforms, pristiophoriforms, squatiniforms and most galeomorphs. In *Heterodontus*, multicuspoid mesial teeth give way to low-crowned laterals with a distinct crown and root morphology (REIF 1976). The multicuspoid crown is typical of very young *Heterodontus* dentitions (REIF 1976, figs. 2 a-d, 3 a-d). As shown below (see p. 144) "Lonchidion-like" teeth of *Lissodus* are conservative and persist throughout the lineage. Thus, I consider that the "Lonchidion-like" teeth of *Lissodus* are mesial in position.

Lissodus minimus (AGASSIZ)

Text-figures 13 a-d, 14 a-d; pl. 2, figs. 3 a-d; pl. 3, figs. 2 a-c

- 1839 *Acrodus minimus* AGASSIZ, p. 145, pl. 22 figs. 6-12.
- 1839 *Acrodus acutus* AGASSIZ, p. 146, pl. 22 figs. 13-15.
- 1843 *Acrodus minimus* - PORTLOCK, p. 107, 469, pl. 14 figs. 18 a-b.
- 1844 *Acrodus minimus* - MEYER & PLIENINGER, p. 115, pl. 10 figs. 25-26, pl. 12, figs. 63, 82.
- 1844 *Thectodus inflatus* MEYER & PLIENINGER, p. 116, pl. 10 fig. 20.
- 1844 *Thectodus glaber* MEYER & PLIENINGER, p. 116, pl. 10 fig. 21.
- 1844 *Thectodus crenatus* MEYER & PLIENINGER, p. 116, pl. 10 fig. 22, pl. 12 fig. 39.
- 1844 *Thectodus tricuspoidatus* MEYER & PLIENINGER, p. 116, pl. 10 fig. 27, pl. 12 fig. 29.
- 1852 *Acrodus minimus* - QUENSTEDT, p. 179, pl. 13 figs. 47-50.
- 1858 *Acrodus minimus* - QUENSTEDT, p. 34, pl. 2 fig. 23-27.
- 1858 *Acrodus minimus* - ROLLE, p. 28, 31, pl. 1 fig. 18.
- 1861 *Acrodus acutus* - SCHMID, p. 17, pl. 2 figs. 33-37.
- 1861 *Acrodus minimus* - SCHMID, p. 17, pl. 2 fig. 38.
- 1865 *Thectodus tricuspoidatus* - ECK, p. 118.
- 1870 *Thectodus inflatus* - ENDLICH, p. 18.
- 1870 *Thectodus glaber* - ENDLICH, p. 18, pl. 2 fig. 55.
- 1870 *Thectodus tricuspoidatus* - ENDLICH, p. 18.
- 1870 *Thectodus crenatus* - ENDLICH, p. 17.
- 1871 *Acrodus minimus* - ETHERIDGE, pl. 2 figs. 15-17.
- 1875 *Thectodus tricuspoidatus* - HENRY, p. 410, pl. 2 fig. 7.
- 1880 *Acrodus minimus* - WINKLER, p. 115, pl. 6 fig. 13.
- 1885 *Acrodus minimus* - QUENSTEDT, p. 279, pl. 21 figs. 46-48.
- 1885 *Acrodus minimus* - WOODWARD, fig. 77.
- 1889 *Acrodus minimus* - WOODWARD, p. 282.
- 1908 *Acrodus minimus* - ENGEL, p. 182, pl. 1 fig. 11.
- 1908 *Acrodus minimus* - PRIEM, p. 11, fig. 4.
- 1928 *Polyacrodus minimus* - CORROY, p. 15.
- 1962 *Acrodus minimus* - DREYER, p. 134, pl. 1 figs. 12-13.
- 1962 *Acrodus lateralis* - DREYER, p. 134, pl. 1 figs. 1-11.
- 1966 *Polyacrodus minimus* - PATTERSON, p. 315, pl. 5 fig. 1.
- 1970 *Acrodus minimus* - SYKES, CARGILL & FRYER, p. 254, pl. 15 figs. 10-14, text-fig. 5 figs. 1-2.
- 1977 *Acrodus minimus* - DUFFIN & GAZDZICKI, p. 335, pl. 1 figs. 1-3.
- 1978 *Acrodus minimus* - DUFFIN, fig. 4.

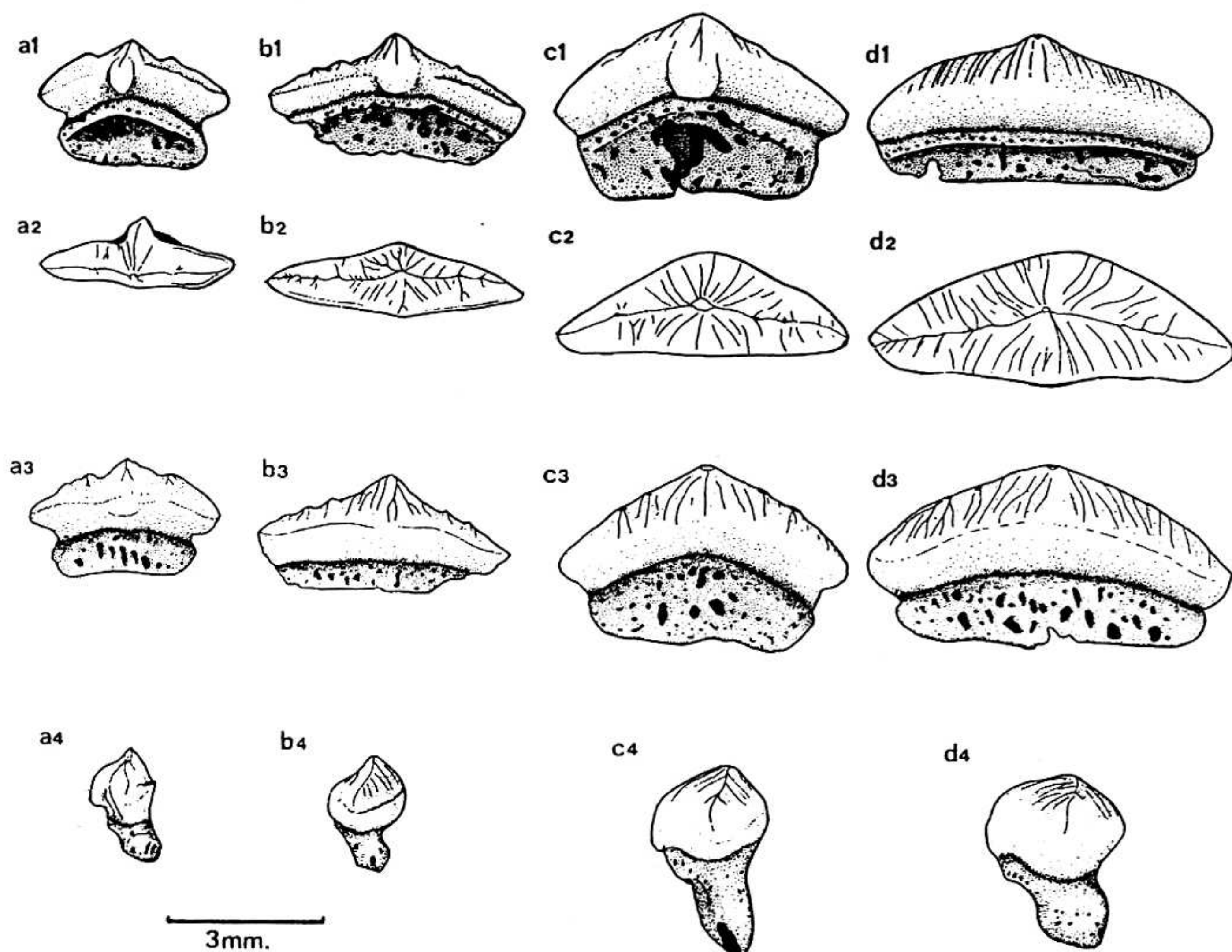
Note on the Holotype: AGASSIZ (1839) figured 7 specimens of *Acrodus minimus*, stating that all were housed in the collections of the Bristol City Museum. WILSON (1890: 4) notes that only two specimens (AGASSIZ 1839 pl. 22, figs. 6, 10) were present when he catalogued the collections. These were catalogued under one number, C 4574. These specimens have not subsequently been traced in the collections, and are believed to have been destroyed when the Museum was bombed in 1940 (M. D. CRANE, written communication).

Neotype: BRSMG Cc735, a complete tooth (pl. 2, figs. 3 a-d) from the bone bed basal to the Westbury Beds, Penarth Group (formerly called "Rhaetic"), Rhaetic, Upper Triassic of Aust Cliff, Avon, England. ST 567895.

Material: many thousands of isolated teeth from the Holwell fissure filling (M 64, MOORE Collection, BGM), including CD 54 (text-figs. 12 a-d) CD 55 text-fig. 11 a), CD 56 (text-fig. 11 b), CD 57 (text-fig. 11 c) and CD 58 (text-fig. 11 d).

Localities: The material listed above is from a ?Rhaetic fissure infill in the Carboniferous Limestone Quarry at Holwell, near Frome, Somerset, south west England. ST 727449. I have examined many hundreds of further teeth from large numbers of localities in Britain and north west Europe.

Diagnosis: Teeth of *Lissodus* up to 7 mm long, showing moderate heterodonty. The principal central cusp is highest in mesial and anterolateral teeth. The labial peg is well developed in mesial teeth, but becomes progressively weaker laterally through the dentition. The occlusal crest is moderate. Lateral cusplets may be developed (up to 5 pairs). The crown is robust and low in lateral teeth. The crown may be ornamented by moderate vertical ridges. The crown/root junction is deeply incised in mesial teeth, but becomes progressively less so laterally. Specialised foramina are present.



Text-fig. 13. Teeth of *Lissodus minimus* (AGASSIZ 1839) from the ?Rhaetic (Upper Triassic) fissure filling at Holwell, near Frome, Somerset, England. All specimens are housed in the MOORE collection, BGM. a, CD 55, a mesial tooth; b, CD 56, an anterolateral tooth; c, CD 57, a lateral tooth; d, CD 58, an extreme lateral tooth. In all cases the views are 1, labial; 2, occlusal; 3, lingual; 4, lateral. Note the specialised foramina on the upper labial root face, vertical ridges and lateral cusplet development.

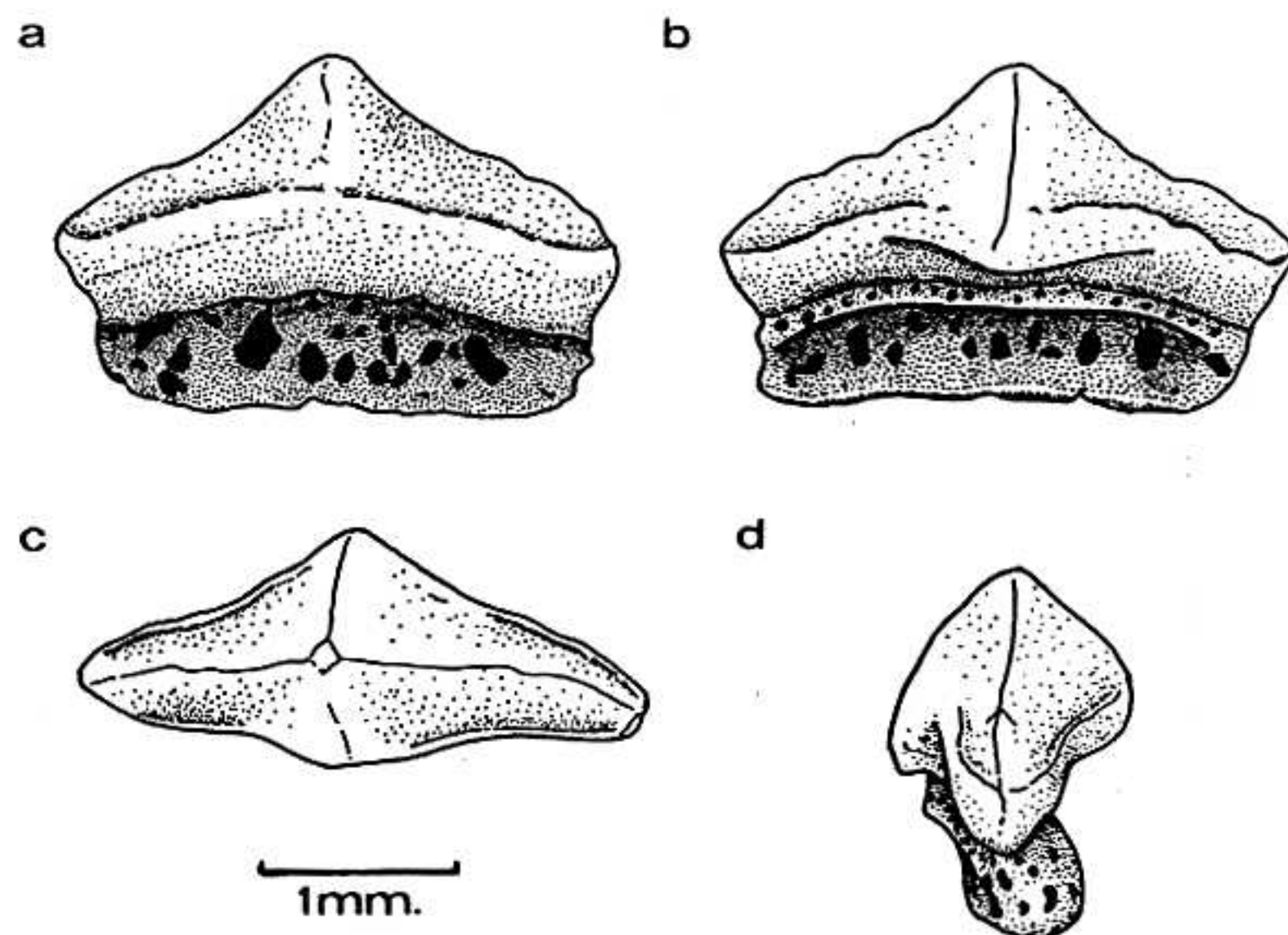
Description: Two main tooth types can be recognised in the teeth of this species; those possessing long and narrow crowns with a relatively high central cusp (text-figs. 13 a, b; pl. 2, fig. 3 a–d); those in which the crown is shorter and wider, with a low profile (text-figs. 13 c, d). Intermediates, and teeth showing a combination of the characters of each of these types, are common. For ease of description and consideration of variation, the two morphological types will be considered separately here.

Those teeth with long and narrow crowns (text-figs. 13 a, b, 14 a–d) possess a medium to high principal cusp, the base of which is diamond-shaped in occlusal view. The base of this central cusp is the widest part of the crown. A well developed labial peg is present at the base of the central cusp. As many as five small lateral cusplets may be developed on either side; when present, they are very low. A moderate occlusal crest runs the length of the crown, through the apices of all the cusps. The crown surface is ornamented by vertical striations. A major vertical ridge forms a crest to the labial peg and ascends the principal cusp. Other, less well developed vertical ridges arise from the principal cusp. Other, less well developed vertical ridges arise from the occlusal crest at the cusp apices and descend the crown on both lingual and labial faces. Most striations terminate at the crown shoulder. Some vertical striations bifurcate basally. The crown shoulder is quite pronounced around the whole tooth. A longitudinal ridge may be present to a greater or lesser extent, passing around the tooth at the level of the crown shoulder (text-figs. 13 a, b, 14). The lateral extremities of the crown may be lingually directed in occlusal view. In lingual view, the extreme lateral margin of the crown varies from being steeply angled to the crown/root junction, and straight, to low and rounded. The former is the more common condition. Toward the base of the crown, the lower lingual crown face undercuts the lingual shoulder moderately sharply, and is deep, leading to the crown/root junction. The lower labial face of the crown is shallower, but undercuts the labial crown shoulder more sharply. The undersurface of the crown in broken teeth shows concentration of the area of root attachment labially. The root attachment is triangular in outline, the lingual border forming the long side, and the apex of the figure situated just lingual to the underside of the labial peg. The crown underside shows slight to fairly pronounced mesiodistal concavity, and the area of root attachment is markedly concave labiolingually.

In the case of the flatter, wider crowns (text-figs. 13 c, d), the central cusp is very low, and lateral cusplets either very low or absent. The occlusal crest is not so pronounced as in higher-crowned teeth. The crown may be heavily ornamented with vertical ridges which descend to the crown shoulders from the occlusal crest, and seldom, if ever, bifurcate basally. The labial peg is small, if present. The lower lingual face of the crown sharply undercuts the lingual crown shoulder and is deeper than the corresponding labial face. The crown undersurface is usually markedly concave mesiodistally, and the root attachment area expanded, but concentrated labially.

In the teeth of both morphotypes, the crown/root junction is moderately incised, often being deeper on the lingual side.

Roots are seldom preserved in teeth belonging to this species. In the smaller, narrow teeth, the lower lingual crown face tends to project straight down to the rather flat crown/root junction.



Text-fig. 14. Tooth of *Lissodus minimus* (AGASSIZ 1839). CD 54, MOORE Collection, BGM, from the Holwell fissure filling (?Rhaetian, Upper Triassic) in a, lingual view; b, labial view; c, occlusal view; d, lateral view; Notice the longitudinal ridge at the crest of the crown shoulder, and specialised foramina on the upper labial root face.

The basal face of the root is flat, punctuated by small, simple foramina, and shows some concavity mesiodistally. On the labial side, a shallow longitudinal ridge runs the length of the root, just below the crown/root junction. This ridge bears a single row of small specialised foramina. From this ridge, the labial face of the root descends lingually to the labial border of the basal root face. The labial root face is concave labiolingually. It bears large vascular foramina.

On the lingual side, a single row of vascular foramina is present just beneath the crown/root junction, giving way to the remainder of the convex lingual root face.

Teeth showing considerable antemortem wear often possess pressure scars on the lingual face of the crown, corresponding in position to the labial face of the succeeding tooth. Occasionally, the lateral extremities of the tooth may possess similar pressure scars, corresponding to the lingually-deflected extremities of teeth in the adjacent tooth family.

Discussion of heterodonty: From an examination of several thousand specimens it can be concluded that a gradation exists from smaller "Lonchidion-like" mesial teeth through to more robust laterals. The following changes take place distally through the dentition:

1. The teeth become longer mesiodistally, increasing in size from approximately 3 mm in mesial to 7 mm in lateral teeth.

2. The coronal profile becomes more shallow. The central principal cusp becomes progressively lower, and the lateral cusplets less obvious.

3. There is an increase in vertical ridge development on the crown, especially on the lateral extremities of the tooth, both labially and lingually.

4. The labial peg becomes less obvious and decreases in importance.

5. Occasional longitudinal ridges on the crown shoulders in mesial teeth are not present in lateral teeth.

6. The incised nature of the crown/root junction, especially at the lateral extremities of the tooth, becomes less marked.

7. The root tends to become sub-equal to the crown in depth; the root is shallower than the crown in mesial teeth.

These progressive changes in tooth morphology through the dentition are reminiscent of those in *L. nodosus* (see p. 121) and reflect the increasing importance of the root in maintaining inter-tooth articulation accompanying expansion of the crown for durophagous diet.

Enameloid ultrastructure: One tooth of *L. minimus* was broken, etched in 2N HCl for three seconds, covered with evaporated gold and studied using a Cambridge Stereoscan 600 Scanning Electron Microscope at an acceleration voltage of 5 KV. The results of this study are shown in pl. 3, figs. 2 a-c. The enameloid layer is approximately 200 μm thick and comprises individual apatite crystallites measuring up to 1.5 μm in length. It is a single crystallite enameloid *sensu* REIF (1973). The individual crystallites tend to be organised into radially arranged groups, and possess more random orientation close to the surface.

REIF (1973, 1978) found that hybodonts and ctenacanth possess single crystallite enameloid in which the individual crystallites are generally longer than 2 μm . Apatite crystallites in *L. minimus* are smaller. Two orientations of the crystallites are common in hybodont enameloid (REIF 1973, 1978); random orientation throughout the enameloid layer (as in *Dicrenodus*, REIF 1978, fig. 7 c), or orientation perpendicular to the tooth surface (as in *Hybodus*, REIF 1978, figs. 7 a, b). Crystallite orientation in *L. minimus* recalls the latter condition.

REIF (1978) has also described the enameloid of *Pseudodalatias barnstonensis* (SYKES, 1971) from the British Rhaetian. In this genus, the crystallites measure only 1 μm in length.

Thus, from the data currently available, the enameloid of *L. minimus* is most similar to that of *Hybodus* and *Pseudodalatias* in terms of crystallite orientation. The enameloid layer is thicker in *Lissodus* than in either *Hybodus* or *Pseudodalatias*. This is to be expected in a comparison between crushing and piercing teeth.

Lissodus leiodus (SMITH WOODWARD)

Text-figures 15 a, b; pl. 4, figs. 3, 4

1844 *Acrodus leiodus* AGASSIZ, p. XXXVIII (name only).

1871 *Acrodus* sp. - PHILLIPS, diagr. XXXVII, p. 177, fig. 10.

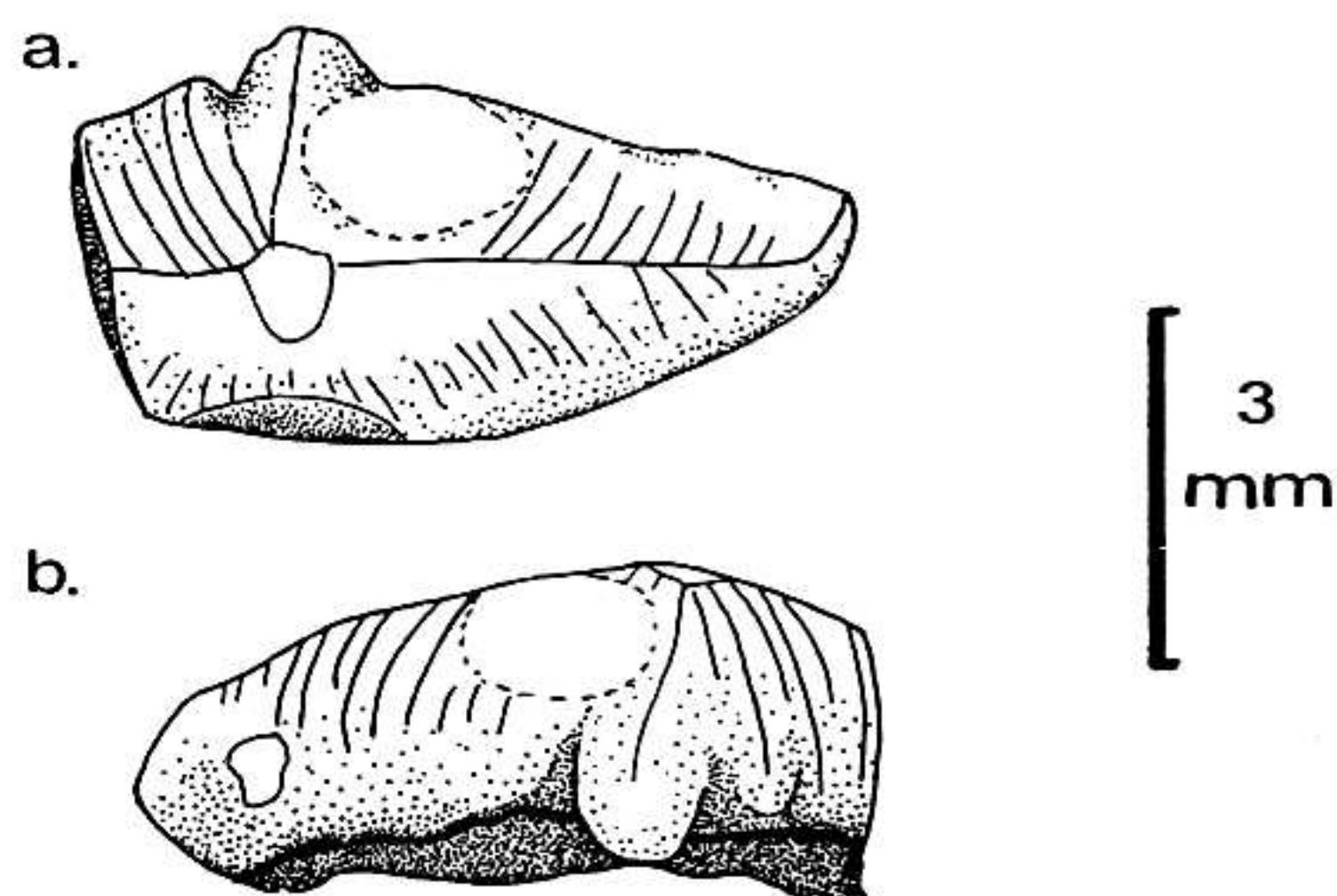
- 1871 *Acrodus* sp. — PHILLIPS, diagr. XXXVII, p. 177, fig. 10.
1887 *Acrodus leiodus* — WOODWARD, p. 101, fig. 1.
1889 *Acrodus leiodus* — WOODWARD, p. 295, pl. 13 figs. 5, 6.
1890 *Acrodus leiodus* — WOODWARD, p. 288, fig. 110.

Holotype: P. 5873 (BM(NH)), an isolated crown (WOODWARD 1887:101, fig. 1; 1889, pl. 13, fig. 6) from the Great Oolite Group (Bathonian, Middle Jurassic) of Minchinhampton, Gloucestershire, England.

Other material: BM(NH) P.12355 (5 crowns) from Brora, Sutherland (specimen label states Bajocian); 41316 (2 crowns), P. 2753 (4 crowns), P. 21043 (1 crown), 36583 (1 crown) from the Stonesfield Slate (Great Oolite Group) of Stonesfield, Oxfordshire; P. 10109 from the Stonesfield Slate of Severnhampton; (?) 30559 from the Forest Marble of Atford, near Bath, Wiltshire; P.2134 (pl. 4, fig. 3) (3 crowns) from the Great Oolite of Stonesfield, Oxfordshire; P.5874 (6 crowns) from the Great Oolite of Minchinhampton, Gloucestershire; P.10110 (locality and horizon unknown) (pl. 4, fig. 4).

Diagnosis: Teeth of *Lissodus* measuring up to 10 mm mesiodistally. The labial peg is moderate when present and surmounted by a vertical ridge. Strong vertical striations tend to cross the crown shoulder. Lateral and accessory cusplets are lacking and the crown has the greatest central expansion in those teeth lacking a labial peg.

Description: All available specimens of this species are isolated crowns varying in length (mesiodistal) from 5 to 10 mm. The coronal profile is low. The central principal cusp is very squat. Lateral and accessory cusplets are absent. The crowns are all quite wide (up to 4 mm labiolingually) in relation to the length, being expanded at the base of the central principal cusp. The labial peg is present in a few specimens only (all 5 specimens in P.12355, 1 specimen in P. 2753, P.21043, 1 specimen in P. 2134 (pl. 4, fig. 3), P. 101100 (pl. 4, fig. 4), and 3 specimens in P. 5874; text-fig. 15 a, b), and is moderately well developed. It is smallest in those specimens with the greatest principal cusp base expansion. Those teeth lacking a labial peg are mostly very expanded centrally (P. 5874; WOODWARD 1889 pl. 13 fig. 5). The labial peg is surmounted by a strong vertical ridge. The whole of the occlusal face of the crown is ornamented by strong vertical striations which descend from the strong occlusal crest to terminate either at the crown shoulder, or in the case of the strongest striae, midway down the lower labial and lingual faces of the crown. Striations passing over the crown shoulder on the labial side often develop into strong vertical ridges (text-fig. 15b).



Text-fig. 15. Tooth of *Lissodus leiodus* (WOODWARD 1887) from the Great Oolite (Bathonian, Middle Jurassic) of Minchinhampton, Gloucestershire, England. BM(NH) P. 5874 in a, occlusal view; b, labial view. Note the moderate labial peg, long and well developed vertical striations and lateral pressure scar.

Many of the teeth show considerable antemortem wear (eg. P. 10110, pl. 4, fig. 4; 1 tooth in P. 2753). One specimen in P.5874 (text-figs. 15 a, b) shows pressure scar development at the base of the central principal cusp on the lingual face of the crown, and toward the lateral extremity on the labial face. These scars would have been produced by the labial peg of the succeeding member of the tooth family, and the lateral extremity of that in the adjacent tooth family. This indicates the alternate overlapping of teeth in adjacent tooth families, as in other species of *Lissodus*.

Discussion: AGASSIZ (1844) listed the name "*Acrodus leiodus*" in the species list introducing his *Recherches sur les poissons fossiles*. He never defined the species, presumably intending to describe it in later supplements to his

work. WOODWARD (1887:101) noted that the teeth acquired from the Stonesfield Slate collection of EGERTON and the Earl of ENNISKILLEN bore labels in AGASSIZ' handwriting, naming them *Acrodus leiodus*. Thus, he retained the name (WOODWARD 1887, 1889, 1890). It may well be that all the specimens listed above belong to this species. More specimens are required before this can be more fully verified, and the heterodonty accurately stated.

The teeth of *L. leiodus* differ from those of *L. wardi*, which is of similar age, in their less well developed labial peg, greater expansion of the base of the principal cusp, tendency for vertical striations to cross the crown shoulder, and the development of occasional strong ridges at the crown shoulder on the labial side.

The teeth of *L. leiodus* are larger than those of *L. nodosus*, and lack the accessory cusplets, lingual and labial nodes found in that species. Although of similar size to the teeth of *L. leiodus*, *L. minimus* possesses occasionally prominent lateral cusplets and a longitudinal ridge at the crown shoulder.

Lissodus levis (WOODWARD)

Text-figures 16 a-f, 17 a-d; pl. 4, figs. 5, 6

1887 *Acrodus levis* WOODWARD, p. 103, figs. 2, 3.

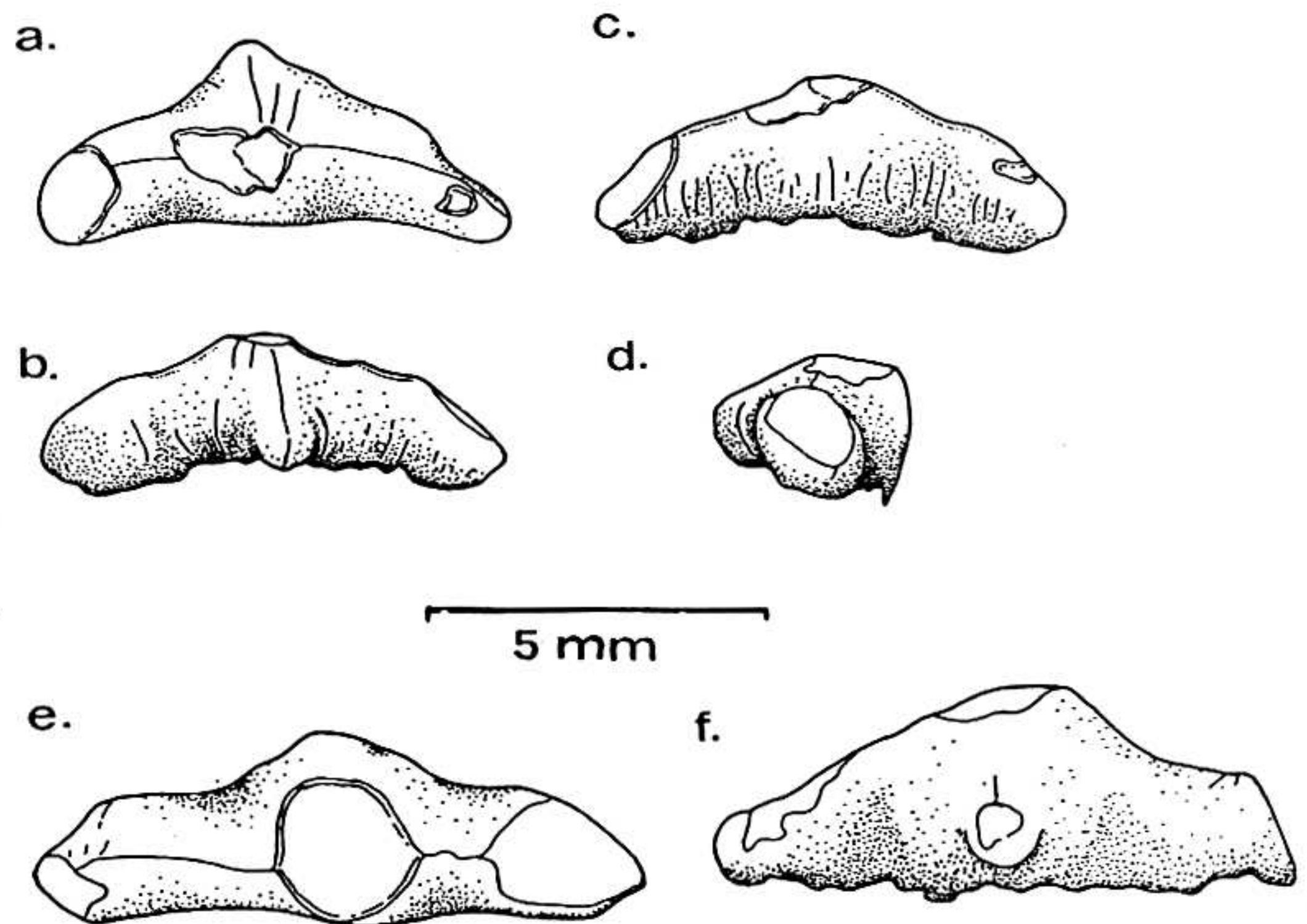
1889 *Acrodus levis* - WOODWARD, p. 296, pl. 14 figs. 5-7.

Syntypes: 10 isolated crowns: P.11 a (BM(NH)), (WOODWARD 1887, fig. 2; 1889:297, pl. 14 fig. 5); P.47293 a, P. 11 b (text-fig. 17 a-b; pl. 4, fig. 5), P.11 c, P.11, P.47223, 47293-4, 47293 a (text-fig. 17 c-d), P.17 (pl. 4, fig. 6), P.4724 and 1 complete tooth (P.17) from the Gault (Lower Cretaceous) of Folkestone, Kent.

Other material: P.51655 (text-fig. 16 c, f); P.47922 (text-fig. 16 a-d), isolated crowns from the Gault Clay (Albian, Lower Cretaceous) of Small Dole, Sussex.

Diagnosis: Teeth of *Lissodus* measuring up to 7 mm mesiodistally, possessing an expanded central part and moderate labial peg. The crown ornament comprises moderate vertical striations which tend to be very short. Lateral and accessory cusplets are lacking. Specialised vascular formaina are absent.

Description of P.47922 (text-fig. 16 a-d): The specimen is an isolated crown measuring 7 mm mesiodistally, 2.7 mm labiolingually and 2 mm high. The crown is elongate and symmetrical with moderately low profile in labial view (text-fig. 16 c, d). The bulk of the wear sustained by the specimen is functional and antemortem, producing a diamond-shaped facet on the apex of the central principal cusp (text-figs. 16 a, d). Additional wear has



Text-fig. 16. Teeth of *Lissodus levis* (WOODWARD 1887) from the Gault Clay (Albian, Lower Cretaceous) of Small Dole, Sussex, England.

BM(NH) P. 47922 in a, occlusal view; b, labial view; c, lingual view; d, lateral view. BM(NH) P. 51655 in e, occlusal view; f, labial view. Note the moderate labial peg and short vertical striations low down on the crown.

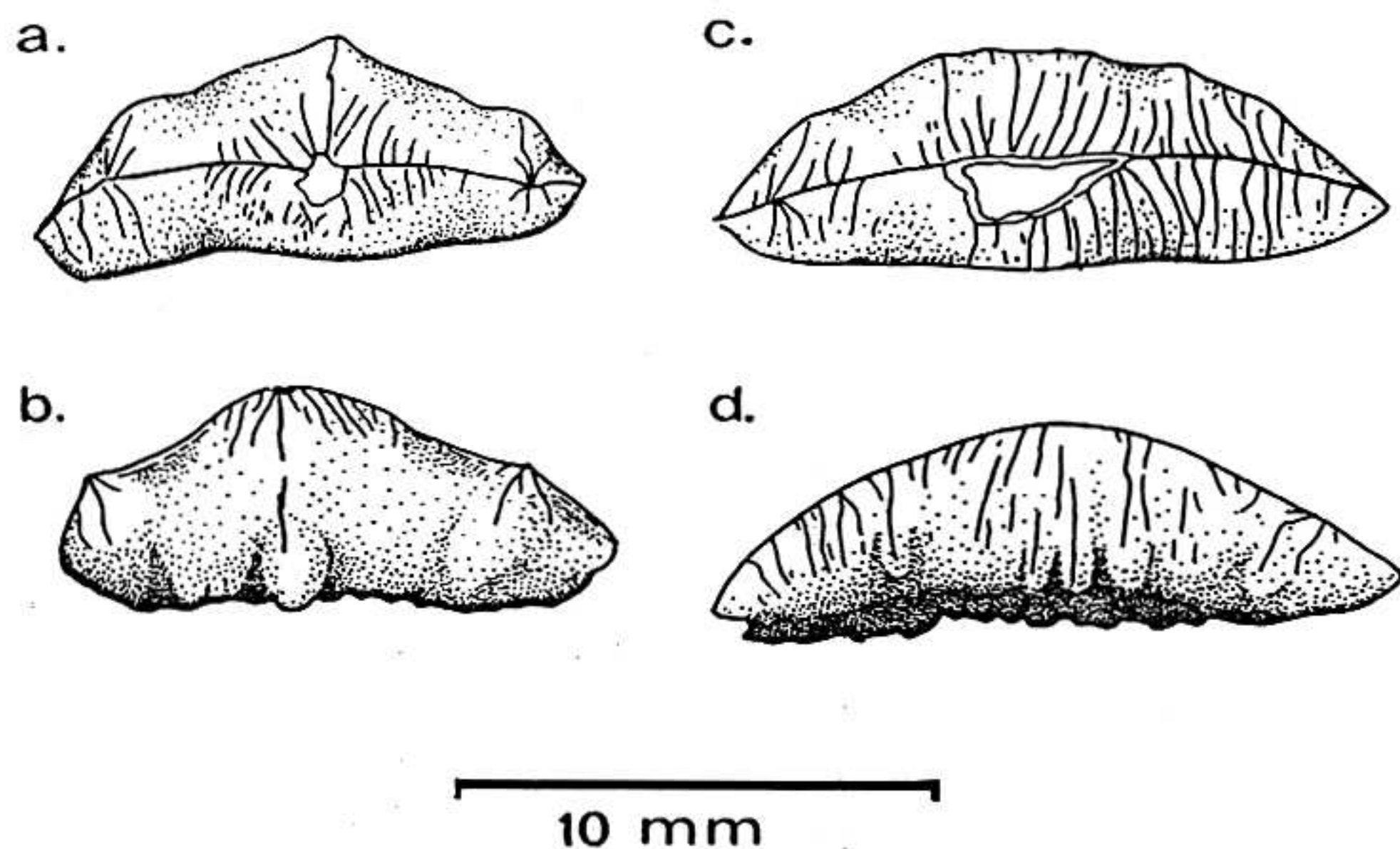
been exploited by solution and is situated on the lateral flanks of the central principal cusp. Further solution scars are present at the lateral extremities of the crown (text-figs. 16 a, c). There are no lateral or accessory cusplets, and the occlusal crest is moderately strong. The crown is arcuate in occlusal view (text-fig. 16 a). The labial peg is well developed, surmounted by a vertical ridge and situated low down on the labial face of the crown, below the crown shoulder and just lateral to the principal cusp base (text-figs. 16 a, b, d). Crown ornament is present in the form of short vertical striations which arise close to the crown/root junction on both labial and lingual faces. These striations do not bifurcate or anastomose. They ascend the crown to a position just below the crown shoulder, where they terminate. The most prominent vertical striation surmounts the labial peg and attains the worn apex of the central principal cusp (text-fig. 16 b). Occasional strong striations are present lateral to the labial peg on the labial face (text-fig. 16 b). A few short striations are present toward the apex of the principal cusp (text-fig. 16 a). Vertical striations are more numerous and closely spaced on the lingual face of the crown (text-fig. 16 c).

The crown undersurface is exposed and damaged by solution. This specimen demonstrates the affinities of this species to *Lissodus* particularly well in the overall crown shape, labial peg development and shape of the crown undersurface.

Variation: P.51655 (text-figs. 16 e, f) is similar in shape to P.47922, but slightly longer (9 mm mesiodistally). The labial peg is less well developed, however, and bears a solution scar on its crest, truncating a very short vertical striation (text-fig. 16 f). Lateral and accessory cusplets are lacking, and apart from a few very short vertical striations close to the occlusal crest labially, the crown is smooth.

Of the remaining material, only 1 specimen shows close resemblance to P.51655 and P.47922; P.47294. This is a larger tooth (11 mm mesiodistally) preserved on a block and exposed in labial view. The principal cusp is high and one pair of very low lateral cusplets is developed. The labial peg is small and situated low down on the principal cusp base, close to the crown/root junction. The crown ornament comprises short vertical striations on the lower labial face of the crown, and some longer striae toward the apex of the principal cusp and the lateral cusplets.

P.47223, 4724, 47293, 47293 a (text-fig. 16 c, d), 11, 11 c and 17 are all longer (up to 14 mm mesiodistally) and more robust teeth. The coronal profile is low and lateral cusplets are lacking. All of the crowns are worn. The labial peg is missing and the crown ornament comprises coarse vertical striations which descend the labial and lingual faces of the crown from the occlusal crest, usually terminating just above the crown shoulder, and occasionally bifurcating basally. Short, weaker striations may be present at the crown shoulder. Some of the stronger vertical striations cross the crown shoulder and reach the crown/root junction (eg. P.17, P.47293 a; text-fig. 17 d), where they become very prominent.



Text-fig. 17. Teeth of *Lissodus lewis* (WOODWARD 1887) from the Gault Clay (Albian, Lower Cretaceous) of Folkestone, Kent, England. BM(NH) P. 11 b, a syntype originally figured in WOODWARD (1889, pl. 14, fig. 6) in a, occlusal view; b, labial view. BM(NH) 47293 a, a syntype, previously figured in WOODWARD (1887, text-fig. 3; 1889, pl. 14, fig. 7) in c, occlusal view; d, labial view.

P. 17 (pl. 4, fig. 6) preserves the root, which has anaulacorhize vascularisation. No specialised vascular foramina are present and the foramina are randomly distributed. The root is essentially *Acrodus*-like.

Because of the difference in crown ornament and overall tooth shape, I should be inclined to retain the 7 teeth described above in *Acrodus*, were it not for P. 11b (pl. 4, fig. 5). This is a robust tooth measuring 10 mm mesiodistally, with a moderate coronal profile, and a central principal cusp flanked by a pair of very low lateral cusplets. A small but distinct labial peg is situated low down on the lower labial face of the crown. Weak, often indistinct vertical striations arise from the crown/root junction and ascend the crown to the crown shoulder. The crown shoulder itself is mostly smooth. Coarser vertical striations pass a short way down the crown from the occlusal crest, and terminate well above the crown shoulder. Small isolated striations are often present between the coarser ones. P. 11a is almost identical in every respect, except that the labial peg is missing.

Heterodonty: It would appear that the teeth described above belong to a single species of *Lissodus* showing considerable heterodonty. P.47922, 51655 and 47294 are presumed mesial teeth and the remainder posterolaterals. Moving posteriorly through the dentition, the following changes take place:

1. General lowering of the coronal profile.
2. Development of one pair of lateral cusplets in anterolateral teeth, followed by loss of lateral cusplets in posterolaterals.
3. Reduction in size and importance of the labial peg.
4. Increase in crown ornament from short vertical striations low down on the labial face, to strong striations on the upper part of the crown.

Discussion: The teeth of *L. levis* are distinct from those of all other Cretaceous species of *Lissodus* in their large size and robust appearance. The crowns most closely resemble those of *L. leiodus* from the Jurassic. They differ from the teeth of this species in the details of the crown ornament. In *L. levis*, the vertical striations are present on both the upper and lower faces of the crown, whereas they are confined to the upper face of the crown in the available specimens of *L. leiodus*. In addition, the striation in *L. levis* often bifurcate basally, whereas this condition has not been observed in teeth of *L. leiodus*.

Teeth of *L. levis* lack the lingual and labial nodes and accessory cusplets of *L. nodosus*, and the longitudinal ridge surmounting the crown shoulder of *L. minimus* amongst other robust tooth forms.

7. Description of new material

Lissodus wirksworthensis n. sp.

Text-figures 18 a-e, 19 a-c, 20 a-e, 21 a-e

Derivation of name: the species is named after Wirksworth in Derbyshire, the locality yielding the material described here. Holotype: P.60740 (BM(NH)), an isolated tooth comprising a complete crown and the greater part of the root (text-figs. 18 c-e).

Other material: 28 isolated fragmentary teeth, P.60739-P.60766. (P.60739 text-fig. 18 b; P.60741 - text-figs. 18 a, b; P.60745 - text-figs. 20 a-c; P.60748 - text-figs. 21 d-e; P.60749 - text-figs. 20 d-e; P. 60752 - text-figs. 21 a-c; P.60758 - text-figs. 19 a-c).

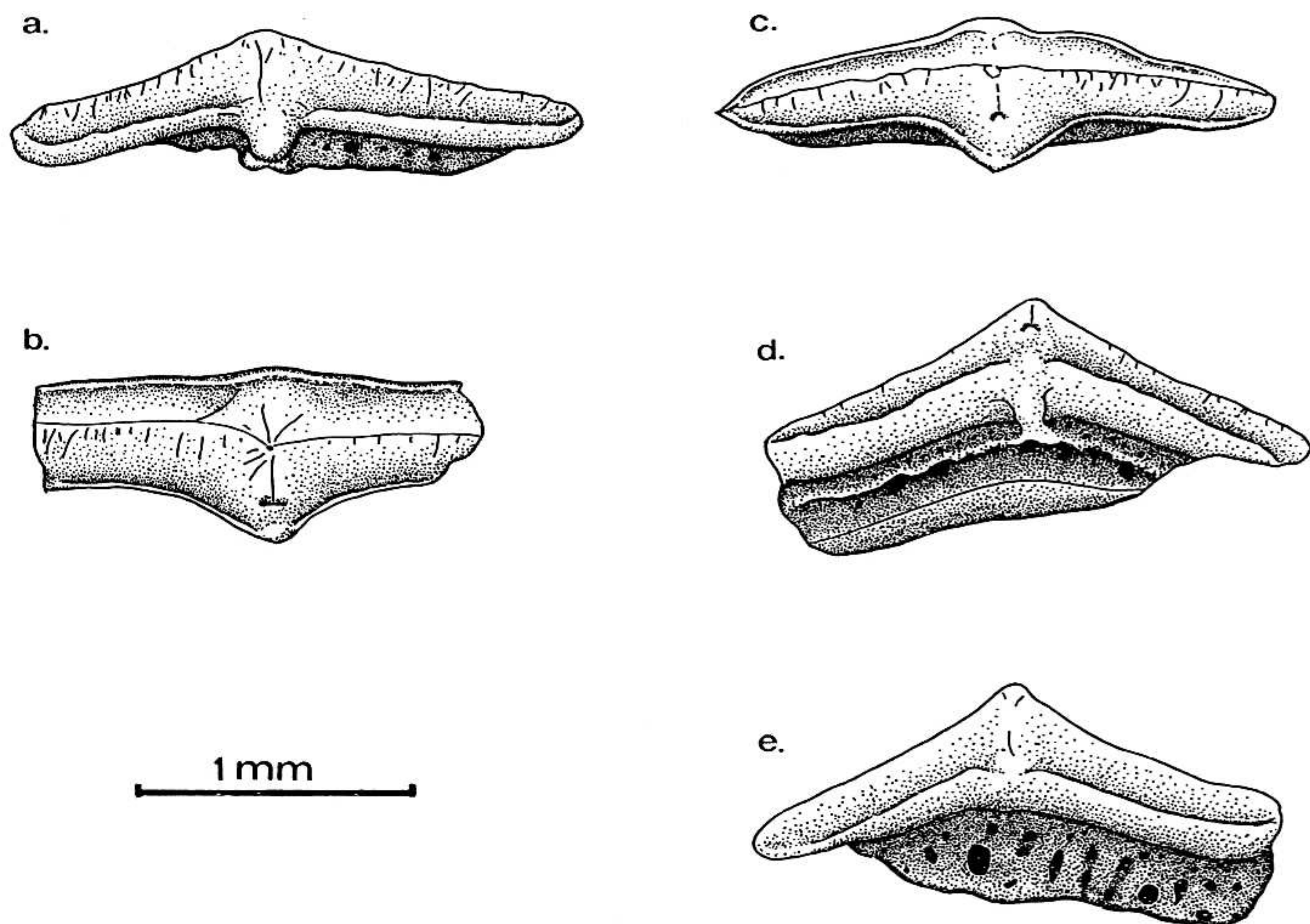
Age: Cawdor Limestones, P₁ sub-zone, Upper Viséan, Dinantian, Lower Carboniferous.

Lithology: Interbedded crinoidal limestone and black shale bands.

Locality: Steeplehouse Quarry (disused), Wirksworth, Derbyshire, England. SK 288554.

Diagnosis: Teeth of *Lissodus* between 1 and 2 mm long. The principal cusp and occlusal crest are moderate. Up to six pairs of very low to moderate lateral cusplets may be developed. The labial peg is moderate to well-developed. A strong vertical ridge surmounts the labial peg, which also bears a small accessory cusp. Further vertical striations are restricted to the labial crown face, are short, and may bifurcate basally. A sharp longitudinal ridge surmounts the crown shoulders, is occasionally crenulate, and may be continuous around the tooth. The root is very shallow and bears specialised foramina. A development of the root supports the underside of the labial peg. Lateral teeth tend to be longer and bear more pronounced lateral cusplets with labial nodes at their bases.

Description of the holotype: The specimen measures 1.1 mm long (mesiodistally), 0.5 mm high at the midpoint of the crown, and 0.3 mm labiolingually.



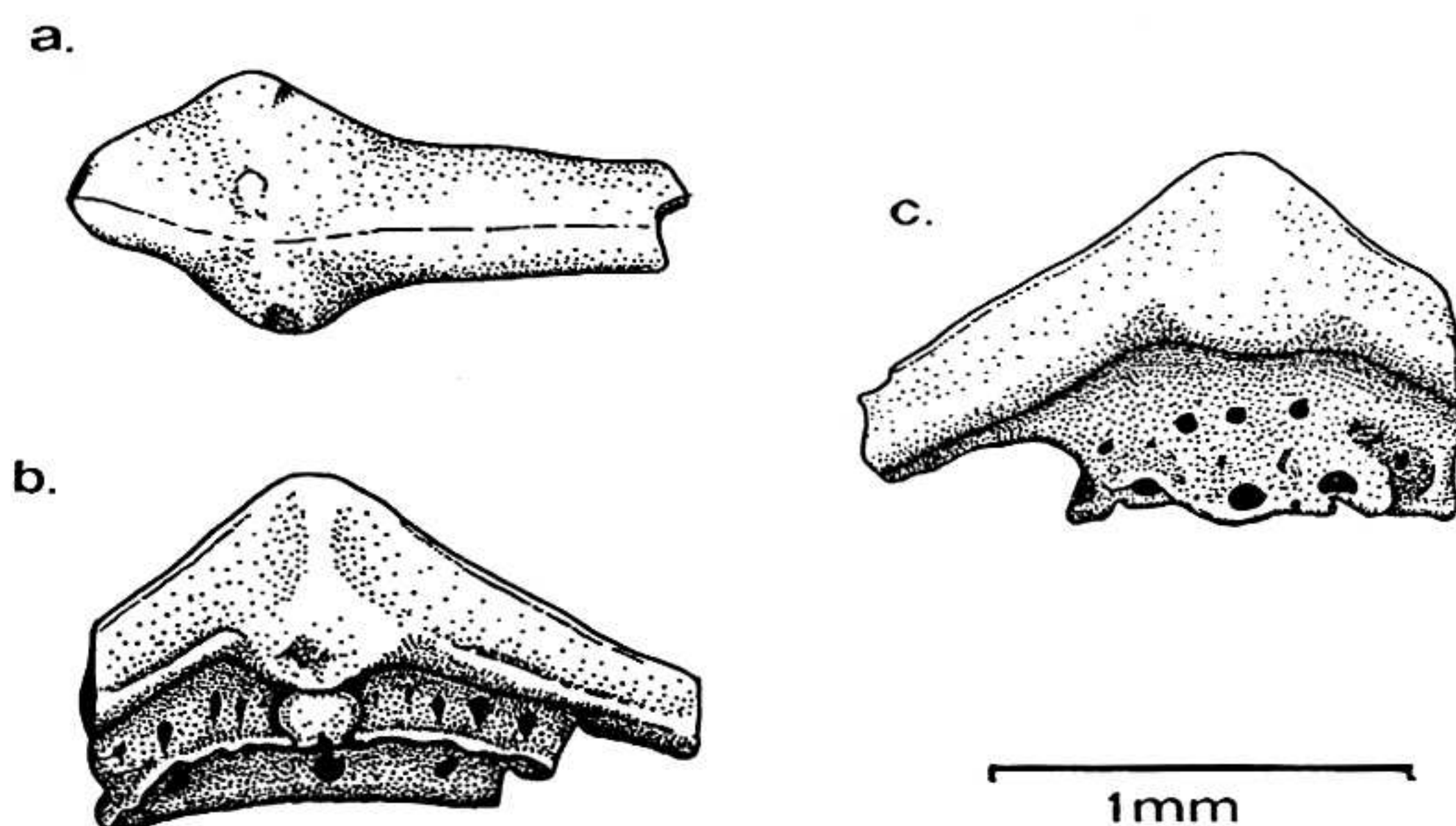
Text-fig. 18. Teeth of *Lissodus wirksworthensis* n. sp., from the Viséan (Dinantian, Lower Carboniferous) of Steeplehouse Quarry, Derbyshire, England. All specimens are housed in the BM(NH). a, P. 60741 in labial view; b, P. 60739 in occlusal view; c, the HOLOTYPE, P. 60740) in occlusal view; d, the holotype in lingual view. Note the crenulate occlusal crest, moderate labial peg buttressed by the upper labial root face, and longitudinal ridges at the crown shoulder.

The crown is elongate and symmetrical. The coronal profile is quite low, the moderate central principal cusp being the highest point. The crown is arched in lateral view (text-fig. 18 d). In occlusal view (text-fig. 18 c) the principal cusp has a diamond shape. The labial peg is moderate and developed at the base of the central principal cusp. The lingual margin of the principal cusp is convex in occlusal view (text-fig. 18 a). A vertical ridge ascends the principal cusp on both labial and lingual sides. Labially, the vertical ridge forms a crest to the labial peg. Just above the crown shoulder, on the crest of the labial peg, a small accessory cusplet is developed.

The occlusal crest is moderate. A series of very low incipient lateral cusplets is developed on either side of the principal cusp on the labial face of the crown. There appear to be six incipient lateral cusplets both mesially and distally. Vertical ridges arising from the occlusal crest descend the crown for a very short distance, occasionally bifurcating basally. The intersection of these ridges with the occlusal crest gives the impression of lateral cusplets. Only one vertical ridge extends to the crown shoulder (text-fig. 18 c). The crown shoulder is marked by a sharp longitudinal ridge which is continuous around the whole tooth, and is occasionally crenulated. The lateral extremities of the crown are only moderately angled to the crown root junction in lateral view (text-figs. 18 d, e). The crown/root junction itself is only moderately incised.

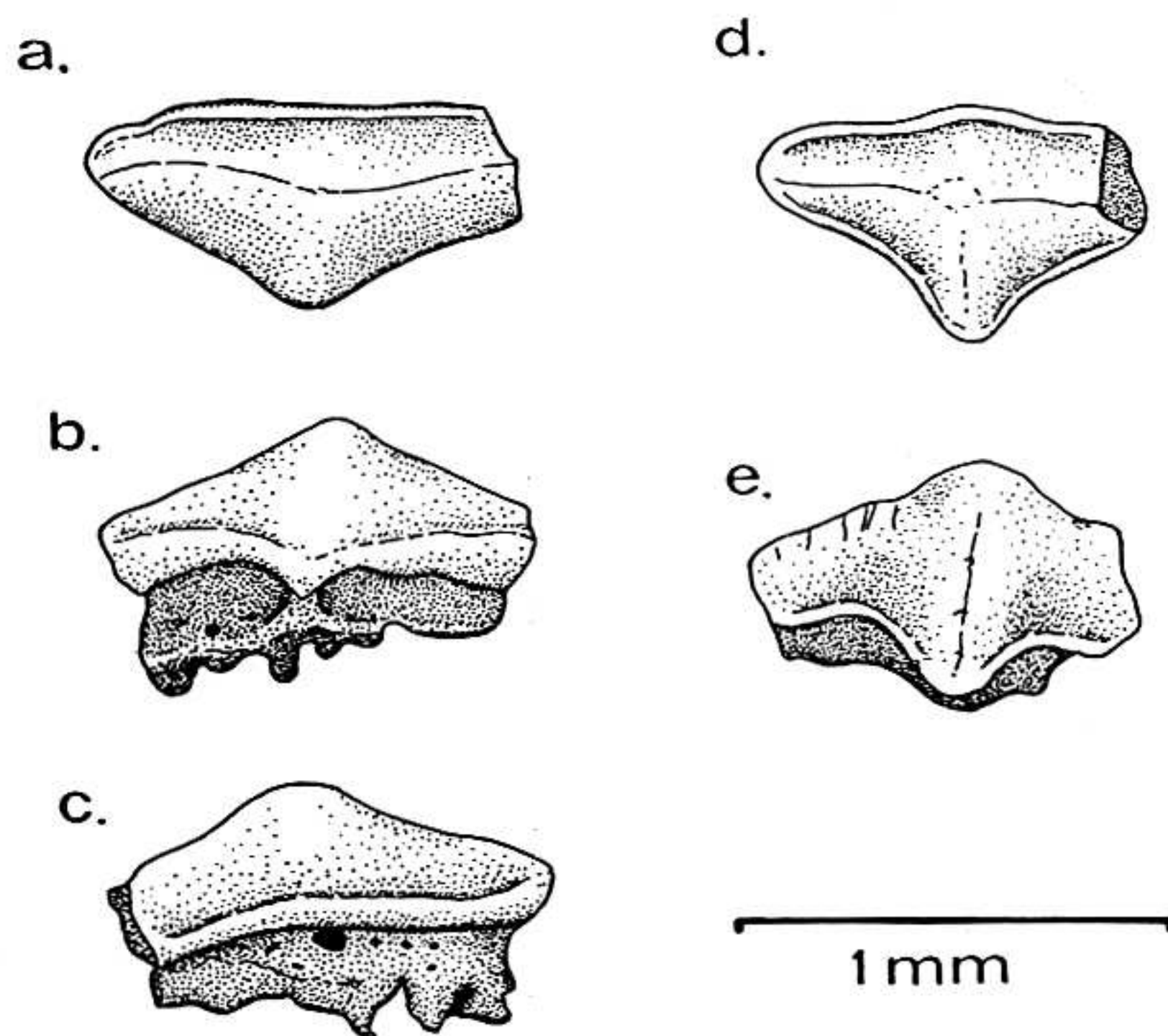
The root is very shallow and forms less than one third the total tooth height. The extremely shallow upper labial root face bears a single row of small specialised foramina along its entire length. Centrally, beneath the

Text-fig. 19. Tooth of *Lissodus wirksworthensis* n. sp., from the Lower Carboniferous of Derbyshire. BM(NH) P. 60758 in a, occlusal view; b, labial view; c, lingual view.



principal cusp, an expansion of the upper labial face of the root underlies the labial peg and buttresses it (text-fig. 18 d). The lower labial root face is angled sharply away to the basal face, and is almost flat, bearing a single row of vascular foramina, which are larger than the specialised foramina on the upper labial root face. The basal face of the root is smooth and slightly concave mesiodistally. The lingual face of the root is angled sharply away from the crown/root junction and bears numerous vascular foramina which are roughly arranged into longitudinal rows (text-fig. 18 e).

Variation: Of the 24 paratypes, all except two (P.60752 and P.60760) are symmetrical. The principal cusp is characteristically moderate. The labial and lingual vertical ridges may be supplemented by oblique vertical ridges (P.60741, text-fig. 18 b; P.60752, text-fig. 21 a; P.60748, text-fig. 21 c; P.60750). The occlusal crest is moderate to strong, and lateral cusplets may become well developed (P.60749, text-fig. 20 e; P.60759). The labial peg is of consistently moderate development, and is supported beneath by a labial expansion of the upper labial root face in



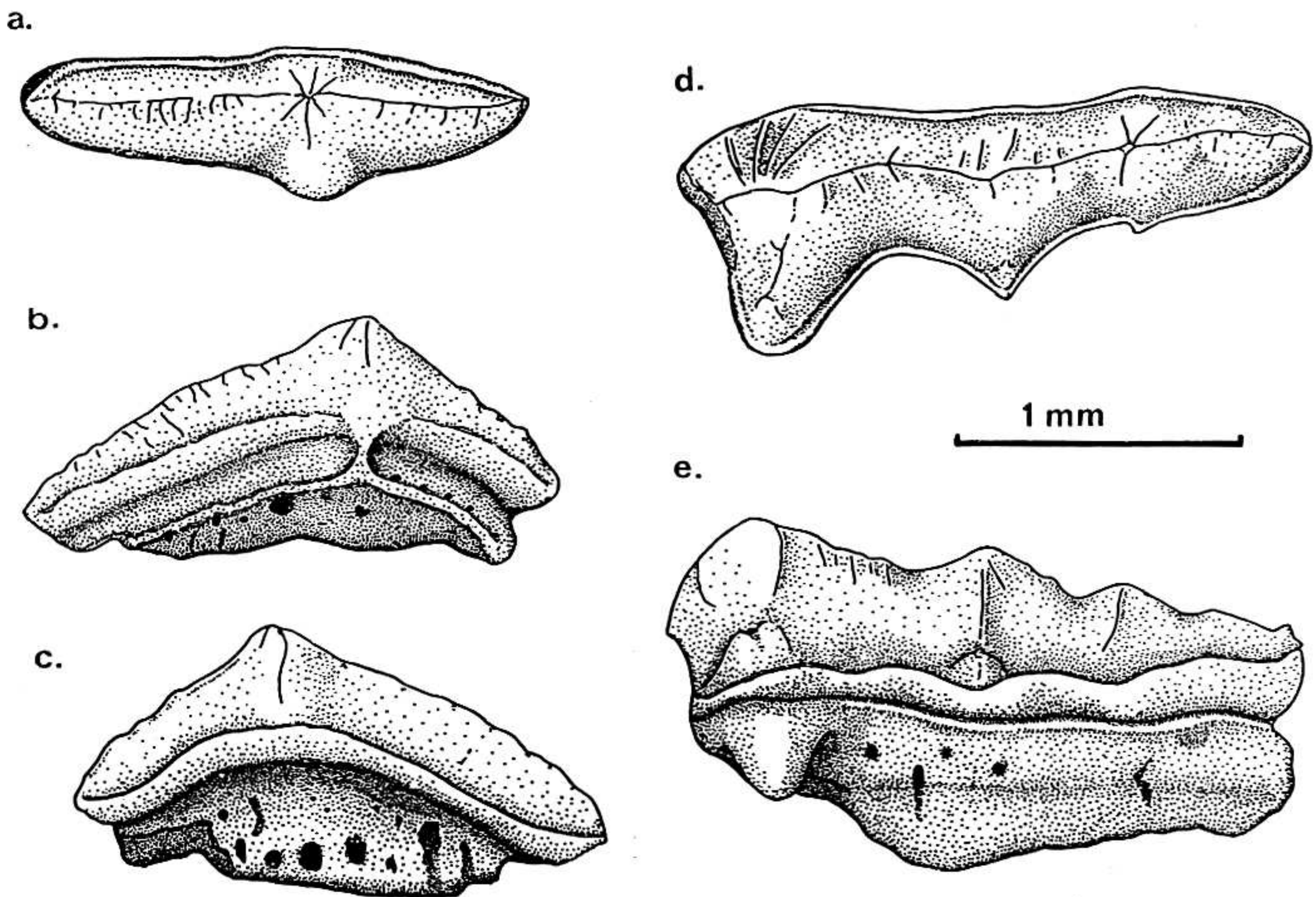
Text-fig. 20. Teeth of *Lissodus wirksworthensis* n. sp., from the Lower Carboniferous of Derbyshire. All specimens are housed in the BM(NH). a, P. 60745 in occlusal view; b, P. 60745 in labial view; c, P. 60745 in lingual view; d, P. 60749 in occlusal view; e, P. 60749 in labial view. Note the longitudinal ridges at the crown shoulder, and buttressing of the labial peg by the upper labial root face.

all but one specimen (P.60760). The vertical ridge ascending the principal cusp and forming a crest to the labial peg always develops an accessory cusplet, and occasionally two small crenulations (P.60749, text-figs. 20 d, e). Other vertical ridges ascending the crown may occasionally be very coarse (P.60748, text-figs. 21 d, e; P.60760). If fine, they are always restricted to the labial face of the crown; only in presumed lateral teeth (P.60748, P.60752) are sparse vertical ridges present lingually. In P.60748, the labial peg and labial bases of the prominent lateral cusplets are markedly expanded.

The longitudinal ridge at the top of the crown shoulder is present in all specimens. In some (P.60741, text-figs. 18 a, b) it may bifurcate and give rise to short oblique vertical striations which begin to ascend the crown. Occasionally, the longitudinal ridge appears to be almost entirely composed of sub-parallel oblique striations (P.60739; P.60743). A labial node is developed on the longitudinal ridge in P.60748 (text-fig. 21 e).

The largest virtually complete tooth (P.60752, text-figs. 21 a–c) is 2 mm long; P.60748 (text-figs. 21 d–e) would have been longer if complete. Both of these specimens are presumed to be laterals. The remainder of the teeth would each have measured approximately 1 mm in length, if entire. Antemortem wear is obvious in only a few specimens (eg. P.60760), and is restricted to the labial face of the crown. Parts of the root are preserved in most specimens, and vary little. Specialised foramina are always present on the upper labial face of the root.

The teeth of *L. wirksworthensis* are distinct from those of all other species of *Lissodus* in possessing accessory cusps restricted to the crest of the labial peg, in the form of the longitudinal striations at the crest of the crown shoulder, and is comparable to *L. pattersoni* in possessing a root buttress beneath the labial peg.



Text-fig. 21. Lateral teeth of *Lissodus wirksworthensis* n. sp., from the Lower Carboniferous of Derbyshire. Specimens held in BM(NH). a, P. 60752 in occlusal view; b, P. 60752 in labial view; c, P. 60752 in lingual view; d, P. 60748 in occlusal view; e, P. 60748 in labial view. Note the lateral cusplets, labial node development and specialised foramina.

Lissodus pattersoni n. sp.

Text-figure 22; pl. 7, figs. 1 a-i

Derivation of name: the species is named in honour of Dr. COLIN PATTERSON (London) in recognition of his work on British Wealden sharks.

Holotype: P.58698 (BM(NH)), a complete tooth (pl. 7, figs. 1 a-d).

Other material: one complete and two fragmentary teeth from Watton Cliff, BM(NH) P.58699 to P.58700 (P.58699 - pl. 7, figs. 1 e-h; P.60734 - pl. 7, fig. 1 i-k; P.60706 - text-figs. 22 a-b). 13 further isolated teeth from Watton Cliff (BM(NH) P.60708 - P.60720), 5 isolated fragmentary crowns from Kirtlington Quarry (BM(NH) P.60721 - P.60725).

Type locality: Watton Cliff, Dorset, England. SY 455907.

Other locality: Old Cement Works Quarry, Kirtlington, Oxfordshire, England. SP 494200.

Age: Watton Cliff - Forest Marble Limestone, Great Oolite Group, Bathonian, Middle Jurassic; Kirtlington - within and immediately adjacent to the Kirtlington Mammal Bed (FREEMAN 1979), ?Kemble Beds, Forest Marble, Great Oolite Group, Bathonian, Middle Jurassic.

Lithology: Watton - uncemented bioclastic sandstone; Kirtlington - clay and oolitic limestone.

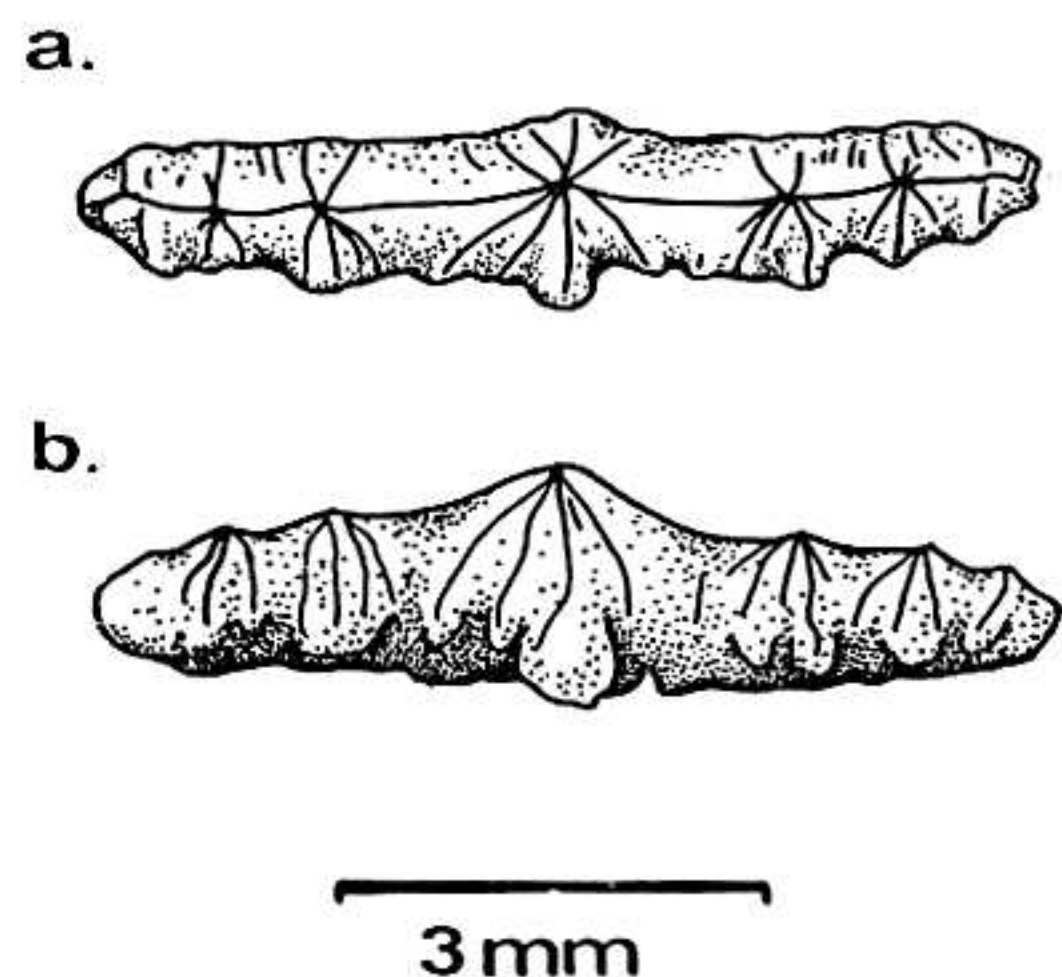
Diagnosis: Teeth of *Lissodus* showing moderate heterodonty. The crown is deep in mesial teeth. A high central principal cusp is flanked by up to two moderately high lateral cusplets on each side. The labial peg is moderate (in laterals) to strong (in mesials). Nodes are developed at the crown shoulder on both labial and lingual faces in some specimens; labial nodes are more pronounced in lateral teeth. Vertical striations are weak in mesials, to strong in lateral teeth. The upper labial root face buttresses the labial peg in mesial teeth, and a few specialised foramina are present.

Description of the holotype: The crown is deep and bears a moderately high central principal cusp flanked by two moderate lateral cusplets on either side (pl. 7, figs. 2 a, b). The central principal cusp base is quadrate in occlusal view and expanded labially in a moderate labial peg (pl. 7, fig. 2 d). A small node is developed at the base of the principal cusp on the lingual side (pl. 7, fig. 2 b). The labial peg is situated low down on the principal cusp base, below the level of the labial crown shoulder. A moderately well developed occlusal crest runs the length of the tooth, through the cusp apices, following a slightly sinusoidal path when seen in occlusal view, reflecting the slight labiolingual bowing of the crown. A single, moderately coarse vertical ridge descends the apex of the principal cusp, down the crest of the labial peg, terminating at the level of the crown shoulder. A similar striation runs from the cusp apex to the lingual node crest, bifurcating basally (pl. 7, fig. 2 b). No other obvious vertical ridges are developed on the labial face, but several ascend the lateral cusplets from just above the crown shoulder on the lingual face. These ridges attain the occlusal crest in most cases. Several small nodes are developed along the base of the lingual crown shoulder. Similar small nodes are developed in a corresponding location on the labial face (pl. 7, fig. 2 a). The lower part of the labial face is relatively shallow and does not undercut the crown (pl. 7, fig. 2 d). The lower lingual face, however, is deeper and undercuts the crown more sharply toward the crown/root junction, especially centrally. At this point, the lower lingual face is concave mesiodistally. The lateral extremities of the crown, in lingual and labial views, are somewhat rounded, but lead quite sharply to the crown/root junction.

The crown/root junction is moderately incised around the tooth. The upper labial face of the root bears a single row of occasional, small, specialised foramina, is arched mesiodistally and is somewhat expanded centrally. This central expansion makes contact with and buttresses the labial peg (pl. 7, fig. 2 a). The lower labial root face slopes lingually to the labial border of the basal face, and is concave labiolingually. The lingual face of the root, however, is convex, and projects lingually from the crown/root junction. The basal face (pl. 7, fig. 2 c) is flat to minimally concave, and shows some curvature. The vascularisation is anaulacorhize.

Variation: Of the other specimens, three (P.58699, P.58700 and P.60725 from Kirtlington) are of comparable size to the holotype. P.58699 is identical to the holotype in possessing two well developed lateral cusplet pairs and a moderate labial peg (pl. 7, figs. 2 e-h). Nodes are developed at the base of the crown shoulder, particularly on the lingual side (pl. 7, figs. 2 e-h). Vertical ridges are sparse and discontinuous in P.58699, seldom attaining the occlusal crest. Most of the vertical ridges are present on the lingual crown face in that specimen (pl. 7, fig. 2 f). The labial peg is situated below the level of the crown shoulder (pl. 7, figs. 2 e, h) and supported beneath by a small buttress from the upper labial root face, as in the holotype. P.58700 possesses a crenulate occlusal crest and small labial peg which is unsupported by the root.

The remaining teeth are larger and more elongate (up to 6 mm long) (text-fig. 22 a-b). In these specimens, the occlusal crest is well defined; up to three pairs of lateral cusplets and the central principal cusp are moderate (pl. 7,



Text-fig. 22. Tooth of *Lissodus pattersoni* n. sp., from the Forest Marble (Bathonian, Middle Jurassic) of Watton Cliff, Dorset, England. BM(NH) 60706 in occlusal view. Note the elongate crown, vertical ridges and labial nodes.

figs. 2 i, k). The labial peg is not so well developed as in the holotype (pl. 7, fig. 2 j). Coarse vertical striations ascend the crown from the lingual shoulder, often attaining the occlusal crest (text-fig. 22). Nodes are commonly well developed at the bases of the lateral cusplets, but apparently not lingually. Roots are not preserved in these specimens, but the impression is gained from the crown underside that the labial peg is not significantly buttressed.

It is assumed that the holotype, P.58699, P.58700 and P.60725 (Kirtlington) are mesial teeth, and the remainder of the specimens laterals. The teeth of *Lissodus pattersoni* thus show moderate heterodonty. Changes occurring distally through the dentition are:

1. Increase in length of the crown.
2. Increase in number of lateral cusplets.
3. Increase in number, length and strength of the vertical ridges.
4. Decrease in size of the labial peg, increase in size and number of labial nodes at the bases of the lateral cusplets.
5. Reduction in lingual crown ornament.
6. Possibly reduction in the buttressing of the labial peg by the upper labial root face.

Discussion: The teeth of this species most closely resembles those of *L. heterodon*. In *L. pattersoni*, the lateral cusplets are larger and the vertical ridges tend to be stronger and more widely spaced. Also, the occlusal crest is not so well developed as in *L. heterodon*, and the labial peg is much more robust.

Buttressing of the labial peg by the upper labial face of the root is a character held in common with *L. wirksworthensis*. The teeth of *L. pattersoni* differ from those of the Carboniferous species in lacking longitudinal ridges at the crown shoulder.

Lissodus wardi n. sp.

Plate 6, figs. 3 a-d; text-figs. 23 a-d

Derivation of name: the species is named in honour of Mr. DAVID WARD (Orpington) in recognition of his work on fossil selachians.

Holotype: P.58701 (BM(NH)), an incomplete tooth preserving the entire crown and upper part of the root (pl. 6, figs. 3 a-d; text-figs. 23 a-d).

Other material: Two fragmentary teeth (P.58702, P.58703 - (pl. 6, figs. 3 a-d) from Watton Cliff, one incomplete tooth from Kirtlington, P.60771.

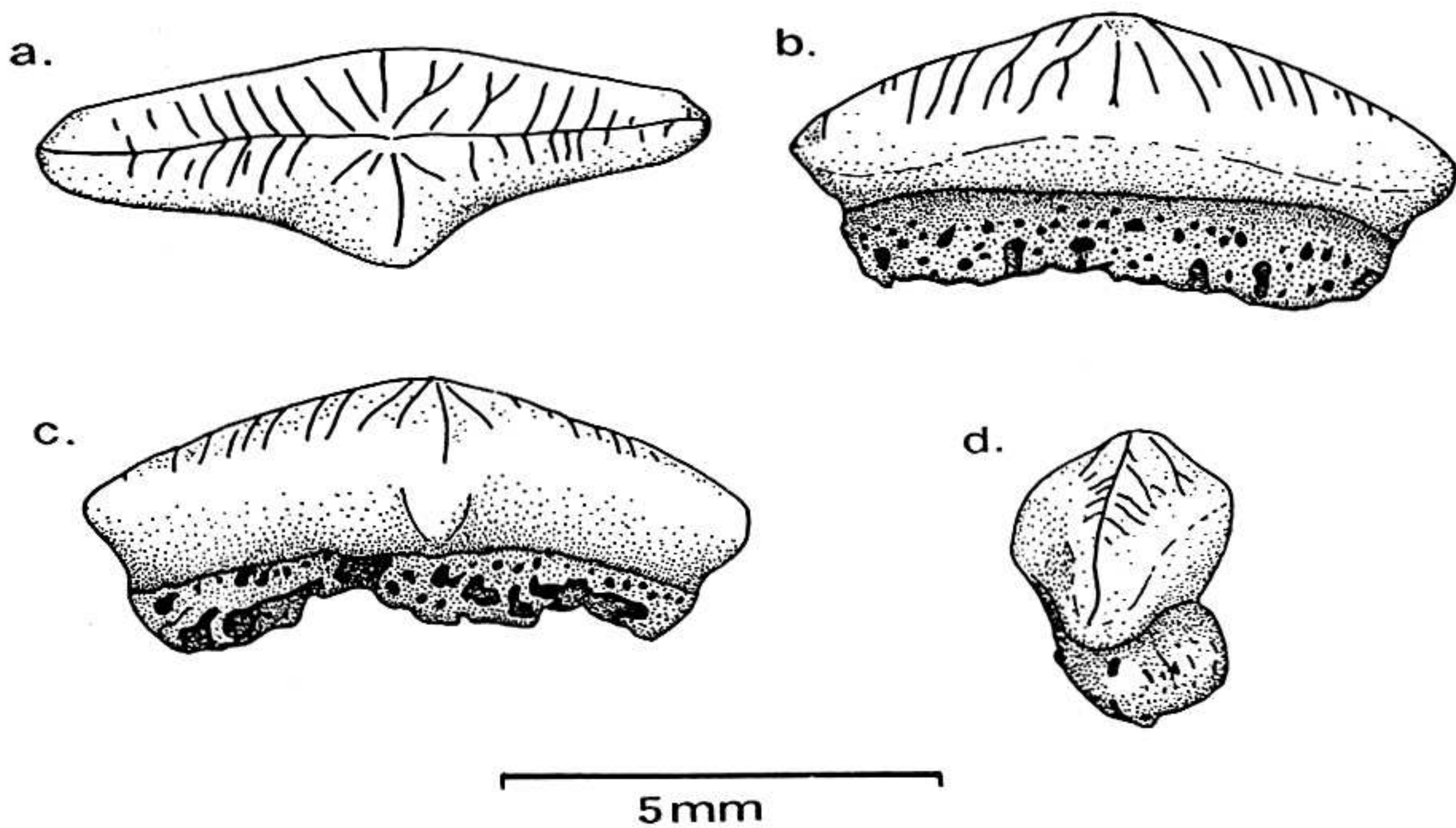
Type locality: Watton Cliff, Dorset, England. SY 455907.

Other locality: Old Cement works Quarry, Kirtlington, Oxford. SP 494200.

Age: Watton Cliff - Forest Marble Limestone, Bathonian, Middle Jurassic; Kirtlington: within and immediately adjacent to the Kirtlington Mammal Bed, ? Kemble Beds, Great Oolite Group, Bathonian, Middle Jurassic.

Lithology: Watton - uncemented bioclastic grit; Kirtlington - clay and oolitic limestone.

Diagnosis: Teeth of *Lissodus* which are large (5.3 to 7.9 mm long, mesiodistally) and robust with a low coronal profile. The central principal cusp is very low; there are no lateral cusplets. The labial peg is robust and the crown ornamented with coarse vertical ridges which may branch basally. Specialised foramina are present.



Text-fig. 23. The holotype (BM(NH) P. 58701) of *Lissodus wardi* n. sp., from the Forest Marble (Bathonian, Middle Jurassic) of Watton Cliff, Dorset, England. a, occlusal view; b, lingual view; c, labial view; d, lateral view. Note the low coronal profile, absence of lateral cusplets, vertical ridge development and specialised foramina.

Description of the holotype: The tooth is large, measuring 7.9 mm mesiodistally, 2.5 mm labiolingually and 3.1 mm high. The coronal profile is very low (text-figs. 23 b, c). There is a very low central principal cusp and no obvious lateral cusplets. A moderate occlusal crest runs the length of the crown. The crown is widest labiolingually at the midpoint of the central cusp. On the labial side, the cusp base is expanded to form a large, robust labial peg (text-figs. 23 a, d). Coarse vertical ridges arise from the apex of the central cusp and from the occlusal crest laterally, descending toward the lingual and labial shoulders of the crown, before which point they terminate. The strongest of these vertical ridges runs from the cusp apex down the crest of the labial peg, bifurcating just before the level of the labial crown shoulder. Other ridges radiate from the cusp apex. Those ridges arising from the occlusal crest run laterally and basally before terminating. The ridges are symmetrically displaced across the occlusal crest, although bifurcation is more common on the lingual side (text-fig. 23 a). The lower labial face of the crown, from the labial crown shoulder to the crown/root junction, is deep and does not markedly undercut the crown. The similarly deep lower lingual face, however, considerably undercuts the crown, terminating beneath the occlusal crest. The lateral extremities of the crown in labial and lingual views slope sharply downward to the crown/root junction (text-figs. 23 b, c).

The crown/root junction is quite deeply incised on the lingual side, but less so labially.

Only the upper part of the root is preserved. The root attachment is concentrated on the labial part of the crown underside and projects somewhat lingually. The upper labial root face bears a row of specialised foramina (text-fig. 23 b). The lower labial root face is concave labiolingually and punctuated by many vascular foramina. The lingual face of the root is convex labiolingually and foraminate (text-fig. 23 c).

Variation: The other three specimens show similar development of a large labial peg, and coarsely ridged crown. P. 58702 shows the incipient development of two lateral cusplets on either side of the central principal cusp, and well lateral to it. In all further specimens, the root is missing. From the crown undersurfaces, the root attachment can be seen to be roughly triangular in shape. The base of the triangle follows the long, straight lingual face, and the other two sides are formed by the two parts of the labial face, converging toward the labial peg. The central longitudinal canal is not visible.

P.58703 has a marked pressure scar situated low down on the lingual shoulder of the crown, due to contact with the succeeding tooth of that file. This indicates the typical *Lissodus* - type tooth disposition within the dentition.

Discussion: The teeth of this species most closely resemble the largest teeth in *L. minimus* and *L. nodosus*. Teeth of *L. wardi* are more elongate than those of *L. nodosus*, and lack nodes. Compared to *L. minimus*, teeth of *L. wardi*, although of comparable size, show a generally lower principal cusp, and a more robust labial peg.

The question arises as to whether or not the teeth of *L. wardi* could be laterals of *L. pattersoni*. The extreme size difference between the teeth of these two species argues against this interpretation. Also, *L. wardi* lacks the prominent lateral cusplets of *L. pattersoni*, and possesses a more clearly defined set of vertical ridges. Teeth of *L. pattersoni* possess nodes, while those of *L. wardi* do not. Further, the teeth of *L. pattersoni* do not grade into those of *L. wardi*.

Lissodus weltoni n. sp.

Text-figures 24 a-d; pl. 7, figs. 2 a-k

Derivation of name: the species is named in honour of Dr. BRUCE WELTON, who found the specimens.

Holotype: P.60772 (BM(NH)), an isolated crown (text-figs. 24 a1-a4; pl. 7, figs. 2 e-h).

Other material: 81 complete and fragmentary crowns. BM(NH) P.60773 (text-figs. 24 b1-b3); P.60774 (text-figs. 24 c1-c4; pl. 7, figs. 2 i-k); P.60775 (text-figs. 24 d1-d4; pl. 7, figs. 2 a-d).

Locality: Suplee, Crook County, Oregon. Map: Dayville Ore, 30 min., B.L.M. quadrant, Dept. of Interior 1970 ed.

Age: Cenomanian, Upper Cretaceous.

Diagnosis: Teeth of *Lissodus* known on the basis of isolated crowns varying from 1.5 to 3.0 mm in length. Presumed lateral teeth possess a well developed central principal cusp ornamented by moderate vertical striations. The labial peg is moderately developed and projects basally. The base of the principal cusp is expanded on the lingual side. The presumed extreme mesial and distal teeth are shorter and possess moderate to well developed labial pegs which may be basally situated and downturned, or situated high up the labial crown shoulder.

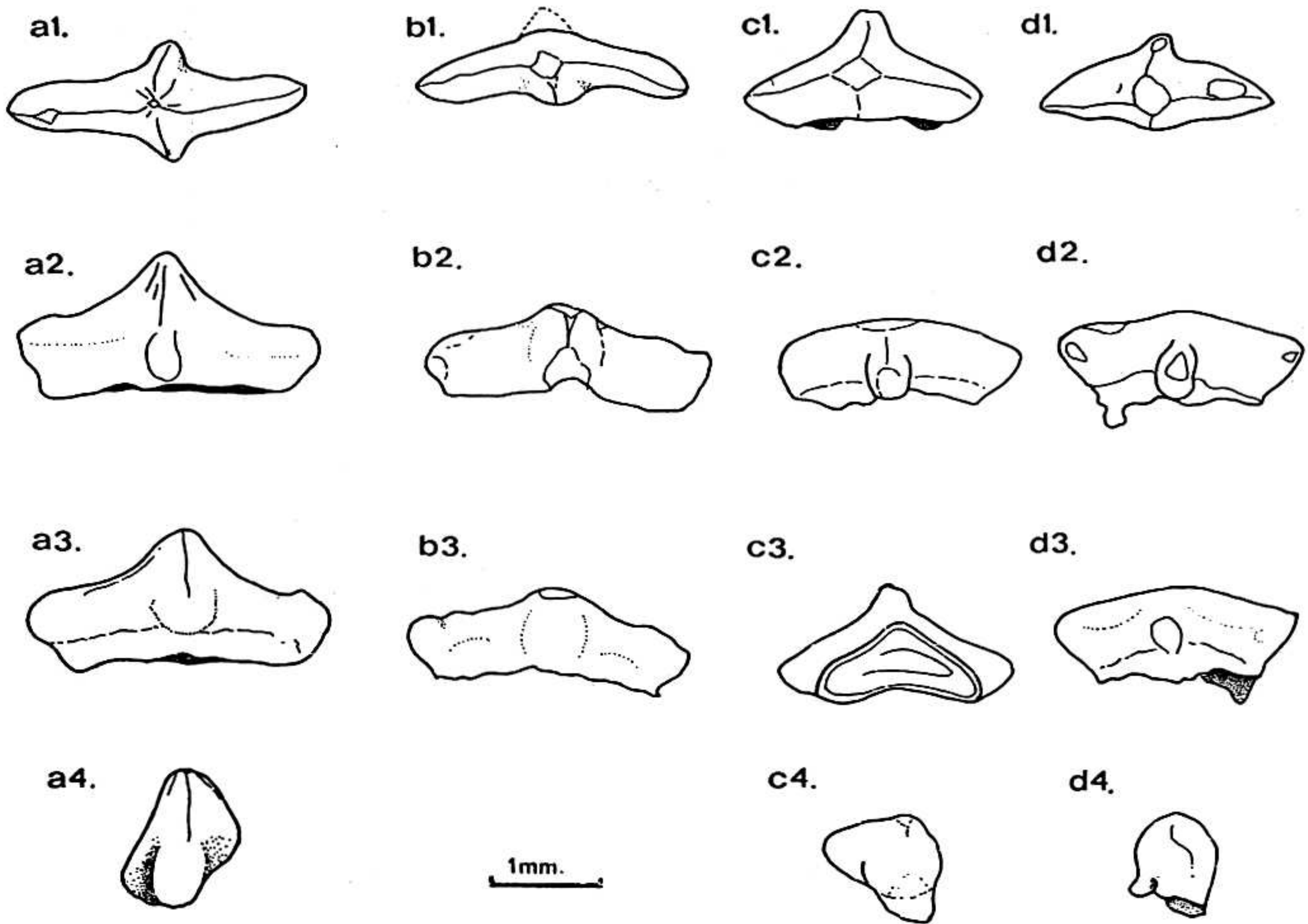
Description of the holotype: The holotype is 2.8 mm long (mesiodistally), 1.1 mm high, and is an isolated crown. It is narrow labiolingually (text-fig. 24 a1; pl. 7, fig. 2f) and elongate. The occlusal crest is moderate. A high central principal cusp is bisected by the occlusal crest and flanked by one incipient lateral cusplet on either side (text-figs. 24 a2, a3; pl. 7, figs. 2e, g). The labial and lingual crown shoulders are weak; occasional vertical striations ascend the central cusp on both labial and lingual sides, and may attain the occlusal crest. A strong vertical ridge is present at the expanded labial and lingual bases of the principal cusp. The labial peg is moderate and sited close to the crown/root junction at the base of the central principal cusp (text-figs. 24 a2, a4; pl. 7, figs. 2g, h). The crest of the labial peg is striated and mildly concave (text-fig. 24 a4; pl. 7, fig. 2h). There is a lingual projection at the base of the central principal cusp (text-fig. 24 a4; pl. 7, fig. 2h). A strong vertical ridge ascends this lingual projection and attains the cusp apex. The underside of the lingual projection slopes sharply toward the crown/root junction. The crown/root junction itself is incised around the whole tooth.

The underside of the crown shows a slightly labially placed elongate triangular root attachment area. No further details of the root or vascularisation are present.

Variation: The crowns in the sample vary from 1.5 to 3.0 mm in length (mesiodistally). The bulk of the complete crowns in the collection (approximately 10 teeth) show the development of a high central principal cusp as in the holotype. Incipient lateral cusplets, up to two on each side, are developed in only nine other teeth in the sample.

In some teeth, the principal cusp may be much lower and the crown more elongate in occlusal view than in the holotype (text-fig. 24 b1). In these teeth (4 specimens) the labial peg is characteristically basally situated and the lingual projection is much reduced or absent (text-fig. 24 a3).

Certain teeth are arcuate in occlusal view (text-fig. 24 b1). The shorter teeth in the sample show a more triangular shape in occlusal view (text-figs. 24 c1, d1; pl. 7, fig. 2b). The labial peg is often very well developed in these specimens; it may form a strong labial expansion to the principal cusp at the level of the labial crown shoulder (text-figs. 24 c2, c4; pl. 7, figs. 2b, d), or it may be basally situated and downward-projecting with a concave upper surface (text-fig. 24 d4; pl. 7, fig. 2k). The lingual projection to the principal cusp may be small or



Text-fig. 24. Teeth of *Lissodus weltoni* n. sp., from the Cenomanian (Upper Cretaceous) of Suplee, Crook County, Oregon, U.S.A. All specimens are housed in the EM(NH). a, P. 60772 (HOLOTYPE); b, P. 60773; c, P. 60774; d, P. 60775. All views are 1, occlusal; 2, labial; 3, lingual; 4, lateral, with the exception of c3, basal view. Notice the very low labial peg.

absent (text-figs. 24 c1, d1, d3; pl. 7, figs. 2b, i, j). In these specimens, the shape of the root attachment in basal view is a well defined triangle concentrated toward the labial underside of the crown (text-fig. 24 c3; pl. 7, fig. 2j). The shorter crowns with low profiles, poorly developed lingual projections and robust labial pegs developed at the crown shoulder are presumed mesial and extreme distal teeth. The longer crowns and those bearing well developed principal cusps are presumed laterals.

Functional antemortem wear tends to be concentrated at the tip of the central principal cusp. In a few specimens, the occlusal surface of the crown is flat, wear having eliminated all signs of the occlusal crest, vertical ridges and cusp apices, exposing the dentine. Certain teeth show isolated wear facets and pressure scars. P.60775 (text-figs. 24 d1–d3; pl. 7, figs. 2i, j) has the central cusp flattened by wear and a large lateral wear facet high up the presumed distal labial face of the crown, reaching the occlusal crest. Smaller wear facets, probably representing pressure scars, are located just above the labial crown shoulder at the mesial and distal crown extremities (text-fig. 24 d2). These pressure scars are due to contact with the lingual crown extremities of mesially and distally adjacent tooth families as a result of the alternate tooth arrangement so typical of *Lissodus* dentitions. A well developed pressure scar is present just below the lingual crown shoulder toward the base of the principal cusp (text-fig. 24 d3; pl. 7, fig. 2j). A corresponding pressure scar is present on the upper surface of the basally directed labial peg (text-fig. 24 d1; pl. 7, fig. 2i). The positions of these pressure scars indicate that the labial peg was in contact with the centre of the lingual face of the preceding member of the tooth family, emphasising again the alternation of teeth in successive files.

8. A note on tooth histology

ESTES (1964:8) described the histology of *L. selachos* as comprising a fan-like radiation of dentine tubules from a central longitudinal cavity. PATTERSON (1966, pl. 5 fig. 3; text-fig. 29E) found that the teeth of *L. breve*, *L. striatus* and *L. heterodon* possessed similar histology. Here, the enameloid layer is thick and the crown comprised "pallial dentine containing long subparallel, much branched tubules which arise from the tips of vascular canals which end shortly after entering the base of the crown" (PATTERSON 1966:315). PATTERSON further compares this histology with that of *L. minimus*, previously believed to belong to *Polyacrodus* (SEILACHER 1943, figs. 7-10; PATTERSON 1966, pl. 5 fig. 1), and notes that the teeth of *Palaeobates* possess longer dentine tubules which are parallel and more regularly branched than in *L. breve*. Further, they arise directly from the longitudinal pulp cavity rather than from short vascular canals in the crown. As remarked by MAISEY (1982:38) the preservation of *Lissodus africanus* teeth is not good, making the preparation of thin sections difficult. Broken teeth show similar histology to those of *L. minimus*, however, so far as can be determined (see also PATTERSON 1966:331; MAISEY 1982:28).

There has currently been some discussion on the nature of "pallial dentine". JOHNSON (1981: 2) indicates that, in his understanding, "pallial dentine represents that part of the orthodentine (or tubular orthodentine) where branching of the dentinal tubules is at a minimum; the dentinal tubules are not as parallel to one another as in the typical orthodentine of most euselachians, osteichthyans and tetrapods".

RIEPEL (1981:345 ff.), on the other hand, examines the history of the usage and understanding of the term "pallial dentine", and suggests that "the term pallial dentine should be restricted to the zones which WEIDENREICH (1926) named Manteldentin, or, more precisely, the term pallial dentine might be restricted to the irregular dentino-enameloid junction as it appears in light microscopy". This definition has been accepted by MAISEY (1982:28). RIEPEL further considers that the tissue forming the crown in *Polyacrodus*, *Palaeobates* and *Lissodus* is orthodentine which has expanded at the expense of the osteodentine. If this is the case, MAISEY (1982:28) may well be correct in surmising that these three genera may form a monophyletic orthodont group within the hybodonts.

If "pallial dentine" is defined in the sense recommended by RIEPEL, there still remains a problem in the type of orthodentine present in the crowns of hybodont sharks. As mentioned above, JOHNSON distinguishes between "typical orthodentine" and tubular orthodentine. The fauna which he describes from the early Permian of Texas contains species with tooth crowns composed entirely of tubular orthodentine (? *Acrodus sweetlacruzensis*; ? *Acrodus olsoni*; ? *Acrodus* sp.), and those which contain mostly typical orthodentine (his *Polyacrodus* spp; *P. wichitaensis*, *P. zideki*, *P. ritchiei* and *P. lapalomensis*), with occasionally considerable histological variety (JOHNSON 1981:22). This suggests the validity of the distinction between these two groups. When one considers morphology, however, "some species of *Polyacrodus* may have been placed in ? *Acrodus*" (*P. lapalomensis*; JOHNSON 1981:22).

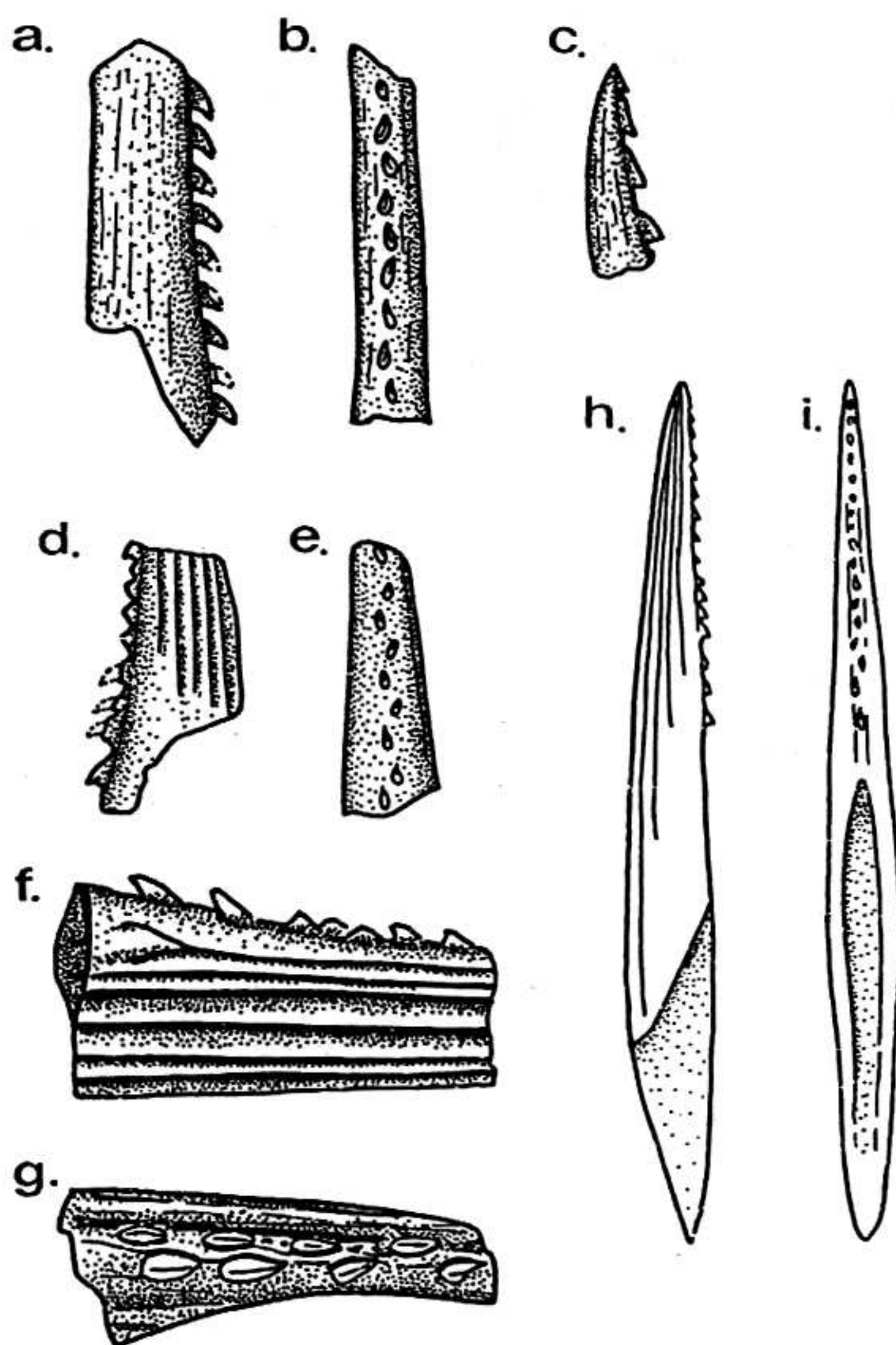
9. Dorsal fin spines

As described above (p.116) the dorsal fin spines of *Lissodus africanus* are costate (MAISEY 1978:658) and possess a row of downturned denticles on the posterolateral margins. This has resulted in *L. africanus* being referred to the hybodonts (BROUGH 1935:38; MAISEY 1978:657, 1982:6; THOMSON 1982:1).

Dorsal fin spines have been found in association with teeth previously described as "*Lonchidion*" by previous authors. ESTES (1964:9, fig. 4 a-b) originally allocated several fin spine fragments to *L. selachos* (text-fig. 25a-c). These fragments are laterally compressed, bearing a single medial denticle row of hooked denticles on the convex posterior spine wall. The denticles are arranged in a herringbone pattern. The lateral walls of the spine are not obviously costate, but bear light striations which are presumably unroofed mantle canals. The complete spine would have been approximately 50 mm long (PATTERSON 1966:329). Other members of the Lance Formation vertebrate fauna would not have possessed fin spines, so the allocation of these fragments to *L. selachos* is reasonable. In addition, LUPTON, GABRIEL & WEST (1980:118) note that a single dorsal fin spine (not figured) from the Hell Creek Formation (Maestrichtian, Upper Cretaceous) of McCone County, Montana, compares well with those illustrated by ESTES.

Dorsal fin spines are well known from the English Wealden (SMITH WOODWARD 1916). PATTERSON (1966:329, figs. 26A, pl. 3 fig. 4) describes and reconstructs fin spines which he allocates to "*Lonchidion*". The spines (text-fig.

Text-fig. 25. Dorsal fin spines possibly belonging to *Lissodus* spp. a, spine fragment of *Lissodus selachos* in lateral view (x 3), UC 56275, after ESTES (1964); b, UC 56275 in posterior view (x 3) after ESTES (1964); c, tip of fin spine referred to *L. selachos* in lateral view (x 6), after ESTES (1964); d, fin spine fragment originally referred to *Hybodus butleri*, but possibly belonging to *Lissodus anitae*, SMU-SMP 62184, in lateral view (x 3), after THURMOND (1972); e, SMU-SMP 62184 in posterior view (x 3) after THURMOND (1972); f, fin spine fragment in lateral view (x 8) referred to *Lissodus humblei*, SMU-SMP 67465 after MURRY (1981); g, SMU-SMP 67465 in posterior view (x 8) after MURRY (1981); h, reconstructed dorsal fin spine (x 1.5) of *Lissodus* from the British Wealden, in left lateral view (after PATTERSON 1966); i, reconstructed dorsal fin spine (x 1.5) of *Lissodus* from the British Wealden in posterior view (after PATTERSON 1966).



25d-e) would have measured about 70 mm in length, were almost straight, with a slight curvature distally (as in fin spines of *L. selachos*, text-fig. 25c). The lateral walls are costate; up to five enamelled ridges are present and show no bifurcation or anastomosis. There is a single row of hook-like denticles in the midline of the posterior face, arranged in a herringbone pattern, as in *L. selachos*. PATTERSON (1966:329) notes that toward the base of the spine the denticles are placed alternately to the right and left of the midline, indicating an origin from a paired series (see also DUFFIN 1981b:473).

THURMOND (1972:215) notes that the fin spine fragments referred by PATTERSON to "*Lonchidion*" are similar to specimens he refers to *Hybodus butleri* from the Butler Farm local fauna of the ?Aptian-Albian of north-central Texas. THURMOND comments that the spines from the British Wealden should perhaps belong to *Hybodus parvidens*. PATTERSON (1966:310) discussed the correlation between teeth and fin spines of Wealden sharks made by SMITH WOODWARD (1916) and suggested that the teeth of *H. parvidens* corresponded with spines named *H. subcarinatus* and possibly *H. sulcatus*.

The fin spines allocated to *H. butleri* have been found only in the Butler Farm local fauna, which also contains *L. anitae*. The fin spine fragments are small, laterally compressed, with a convex posterior wall bearing denticles in a rough median row. The denticles alternate with each other either side of the midline of the posterior face. If ESTES and PATTERSON are correct in allocating the fin spine fragments they describe to "*Lonchidion*" spp., then perhaps the fin spines described by THURMOND belong to *L. anitae*.

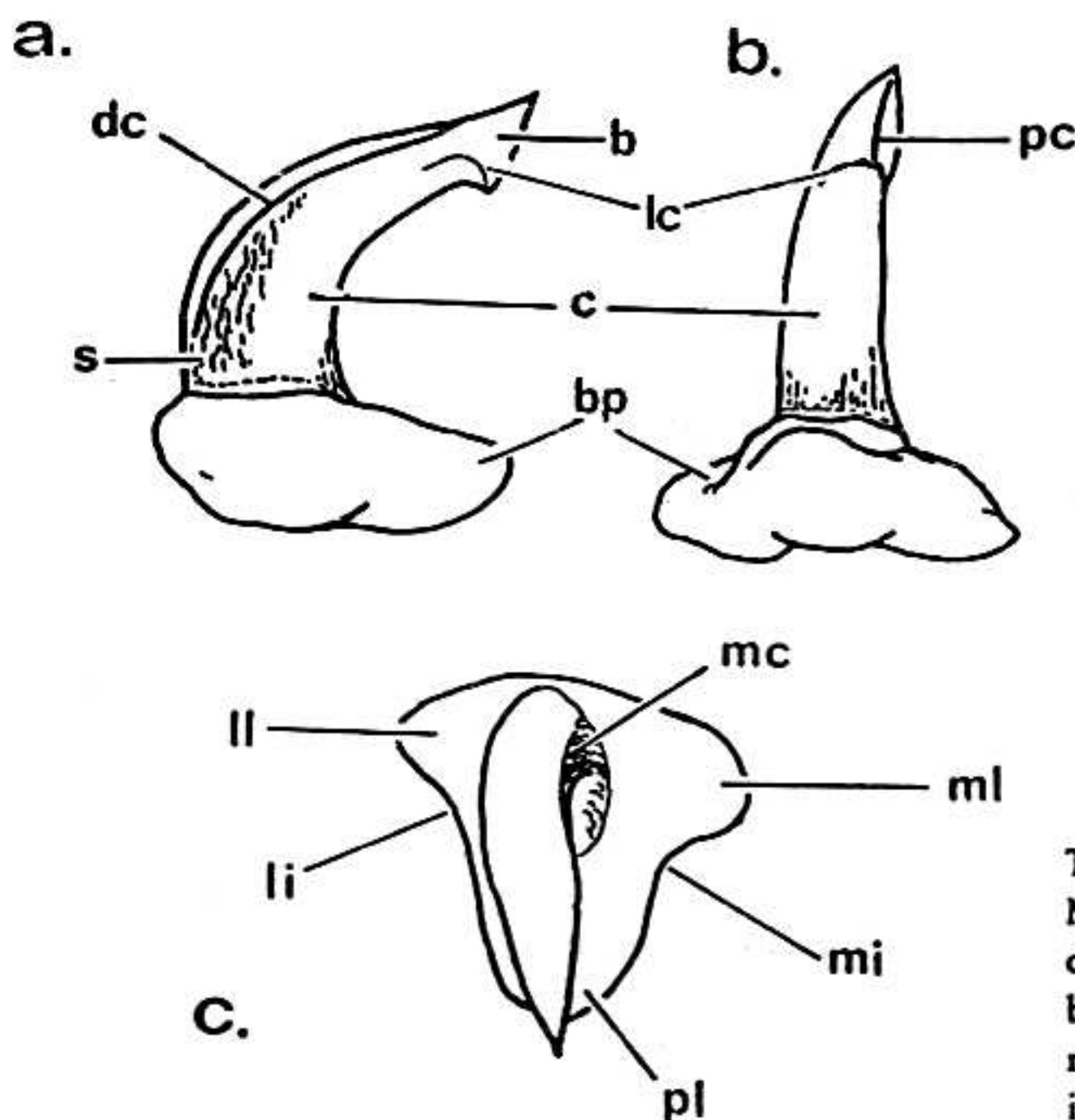
MURRY (1981:603, pl. 1 fig. 7 A-B) refers costate dorsal fin spine fragments with oval cross-section to *L. humblei* (Carnian, Upper Triassic of Texas). The posterior denticles are arranged in a single median row on the distal part of the posterior spine wall, giving way to two denticle rows proximally (text-fig. 25 f-g).

It should be noted that MAISEY (1978 fig. 1 B) illustrates considerable variation in ornament of the posterior face of hybodont fin spines (see also RIEPPEL 1981:330). There appears to be a tendency toward the production of a single median denticle row in place of two posterolateral denticle rows in several hybodont genera. It is therefore virtually impossible to define certain hybodont genera from fin spine morphology.

The question of the affinities of certain Triassic and Jurassic dorsal fin spines will be discussed elsewhere in a review of the Upper Triassic marine vertebrate faunas of north west Europe (DUFFIN, in preparation).

10. Cephalic spines

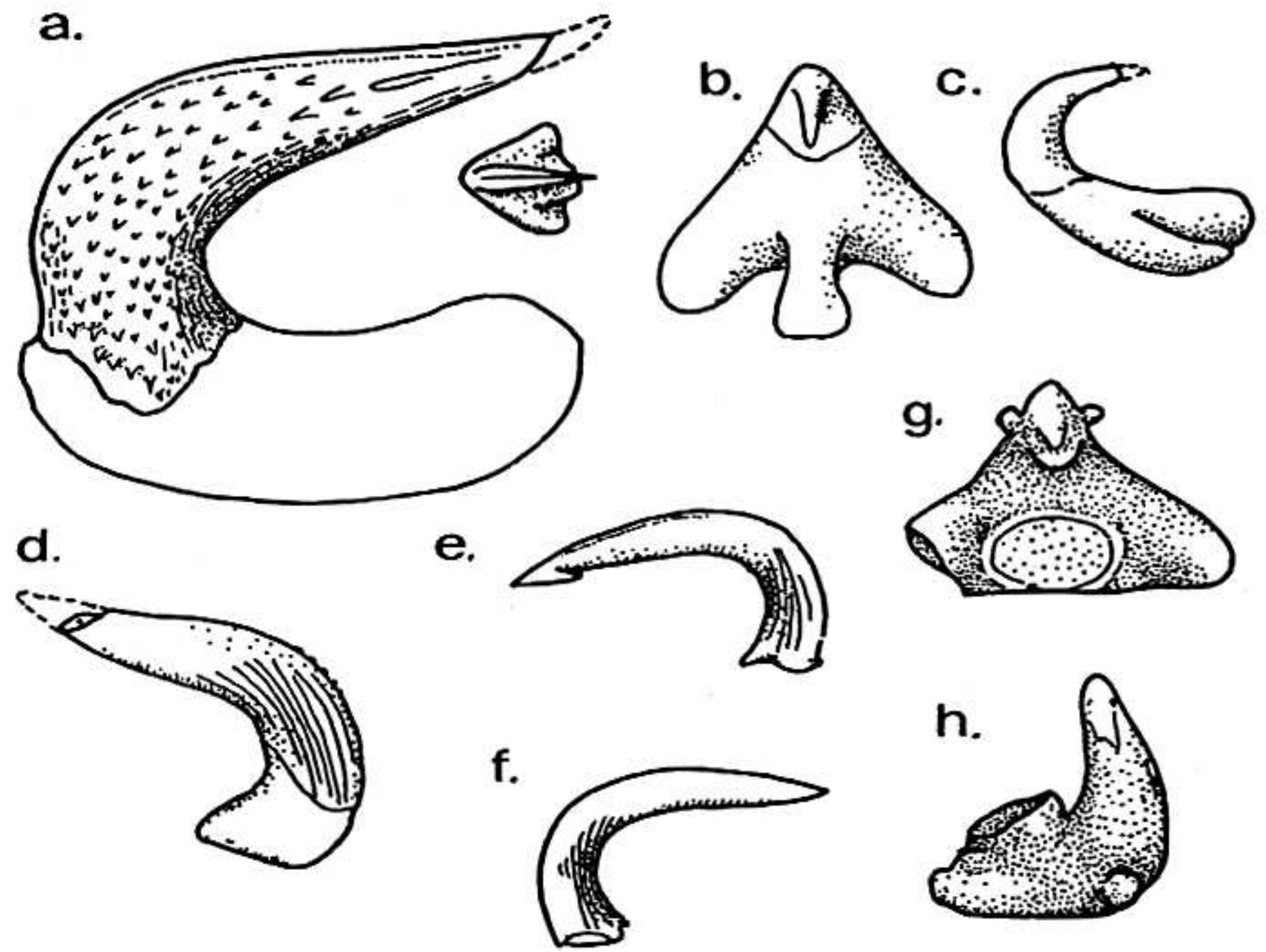
For a long time referred to a form genus, "*Sphenonchus*", cephalic spines are now known to be postorbital head spines from male hybodont sharks. MAISEY (1982), in his review of Mesozoic hybodonts, introduces several descriptive terms for cephalic spines (text-fig. 26 a-c). The cephalic spine comprises a triadial basal platform; the three lobes are mesial, posterior and lateral, separated by mesial and lateral indentations respectively. The cephalic spines are often asymmetric in shape, and paired; the anterior extremity of the mesial lobe is usually posterior to that of the lateral lobe. The basal platform is surmounted by an enamelled crown which is strongly recurved and possesses an apical retrorse barb. The barb is surmounted by a posterior crest; a dorsal crest ornaments the anterodorsal face of the crown; mesial and lateral crests may arise from the base of the crown posteriorly. Striations are developed around the base of the crown. It is presently unclear as to whether the spines were protective or functioned during copulation (RIEPEL 1981:332).



Text-fig. 26. Terms used to describe hybodont cephalic spines, after MAISEY (1982). Cephalic spines in a, lateral view; b, posterior view; c, dorsal view. Abbreviations: c, crown; bp, basal platform; dc, dorsal crest; b, barb; s, vertical striations; lc, lateral crest; pc, posterior crest; mc, mesial crest; ll, lateral lobe; ml, mesial lobe; pl, posterior lobe; li, lateral indentation; mi, mesial indentation.

Two pairs of cephalic spines are known in *Lissodus africanus* (BROUGH 1935:38; MAISEY 1982:30), placed "on each side of the head....more or less in their natural position (for hybodont sharks) behind the orbits" (BROUGH 1935:38). MAISEY (1982) suggests that in *L. africanus* the cephalic spines correspond in position to those of *Hybodus hauffianus* (MAISEY 1982, fig. 15 B), ie., one pair lies in the regions of the lateral otic processes and the other closer to the endolymphatic (parietal) fossa, based upon the statement by BROUGH quoted above. BROUGH (1935, pl. 3, fig. 2), however, in his reconstruction of *L. africanus*, inserts the cephalic spines in positions more

Text-fig. 27. Cephalic spines possibly belonging to *Lissodus* spp. a, cephalic spine of *Lissodus selachos* in lateral view, with basal platform restored (x 6). U.C. No 53906, after ESTES (1964). Inset, restored cephalic spine in dorsal view, slightly larger than natural size (after ESTES 1964); b, spine from the Wadhurst Clay (BM(NH) P. 11895) of Brede, Hastings, Sussex, in dorsal view (x 3.5), after PATTERSON (1966); c, P. 11895 in lateral view (x 3.5) after PATTERSON (1966); d, incomplete cephalic spine in lateral view, from the Weald Clay of Henfield, Sussex (BM(NH) P. 47207, after PATTERSON 1966); e, cephalic spine crown in lateral view (SMU-SMP 62180, x 5.5) from the Butler Farm local fauna, formerly referred to *Hybodus butleri*, but possibly belonging to *Lissodus anitae* (after THURMOND 1972); f, SMU-SMP 62180 in lateral view, after THURMOND (1972); g, cephalic spine of *Lissodus humblei* with posterior lobe of basal platform missing, drawn in dorsal view after MURRY (1981). SMU-MMP 67955 (x 10); h, SMU-SMP 67955 in lateral view (x 10), after MURRY (1981).



closely corresponding to the condition of *Hybodus delabèchei* (MAISEY 1982, fig. 15 C): a posterior pair in the vicinity of the lateral otic process and a supraorbital anterior pair.

ESTES (1964:9, fig. 3 d), allocates cephalic spines to *L. selachos* (text-fig. 27 a-b). These specimens are fairly symmetrical; the mesial and lateral lobes of the basal platform are posteriorly directed, possibly slightly curved, and separated from the posterior lobe by weak indentations. The crown is very recurved, but apparently lacks a terminal barb. A dorsal crest runs down the greater part of the length of the crown, but the lateral, posterior and mesial crests are missing. The crown ornament is "punctate" (ESTES 1964:9), although some striations are obvious on the anterior and posterior basal crown faces.

SMITH WOODWARD (1916, pl. 1, fig. 14) figured a complete cephalic spine from the Wadhurst Clay, which PATTERSON (1966) considered, together with further specimens from Cliff End (text-figs. 27 c-d), might belong to "*Lonchidion*". The lateral and mesial lobes of the basal platform are posteriorly-directed and somewhat curved, but more obviously separated from the posterior lobe than in the specimen described by ESTES. The crown is shorter and possesses a striated base, but apparently lacks the apical barb.

THURMOND (1972, fig. 5) describes cephalic spines from the Butler Farm local fauna and refers them to *Hybodus butleri*. These are very similar to those described by PATTERSON, but complete crowns possess a terminal barb (text-fig. 27 f-g), are striate basally and possess a prominent dorsal crest. It remains possible that some of the cephalic spines described by THURMOND belong to *L. anitae* on the basis of coincident geographical and stratigraphical occurrence.

MURRY (1981:603, pl. 1, fig. 6 A-B) describes a peculiar symmetrical cephalic spine from the Carnian (Upper Triassic) of Texas (text-fig. 27 h-i). The crown is upright, rather than strongly recurved, and lacks ornament (MURRY 1981:605). A pair of accessory denticles is developed just below the crown base. The basal platform is triradiate; the lateral and mesial lobes are laterally-directed and only slightly curved. The posterior lobe is broken, but from the attitude of its base, projects posterodorsally.

The question of the affinities of certain further Triassic cephalic spines will be discussed in a later publication (DUFFIN, in preparation).

11. Summary of taxonomy

The teeth of *Lissodus* are morphologically distinct from those of other comparable and contemporary hybodont genera. The distinction of teeth previously described as "*Lonchidion*" led HERMAN (1973:58, 1977:40) to erect the family Lonchidiidae, an act criticised by CAPPETTA & CASE (1975:6) on the basis that there was insufficient unequivocal evidence to warrant establishment of a new family. The recognition that the teeth described as "*Lonchidion*" are congeneric with those of *Lissodus* provides more evidence bearing on taxonomic discussion.

The hybodontiform sharks are poorly known apart from isolated mineralised elements of the dermal skeleton. The rarity of well preserved articulated hybodont material has led to much confusion concerning the relationships of the group. A welcome comprehensive anatomical review of the hybodonts by MAISEY (1982) has shed considerable light on the hybodonts as a whole. MAISEY (1982:40) was forced to conclude, however, that "it is not possible to establish the interrelationships of these taxa with any degree of confidence". A taxonomic review of the hybodontiform sharks is beyond the scope of this paper. In order to avoid adding to an already confused classification, it is best to distinguish *Lissodus* at generic level only. My feeling, based mostly upon dental characters, is that *Lissodus* may transpire as deserving the status of genotype of a distinct family of hybodontiform shark. If this proves to be the case, it is unfortunate that although *Lissodus* has priority as a genus, the family name Lonchidiidae takes priority.

The taxonomy of *Lissodus* is summarised below:

Genus *Lissodus* BROUGH 1935

Type species: *Hybodus africanus* BROOM, Upper Beaufort Series, Lower Triassic, South Africa.

Diagnosis: Hybodont sharks in which some members possess a sub-terminal mouth. The teeth are small to moderately large with deep crowns. A small to well developed labial peg is present and supported by a labial root buttress in some species. The occlusal crest is strong to moderate. The crown possesses a single low central cusp, usually flanked by very low lateral cusplets. Accessory cusplets are developed in some species. A longitudinal ridge may be present on the crown shoulders. The lateral margins of the crown incline steeply to an incised crown/root junction. The root is hybodontoid with simple and large vascular foramina, with anaulacorhize organisation. A central longitudinal pulp cavity is situated high up inside the tooth, at the level of the crown/root junction. A single row of small specialised foramina is usually present on the upper labial root face. The root is directed lingually, but not developed into a torus. The crown/root attachment is concentrated on the labial underside of the crown. A thick single, crystallite enameloid layer is present over the crown, and is thickest labially. There is overlap of the teeth in successive tooth files. Strong occlusal wear facets indicate a durophagous feeding habit.

The contained species, in stratigraphical order and with brief locality data, are as follows:

1. *L. wirksworthensis* n. sp., Cawdor Limestone, P1 subzone, Viséan, Lower Dinantian, Lower Carboniferous of Derbyshire, England.
2. *Lissodus* sp. (TWAY & ZIDEK 1983), Iowa Point Shale (Shawnee Group), Late Pennsylvanian, Upper Carboniferous of Shawnee County, Kansas, USA.
3. *L. zideki* (JOHNSON 1981); Upper Admiral to Middle Lueders Formation, Wichita-Albany Group, Early Permian of Texas, U.S.A.
4. *L. africanus* (BROOM 1909); Fish Bed, Lower Cynognathus Zone, Upper Beaufort Series, Scythian, Lower Triassic of Bekker's Kraal, Orange Free State, South Africa.
5. *L. angulatus* (STENSIÖ, 1921); Scythian, Lower Triassic of Spitsbergen.
6. *L. humblei* (MURRY 1981); Tecovas Formation, Dockum Group, ?Upper Carnian, Upper Triassic of Crosby County, Texas, U.S.A.
7. *L. nodosus* (SEILACHER 1943); Upper Muschelkalk and Keuper (Norian), Upper Triassic of south west Germany.
8. *L. minimus* (AGASSIZ 1834); Carnian to Rhaetian of north west Europe.
9. *L. pattersoni* n. sp., Forest Marble, Great Oolite Group, Bathonian, Middle Jurassic of Oxfordshire and Dorset, England.
10. *L. wardi* n. sp., Forest Marble, Great Oolite Group, Bathonian, Middle Jurassic of Oxfordshire and Dorset, England.
11. *L. leiodus* (WOODWARD 1887); Great Oolite and Stonesfield Slate, Great Oolite Group, Bathonian, Middle Jurassic of Gloucestershire, Oxfordshire and Wiltshire, England.
12. *L. heterodon* (PATTERSON 1966); Upper Purbeckian (Upper Jurassic) to "Wealden" (Lower Cretaceous) of Friar Waddon, Dorset, England.

13. *L. breve* (PATTERSON 1966); Ashdown Beds to Atherfield Clay, Wealden, Lower Cretaceous of southern England.
14. *L. crenulatus* (PATTERSON 1966); Wadhurst Clay and Grinstead Clay, Wealden, Lower Cretaceous of Sussex, England.
15. *L. pustulatus* (PATTERSON 1966); Atherfield Clay, Wealden, Lower Cretaceous of the Isle of Wight, England.
16. *L. striatus* (PATTERSON 1966); Weald Clay, Wealden, Lower Cretaceous of Henfield, Sussex, England.
17. *L. anitae* (THURMOND 1972); Butler Farm local fauna, Middle Paluxy Formation, ?Aptian-Albian, Lower Cretaceous of Wise County, Texas, U.S.A.
18. *L. levis* (WOODWARD 1887); Gault Clay, Albian, Lower Cretaceous of Sussex and Kent, England.
19. *L. weltoni* n. sp., Cenomanian, Upper Cretaceous of Suplec, Crook County, Oregon, U.S.A.
20. *L. babulskii* (CAPPETTA & CASE 1975); Upper Campanian, Upper Cretaceous of New Jersey, U.S.A.
21. *L. selachos* (ESTES 1964); Lance Formation, Maestrichtian, Upper Cretaceous of Wyoming, U.S.A.

12. Palaeoecological significance

The question now arises as to whether *Lissodus* might be taken as an environmental indicator. BROUGH (1935:37) points out that *L. africanus* was recovered from freshwater deposits. The accompanying fish fauna (eg. BROOM 1909; BROUGH 1931, 1934; HUTCHINSON 1973, 1975, 1978; JUBB & GARDINER 1975) includes redfieldiiforms, perleidiforms and the palaeoniscoid *Dicellogyge*. The environment of deposition and provenance of many of the other species of *Lissodus* are subjects of debate; in many cases, *Lissodus* could be either freshwater or marine. The associated faunas and supposed environments of deposition for each of the species of *Lissodus* is briefly summarised below.

The teeth of *L. wirksworthensis* were recovered from limestones and intercalating black shales believed by FORD (1964) to represent deposition in an off-reef area. The presence of coral bioherms indicates a marine depositional environment, a conclusion corroborated by the rich invertebrate fauna (FORD 1964, DUFFIN & WARD 1983 a). The associated vertebrate fauna includes teeth of the oldest presumed neoselachian shark (DUFFIN & WARD 1983 a) the problematic selachian *Harpagodonts* (TURNER 1982, 1983), and as yet undetermined isolated cladodont, xenacanth, petalodont and palaeoniscid remains.

The Wichita-Albany Group of north-central Texas, yielding *L. zideki*, is part of a largely terrestrial sequence, although some ammonites have been recorded from the region (SHERLOCK 1948). JOHNSON (1981:20) found several species of *Hybodus* and *Polyacrodus*, xenacanths, cladodonts and petalodonts in association with *L. zideki*, suggesting that the fauna is marine (although at least some xenacanth sharks are known to occur in freshwater).

L. angulatus from the Vardebukta Formation of the Spitsbergen Lower Triassic (Scythian) was recovered from fully marine deposits (BIRKENMAJER and JERZMAŃSKA 1979:8). The associated vertebrates include teeth of *Hybodus*, *Acrodus*, edestids, saurichthyids and other actinopterygians.

L. humblei from the ?late Carnian (Upper Triassic) Dockum Formation of Texas has been found in association with "a diverse fauna of Upper Triassic vertebrates including...xenacanth sharks..." (MURRY 1981:603). The Dockum Formation is regarded as fluvial or lacustrine in origin (SHERLOCK 1948:200; MURRY 1981:603).

The teeth of *L. nodosus* from the Norian (Upper Triassic) of south west Germany form part of a diverse selachian fauna including *Acrodus*, *Hybodus* spp., *Polyacrodus*, *Palaeobates*, *Doratodus*, the neoselachian *Reifia*, together with *Ceratodus*, various actinopterygians, coelacanthids, labyrinthodonts, nothosaurs and tetrapods (SEILACHER 1943; DUFFIN 1980 a, 1981 a). The fauna probably represents an admixture of several thanatocoenoses, the best represented being marine.

Teeth of *L. minimus* are characteristic of the Rhaetian (Upper Triassic) of north west Europe, particularly Britain. The vertebrate faunas of the Penarth Group (lower Rhaetic) occur in bone beds and black shale sequences. At several localities (eg. Aust cliff, Avon, south-west England) a basal bone bed contains palaeoniscids, *Ceratodus*, holosteans, hybodont sharks (*Polyacrodus Hybodus*), neoselachian sharks (*Pseudodalatias*, *Vallisia*, *Palaeospinax*, *Nemacanthus*), ?placodonts (*Psephoderma*), ichthyosaurs and plesiosaurs, ?crocodilians (*Rysosteus*), ?labyrinthodonts and prosauropods (SYKES, CARGILL & FRYER 1970, DUFFIN 1978, 1980 a, 1982 a, 1982 b) indicating terrestrial, possibly freshwater and marine sources. Elsewhere in the British Rhaetic (DUFFIN 1980 b, 1980 c) *L. minimus* is associated with echinoid spines, bivalves and gastropods, indicating marine conditions. It is probable that *L. minimus* was euryhaline.

Teeth of *L. pattersoni* and *L. wardi* were recovered from the Forest Marble of Kirtlington in Oxfordshire and Watton Cliff in Dorset, England. The Watton Cliff deposit is a bioclastic grit containing marine bivalve fragments, rare hybodont selachian teeth of *Polyacrodus* type, and a sparse fauna of as yet undescribed neoselachians. A terrestrial element is present, as indicated by the discovery of rare mammal teeth (FREEMAN 1976). At Kirtlington, the *Lissodus* teeth were collected from friable oolitic limestones and an unconsolidated brown marl in the ?Kemble Beds. The teeth were more common in the oolitic limestone than in the marl. The marl contains a rich vertebrate fauna including mammalian, crocodylian, ornithischian, theropod, pterosaur, chelonian, lepidosaur, anuran, actinopterygian and rare selachian remains (FREEMAN 1977, 1979). This, and the presence of abundant plant debris and freshwater ostracods indicates non-marine deposition. The sparse selachian fauna may have been derived from the oolitic limestones which underlie and form impersistent lateral equivalents to the Kirtlington Mammal Bed. The selachian fauna, as yet undescribed, is identical to that from Watton Cliff, and contains hybodont teeth and dermal denticles, *Heterodontus*, two species of scyliorhinid and two species of belemnobatid, suggesting thoroughly marine conditions.

L. leiodus is known from the Great Oolite of Gloucestershire and Oxfordshire. While the Stonesfield slate shows some terrestrial influence (mammals, lepidosaurs), the bulk of the Great Oolite Group is demonstrably marine comprising carbonate bank deposits containing abundant echinoids and other marine invertebrates. *L. heterodon* from the Purbeckian, *L. brevis*, *L. crenulatus*, *L. pustulatus* and *L. striatus* from the British Wealden (Lower Cretaceous) form part of what is believed to be a freshwater fauna including other hybodont sharks, actinopterygians, reptiles, non-marine ostracods and charophytes (PATTERSON 1966).

L. levis from the Gault Clay (Albian, Lower Cretaceous) forms part of an as yet undescribed marine selachian fauna.

L. anitae was recovered from the Butler Farm local fauna, a channel fill in the Middle Paluxy Formation, ?Aptian/Albian, Lower Cretaceous of Texas. The only associated selachian is *Hybodus butleri*, which THURMOND (1972:215) believes to have been restricted to fresh and brackish water conditions. The vertebrate fauna also contains frog, salamander, lepidosaur, crocodile, dinosaur, multituberculate and triconodont mammal, amiid and lepisosteid material (SLAUGHTER 1971:132), indicating freshwater conditions.

CAPPETTA & CASE (1975) describe *L. babulskii* from a diverse, thoroughly marine selachian fauna recovered from Upper Campanian (Upper Cretaceous) deposits of New Jersey, U.S.A.

ESTES (1964) describes a subtropical freshwater deposit containing *L. selachos*, in addition to orectolobid, ganopristine and dasyatid selachians and a diverse association of actinopterygians, amphibians and reptiles, including crocodylians, ornithischians, saurischians, ophidians, testudines and lepidosaurs.

The isolated fin spine cited by LUPTON, GABRIEL, & WEST (1980) from the Upper Cretaceous Hell Creek Formation of Montana was recovered from sediments which form part of a fluvial sequence. The associated vertebrate fauna includes a dasyatid, amiid and lepisosteid actinopterygians, amphibians, champsosaurs, crocodylian, trionychid, saurischian and ornithischian dinosaurs, and multituberculate and condylarthran mammals.

Thus, certain of the species of *Lissodus* may well have been restricted to freshwater (*L. africanus*, *L. anitae*, *L. selachos* and the British Wealden species); certain species may have been euryhaline (*L. minimus*, and possibly *L. pattersoni* and *L. wardi*), while others have been recovered from deposits which are demonstrably marine.

13. Evolution

The teeth of *Lissodus* show little structural diversity throughout their range from Lower Carboniferous to Upper Cretaceous, and are distinct from those of other hybodontiforms from their earliest record. The dentition of *L. africanus* in the Lower Triassic shows a specialised tooth arrangement in which the teeth in any tooth file alternate with those of the preceding and succeeding files. This gives rise to extreme conservation of space along the jaw and provides a battery of closely associated tooth crowns, well suited to a durophagous habit, with concomitant increase in rigidity of the portion of the dental battery employed during occlusion. The dental configuration is taken to be characteristic of *Lissodus*, and is indicated in most species by the pattern of pressure scars produced by contact of adjacent teeth *in vivo*. The lateral extremities of the teeth possess pressure scars

produced by contact with teeth in adjacent rows. Also, the earlier tooth in the file produced a pressure scar on the lingual crown face of the succeeding tooth. Certain species (*L. nodosus*, *L. minimus*) show inflation of the crown in lateral teeth, and additional means of inter-tooth articulation.

Within the genus, inter-specific relationship is clouded by gaps in the record. The species are united in possessing a labial peg, a synapomorphy, so far as can be presently judged. The members of the genus appear to represent a continuously evolving lineage.

HERMAN (1977:42) remarks that evolutionary trends in the teeth of "*Lonchidion*" include the reduction of coronal striation, progressive reduction in number of lateral cusplets and progressive accentuation of the labial peg. Table 1 summarises the dental characters of individual species of *Lissodus*. From this it can be seen that size has varied throughout the history of the group. There are two rough size groupings: those with mean tooth length less than 4 mm (*L. wirksworthensis*, *L. zideki*, *L. africanus*, *L. humblei*, *L. pattersoni*, *L. breve*, *L. crenulatus*, *L. pustulatus*, *L. striatus*, *L. anitae*, and *L. weltoni*) and those with crown length exceeding 4 mm (*L. angulatus*, *L. nodosus*, *L. minimus*, *L. wardi*, *L. leiodus*, *L. heterodon*, *L. babulskii* and *L. selachos*).

Crown shape has tended to remain simple throughout the history of the genus, being moderately elongate with a moderate labial peg. Several of the Cretaceous species (*L. striatus*, *L. selachos*) show elongation of the crown, while several pre-Cretaceous species show medial expansion of the crown. Lateral cusplets are variously developed. Present in the earliest species, they appear several times in the history of the group, and persist in the final member.

Coronal striation appears to be variable. The feature is common and coarsely developed in certain Triassic and Jurassic forms (*L. nodosus*, *L. minimus*, *L. wardi*) but is less frequent in Cretaceous species.

The development of the labial peg varies through the history of the genus. It tends to be strongly developed in early species, and weaker in Cretaceous ones.

The crowns of most species of *Lissodus* are of simple shape and show little heterodonty. Certain species, such as *L. nodosus*, show the development of progressively centrally expanded tooth crowns laterally. In the larger Triassic and Jurassic species, central expansion of the crown may have disrupted the tooth file interdigitation laterally.

Secondary characters developed within the genus include the presence of nodes on the crown shoulder (*L. nodosus*, *L. weltoni*), a longitudinal ridge on the crown shoulder (*L. wirksworthensis*, *L. pattersoni*), accessory cusplets on the labial crown face (*L. wirksworthensis*, *L. pustulatus*), and buttressing of the labial peg by a development of the upper labial root face (*L. wirksworthensis*, *L. pattersoni*).

It is interesting that the simple crown shape, exemplified by *L. africanus*, is maintained throughout the history of the genus. The record, so far as it is presently known, indicates specialisation of this simple crown shape in the Upper Triassic (*L. nodosus* and *L. minimus*) and Middle Jurassic (*L. wardi*). The tendency, at least in the former two species, is to develop larger teeth, with considerable heterodonty. All three species show expansion of the crown centrally in lateral teeth. The teeth of *L. nodosus* vary from forms of very simple, generally elongate shape, possessing a large labial peg, to those which are larger, centrally expanded and with little or no development of the labial peg. Reduction of the labial peg in the larger teeth is also noticed in *L. minimus*, and may well prove to be the case in *L. wardi* and *L. pattersoni* as more material is discovered. So far as can be judged at the present time, the earliest representative of the genus *Lissodus*, *L. wirksworthensis*, was marine, inhabiting reef environments of the Carboniferous Limestone of Britain. Like all subsequent species of *Lissodus*, its tooth morphology suggests durophagous feeding on benthonic organisms. It may well have been in direct competition for food with other vertebrates, notably certain bradyodonts and the earliest neoselachian (DUFFIN & WARD 1983 a:108). *L. wirksworthensis* presumably developed from less specialised *Lissodus* stock in the Lower Carboniferous. Its effectiveness as a bottom feeder was enhanced by the development of a labial buttress to the labial peg. This labial buttressing of the labial part of the crown has been independently acquired by a later species of *Lissodus* (*L. pattersoni*) in the Jurassic, and by several neoselachian groups (*Anachronistes* in the British Lower Carboniferous and Permian of the U.S.A., DUFFIN & WARD 1983 a; Jurassic orectolobid, *Agaleus*, from the British Lower Jurassic, DUFFIN & WARD 1983 b).

The conservative tooth morphology of *L. zideki* indicates a position close to the basal *Lissodus* stock. The teeth of this species are marine.

During the Triassic there appear to have been several incursions to freshwater conditions (*L. africanus* in the Scythian, *L. humblei* in the Carnian) and possibly the production of euryhaline species (*L. minimus*), although there

remain several marine species (*L. angulatus* in the Scythian and *L. nodosus* in the Norian). *L. africanus* is very conservative and might well be part of the central *Lissodus* stock. *L. angulatus* showed elongation of the teeth, while *L. nodosus* and *L. minimus* have much enlarged and more robust laterals. This required slight modification of the conservative alternate tooth arrangement; the labial peg is reduced in lateral teeth, and in *L. nodosus* tooth position is maintained by labial nodes on the crown.

The environment inhabited by *L. wardi* and *L. pattersoni* is debatable. *L. wardi* shows similar structure to *L. minimus* and may well be closely related. *L. pattersoni* is probably closer to the central *Lissodus* stock, and shows considerable similarity in coronal striation and development of lateral cusplets to the Upper Jurassic *L. heterodon*. *L. leiodus* was marine, and is again similar to *L. minimus* and *L. wardi*.

Amongst the British Cretaceous species, PATTERSON'S (1966:347) suggestions of interrelationship are accepted here, with *L. brevis* lying close to the main line of *Lissodus* evolution. *L. crenulatus* probably developed from *L. brevis* early in Wadhurst Clay times, developing a crenulate occlusal crest. *L. pustulatus* probably also arose directly from *L. brevis*, but appeared during Weald Clay times. *L. striatus* may have evolved from *L. crenulatus* by elongating the teeth, strengthening the surface ornament of the crown and reducing the labial peg.

L. levis from the marine Gault Clay (Albian) shows broadening of the crown and loss of the labial peg in lateral teeth. This species possibly arose from an unspecialised *L. brevis* - like stock in Aptian times. *L. anitae*, *L. weltoni* and *L. babulskii* are unspecialised and probably arose from primitive stock during Albian, Cenomanian and Campanian times respectively. Although slightly larger and possessing a crenulate occlusal crest, *L. selachos* probably also lies close to generalised *Lissodus* stock. It is most similar to *L. anitae* amongst the species from the American Cretaceous.

The Upper Jurassic and Cretaceous species of *Lissodus* mark another radiation into freshwater conditions, with marine stock being represented by *L. babulskii*.

PATTERSON (1966: 333) redescribes the teeth of *Hylaeobatis ornata* (SMITH WOODWARD) from the Weald Clay and Lower Greensand of south east England, the teeth in the latter deposit being derived. He shows that the symphyseal tooth was rectangular in coronal view, elongate and symmetrical. The teeth decrease in size posteriorly, with concomitant deterioration of symmetry and simplification of the coronal ornament. The smallest teeth of this species (possibly juvenile) resemble those of *L. pustulatus* with regard to overall crown shape and ornamentation. PATTERSON (1966: 341) points out that with specialisation of the anterior teeth in the dentition, the extreme posterior lateral positions will contain teeth most closely resembling the ancestral form. The converse is usually the case (see p. 122); the lateral teeth are usually specialised and the anteriors retain primitive characters. Bearing in mind the similarity of *H. ornata* to *L. pustulatus*, PATTERSON (1966: 342) suggests that *Hylaeobatis* "arose from a homodont species of the hybodont genus *Lonchidion* primarily by reduction in the labial process, by increase in the surface ornament, by specialisation in the anterior teeth, and by loss of fin and cephalic spines".

Hylaeobatis is placed in the Family Ptychodontidae, primarily on the basis that *Ptychodus* also possesses specialisation of the anterior teeth, and apparent absence of fin spines. After a very thorough comparison of the teeth of the two genera, PATTERSON (1966: 340, 345) concludes that *Hylaeobatis* is intermediate in form between the hybodontids and the ptychodontids, but that *Ptychodus* did not evolve directly from *H. ornata*. It appears that *Ptychodus* is a neoselachian shark (STEWART 1980), since it possesses calcified vertebral centra, and is unlikely to have been derived from *Lissodus* or any other hybodontiform stock in the Cretaceous. Also, its relation to *Hylaeobatis* might be better assessed if data were available on the enameloid ultrastructure of the two genera. While it is possible to derive *Ptychodus* from *Lissodus* via *Hylaeobatis* on morphometric transformations, it may well transpire that *Hylaeobatis* and *Ptychodus* are phylogenetically very distinct from *Lissodus*. In his diagnosis of the Family Lonchidiidae, HERMAN (1977: 40) states that the teeth of species formerly placed in the genus *Lonchidion* show degeneration of their original hybodont polycuspidity, and the acquisition of a secondary pseudopolycuspidity. It is regrettable that the scope of HERMAN'S paper does not allow him to pursue his speculation on this topic, and to define the comparative characters of his "polycuspidae originelle" and "pseudopolycuspidae secondaire", especially since he earlier (HERMAN 1977: 18) lists unicuspid or "pluricuspid" crowns as diagnostic of the Family Hybodontidae. Moreover, he emphasises that the original cusps are little pronounced.

HERMAN'S remarks on the nature of the crown of "*Lonchidion*", it should be realised, are born out of his assumption that it evolved from *Hybodus* during the Jurassic (HERMAN 1977: 40). The origin of *Lissodus* is probably pre-Carboniferous and remains obscure at the present time.

14. Conclusions

1. The genus *Lonchidion* is a junior synonym of *Lissodus*. All previously erected valid species of *Lonchidion* belong to *Lissodus*.
2. "*Lonchidion*" *rhizion* PATTERSON (1966) from the Wealden (Lower Cretaceous) of Britain is not a *Lissodus* tooth, but a vertebrate fragment of unknown affinity.
3. From the description of new material, and by synonymy, the genus *Lissodus* ranges from Lower Carboniferous to Upper Cretaceous times.
4. The overall crown shape and presence of a labial peg are the most reliable characters for distinguishing teeth of *Lissodus* from those of other hybodontiforms.
5. Further to "*Lonchidion*" spp., the following species belong to *Lissodus* by synonymy:
 - I) *L. zideki* (JOHNSON 1981) from the Early Permian of the U.S.A.
 - II) *L. angulatus* (STENSIÖ 1921) from the Lower Triassic of Spitsbergen.
 - III) *L. nodosus* (SEILACHER 1943) from the Upper Triassic of southern Germany.
 - IV) *L. minimus* (AGASSIZ 1839) from the Upper Triassic of north west Europe.
 - V) *L. leiodus* (WOODWARD 1887) from the Middle Jurassic of Britain.
 - VI) *L. levis* (WOODWARD 1887) from the Lower Cretaceous of Britain.
6. The following new material belongs to *Lissodus*:
 - I) *L. wirksworthensis* n. sp. from the Lower Carboniferous of Britain.
 - II) *L. pattersoni* from the Jurassic of Britain.
 - III) *L. wardi* from the Jurassic of Britain.
 - IV) *L. weltoni* from the Upper Cretaceous of the U.S.A.
7. *Lissodus* was a benthonic shark of durophagous habit. Essentially a marine stock, it radiated to freshwater habitats during the Triassic and Cretaceous, possibly in response to competition with various groups of marine actinopterygians.

Acknowledgements

I am very grateful for the following for access to specimens held in their care: Dr. COLIN PATTERSON (BM(NH)), Prof. W. A. CLEMENS (U.C.), Dr. J. A. VAN DEN HEEVER (South African Museum), Prof. B. SLAUGHTER and Dr. G. JOHNSON (Southern Methodist University, Texas), Mr. R. F. PICKFORD (Bath), Dr. M. L. K. CURTIS (Bristol), Prof. F. WESTPHAL (Tübingen), Dr. O. RIEPPEL and Prof. Dr. H. RIEBER (Zürich), and Dr. R. WILD (Ludwigsburg). Dr. M. D. CRANE (BCM) provided information on the history of the holotype of *L. minimus*. Miss PAT GASSER kindly made the drawing of *Lissodus anitae* from the holotype. Some of the photography was kindly done by the Photography Departments of the BM(NH) and SAM. I am particularly grateful to Mr. DAVID WARD, Dr. BRUCE WELTON, Mr. ERIC F. FREEMAN and Mr. GERARD R. CASE for providing specimens for my study. Dr. COLIN PATTERSON and Mr. D. WARD kindly read the manuscript. Dr. R. P. S. JEFFERIES and Ms. E. MATEAR helped with the German summary. The manuscript was written on a Xerox 850 Page Display System through the kindness of Mr. D. WARD (Orpington).

Literature

- AGASSIZ, L. (1833-1843): *Recherches sur les Poissons Fossiles*. - 5 vols., 1420 pp., and suppl.; Neuchatel.
- BIRKENMAJER, K. & JERZMAŃSKA, A. (1979): Lower Triassic shark and other fish teeth from Hornsund, South Spitsbergen. - *Studia geol. pol.*, 40 10: 7-37, 2 pls., 3 tabs. Warszawa.
- BIRKENMAJER, K. & TRAMMER, J. (1975): Lower Triassic conodonts from Hornsund, south Spitsbergen. - *Acta geol. pol.*, 25, 2: 299-308. Warszawa.
- BROOM, R. (1909): Fossil Fishes of the Upper Karroo Beds of South Africa. - *Ann. S. Afr. Mus.* 7, 3: 251-269, pls. 12, 13. Cape Town.
- BROUGH, J. (1931): On fossil fish from the Karroo System, and some general considerations of the bony fishes of the Triassic period. - *Proc. zool. Soc. Lond.*, 1931: 235-296, 4 pls. London.
- (1935): On the Structure and Relationships of the Hybodont Sharks. - *Mem. Manchr. lit. phil. Soc.*, 79: 35-49, pls. 1-3. Manchester.
- CAPPETTA, H. & CASE, G. R. (1975): Contribution à l'étude des sélaciens du Groupe Monmouth (Campanien-Maestrichtien) du New Jersey. - *Palaeontographica*, (A), 151: 1-46, 9 pls., 11 figs., 3 tabs. Stuttgart.
- CASE, G. R. (1979): Additional fish records from the Judith River Formation (Campanian) of Montana. - *Geobios.*, 12,2: 223-233, 1 fig., 2 pls. Lyon.
- CASIER, E. (1947): Constitution et évolution de la racine dentaire des Euselachii. 3. Evolution des principaux caractères morphologiques et conclusions. - *Bull. Mus. r. Hist. nat. Belg.*, 23, 15: 1-45. Brussels.

- CORROY, G. (1928): Les vertébrés du Trias de Lorraine et le Trias lorrain. — Ann. Paléont., 17, 3: 81–136, figs. 16–19, pls. 10–14. Paris.
- DREYER, D. (1962): Zur Entstehung und Paläontologie der Bonebedlagen im Unteren Rät Thüringens. — Freib. Forsch., 125: 129–143, 10 figs., 6 pls. Berlin.
- DUFFIN, C. J. (1978): The Bath Geological Collections. f. The importance of certain vertebrate fossils collected by CHARLES MOORE: an attempt at scientific perspective. — Geological Curators Group Newsletter., 2, 2: 59–67. Keele.
- , (1980 a): A new euselachian shark from the Upper Triassic of Germany. — N. Jb. Geol. Paläont., Mh. 1980, 1: 1–16, 8 figs. Stuttgart.
- , (1980 b): Marine Vertebrates from the North West European Rhaetic (Upper Triassic). — 326 pp. Unpublished Ph. D. thesis, London University.
- , (1980 c): The Upper Triassic section at Chilcompton, Somerset, with notes on the Rhaetic of the Mendips in general. — Mercian Geol. 7, 4: 251–268, 2 figs., pl. 24. Nottingham.
- , (1981 a): Comments on the selachian genus *Doratodus* SCHMID (1861) (Upper Triassic, Germany). — N. Jb. Geol. Paläont. Mh., 1981, 5: 289–302, 4 figs. Stuttgart.
- , (1981 b): The fin spine of a new holocephalan from the Lower Jurassic of Lyme Regis, Dorset, England. — Geobios, 14, 4: 469–475, 1 fig., 1 pl. Lyon.
- , (1982 a): A palaeospinacid shark from the Upper Triassic of south-west England. — Zool. J. Linn. Soc., 74, 1: 1–7, 2 figs. London.
- , (1982 b): Teeth of a new selachian from the Upper Triassic of England. — N. Jb. Geol. Paläont., Mh, 1982, 3: 156–166, 4 figs., 1 tab. Stuttgart.
- DUFFIN, C. J. & GAŹDZICKI, A. (1977): Rhaetic fish remains from the Tatra Mountains. — Acta geol. pol., 27, 3: 333–348, 10 figs., 2 pls. Warsaw.
- DUFFIN, C. J. & WARD, D. J. (1983 a): Neoselachian sharks teeth from the Lower Carboniferous of Britain and the Lower Permian of the U.S.A. — Palaeontology, 26, 1: 93–110, pls. 13–14. London.
- , (1983 b): Teeth of a new neoselachian shark from the British Lower Jurassic. — Palaeontology, 26, 4: 839–844, 3 figs., 1 table. London.
- ECK, H. (1865): Über die Formationen des bunten Sandsteins und des Muschelkalks in Oberschlesien und ihre Versteinerungen. — Diss. Berlin.
- ENDLICH, F. M. (1870): Das Bonebed Württembergs. — 30 pp., Diss. Tübingen.
- ENGEL, T. (1908): Geognostischer Wegweiser durch Württemberg. — 3 Aufl. Schweizerbart, Stuttgart.
- ESTES, R. (1964): Fossil Vertebrates from the Late Cretaceous Lance Formation, Eastern Wyoming. — Univ. Calif. Publ., geol. Sci., 49: 1–187, 5 pls., 73 figs. Berkeley.
- ETHERIDGE, R. (1871): On the physical structure and organic remains of the Penarth (Rhaetic) beds of Penarth and Lavernock; also with description of the Westbury-on-Severn section. — Trans. Cardiff nat. Soc. 3: 39–62. Cardiff.
- FORD, T. D. (1964): A new fish bed in the Carboniferous Limestone of Derbyshire. — Mercian Geol., 1: 3–9. Nottingham.
- FREEMAN, E. F. (1975): The isolation and ecological implications of the microvertebrate fauna of a Lower Cretaceous lignite bed. — Proc. Geol. Ass., 86, 3: 307–312, 1 table. London.
- , (1976): A mammalian fossil from the Forest Marble (Middle Jurassic) of Dorset. — Proc. Geol. Ass., 87, 2: 231–236, 1 pl. London.
- , (1977): Triassic extinction or Jurassic vacuum? — Nature, 266, No. 5600: 305. London.
- , (1979): A Middle Jurassic mammal bed from Oxfordshire. — Palaeontology, 22, 1: 135–166, pls. 15–21. London.
- HENRY, J. (1875): L'Infralias dans la Franche-Comte. — Mémoires. Soc. Émul. Doubs. 4, 10: 285–476, 5 pls. Besançon.
- HERMAN, J. (1973): Les Sélaciens des terrains Néocrétacés et Paléocènes de Belgique et contrées limitrophes. Eléments d'une biostratigraphie intercontinentale. — 3 vols. 598 pp., 15 pls., Thesis, University of Brussels.
- , (1977): Les Sélaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. Eléments d'une biostratigraphie intercontinentale. — Mém. Servic. Explic. Cartes. geol. min. Belg. No. 15: 450 pp., 25 figs., 21 pls. Brussels.
- HUTCHINSON, P. (1973): A revision of the Redfieldiiform and Perleidiform fishes from the Triassic of Bekker's Kraal (South Africa) and Brookvale (New South Wales). — Bull. Br. Mus. nat. Hist. (Geol.), 22: 233–354, 54 figs. London.
- , (1975): Two Triassic fish from South Africa and Australia, with comments on the evolution of the Chondrostei. — Palaeontology, 18: 613–629, 1 pl. London.
- , (1978): The anatomy and phylogenetic position of *Helichthys*, a Redfieldiiform fish from the Triassic of South Africa. — Palaeontology, 21, 4: 881–891, 4 figs. London.
- JOHNSON, G. D. (1979): Early Permian vertebrates from Texas: Actinopterygii (*Schaefferichthys*), Chondrichthyes (including North American Pennsylvanian and Triassic *Xenacanthodii*), and Acanthodii. — Unpublished Ph. D. thesis, 653 pp., Southern Methodist University, Dallas, Texas.
- , (1981): Hybodontoides (Chondrichthyes) from the Wichita-Albany Group (Early Permian) of Texas. Journ. Vert. Paleont. 1, 1: 1–41, 195 figs. Norman.
- JUBB, R. A. & GARDINER, B. G. (1975): A preliminary catalogue of identifiable fossil fish material from Southern Africa. — Ann. S. Afr. Mus., 67, 11: 381–440, 38 figs. Cape Town.
- LANG, R. (1910): Der mittlere Keuper im südlichen Württemberg. — Jh. Ver. vaterl. Naturk. Württ., 65: 77–131; 66: 1–54. Stuttgart.
- LUPTON, C., GABRIEL, D. & WEST, R. M. (1980): Paleobiology and depositional setting of a Late Cretaceous vertebrate locality, Hell Creek Formation, McCone County, Montana. — Contr. Geol. Univ. Wyo., 18, 2: 117–126, 7 figs., 2 tabs. Laramie.
- MAISEY, J. G. (1978): Growth and form of finspines in hybodont sharks. — Palaeontology, 21, 3: 657–666, pl. 72. London.
- , (1982): The Anatomy and Interrelationships of Mesozoic Hybodont Sharks. — Am. Mus. Novit. No. 2724: 1–48, 17 figs. New York.
- MEYER, H. VON & PLEININGER, T. (1844): Beiträge zur Paläontologie Württembergs, enthaltend die fossile Wirbelthierreste aus dem Triasgebirgen mit besonderer Rücksicht auf die Labyrinthodonten des Keupers. — Fol. 1–132. Stuttgart.

- MEYER, R. L. (1970): Late Cretaceous elasmobranchs from the Mississippi and East Texas embayments of the Gulf Coastal Plain. - Unpublished Ph. D. thesis, University of Texas at Arlington.
- MURRY, P. A. (1981): A new species of freshwater hybodont from the Dockum Group (Triassic) of Texas. - *J. Paleont.*, 55, 3: 603-607, 1 pl. Chicago.
- OERTLE, G. (1928): Das Vorkommen von Fischen in der Trias Württembergs. - *N. Jb. Miner. Geol. Paläont., Beil.Bd., Abt. B*, 60: 325-472, pls. 30-32. Stuttgart.
- PATERSON, C. (1966): British Wealden Sharks. - *Bull. Br. Mus. nat. Hist. (Geol.)*: 11, 7: 283-350, 5 pls., 31 figs. London.
- PHILLIPS, J. (1871): Geology of Oxford and the valley of the Thames. - 24+529 pp., 207 figs., 17 pls. Oxford.
- PORTLOCK, J. E. (1843): Report on the geology of the county of Londonderry, and parts of Tyrone and Fermanagh. - XXXI+784 pp., pls. 1-38. Dublin.
- PRIEM, F. (1908): Etude des Poissons Fossiles du Bassin Parisien. - *Ann. Paléont.*, 1-144, 74 figs., 5 pls. Paris.
- QUENSTEDT, F. A. (1852): Handbuch der Petrefaktenkunde. - 792 pp., 62 pls. (2nd. Ed. 1866). Tübingen.
- , — (1858): Der Jura. VI+842 pp., 42 figs., 100 pls. Tübingen.
- , — (1885): Handbuch der Petrefaktenkunde. - 3rd Ed. 1239 pp., 100 pls (Atlas). Tübingen.
- RAWSON, P. F., CURRY, D., DILLEY, F. C., HANCOCK, J. M., KENNEDY, W. J., NEALE, J. W., WOOD, C. J. & WORSSAM, B. C. (1978): A correlation of Cretaceous rocks in the British Isles. - *Geol. Soc. Lond., Special Report No. 9*, 70 pp. London.
- REIF, W.-E. (1976): Morphogenesis, Pattern Formation and Function of the Dentition of *Heterodontus* (Selachii). - *Zoomorphologie*, 83: 1-47, 39 figs., Berlin.
- , — (1978): Types of morphogenesis of the dermal skeleton in fossil sharks. - *Palaont. Z.*, 52, 1/2: 110-128, 10 figs. Stuttgart.
- REIFF, W. (1938): Obere bunte Estheriensichten, Schilfsandstein und Dunkle Mergel im mittleren Württemberg. - *Tübinger geogr. geol. Abh.*, 1, 26. Rau, Öhringen.
- RIEPEL, O. (1981): The hybodontiform sharks from the Middle Triassic of Mte. San Giorgio, Switzerland. - *N. Jb. Geol. Paläont., Abh.* 161, 3: 324-353, 14 figs., 1 table. Stuttgart.
- ROLLE, F. (1858): Ueber einige an der Grenze von Keuper und Lias in Schwaben auftretende Versteinerungen. - *Sber. Akad. Wiss. Wien*. 26: 13-32. Wien.
- SCHMID, E. E. (1861): Die Fischzähne der Trias bei Jena. - *Nova Acta Akad. Leop. - Carol.*, 29, 9: 42 pp., 4 pls. Halle.
- SEILACHER, A. (1943): Elasmobranchier-Reste aus dem oberen Muschelkalk und dem Keuper Württembergs. - *N. Jb. Min. Geol. Paläont., Mh., B* (10): 256-271. Stuttgart.
- SHERLOCK, R. L. (1948): The Permo-Triassic Formations. - 367 pp., 16 figs. Hutchinson, London.
- SLAUGHTER, B. H. (1971): Mid-Cretaceous (Albian) therians of the Butler Farm local fauna, Texas. - In KERMACK, D. M. & KERMACK, K. A. (Eds.): *Early Mammals*. - *Zool. J. Linn. Soc.*, 50. Supplement 1: 131-143, 10 pls. London.
- STENSIÖ, E. A. (1921): Triassic fishes from Spitsbergen. - Part 1 307 pp. Vienna.
- STEWART, J. D. (1980): Reevaluation of the phylogenetic position of the Ptychodontidae. - *Trans. Kansas Acad. Sci.*, 83, 3: 154. Topeka. (Abstract only).
- SYKES, J. H., CARGILL, J. S. & FRYER, H. G. (1970): The stratigraphy and palaeontology of the Rhaetic Beds (Rhaetian: Upper Triassic) of Barnstone, Nottinghamshire. - *Mercian Geol.* 3, 3: 233-264, pls. 15-18, 5 figs. Nottingham.
- THIES, D. (1983): Jurazeitliche Neoselachier aus Deutschland und S-England. - *Cour. Forsch.-Inst. Senckenberg*, 58, 117 pp., 11 figs., 15 tables. Frankfurt.
- THOMSON, K. S. (1982): An Early Triassic Hybodont shark from Northern Madagascar. - *Postilla No. 186*: 1-15, 8 figs. New Haven.
- THÜRACH, H. (1888): Übersicht über die Gliederung des Keupers im nördlichen Franken. - *Geogn. Jh.* 1: 75-102. München.
- THURMOND, J. T. (1970): Lower vertebrates and paleoecology of the Trinity Group (Lower Cretaceous) in north-central Texas. - 127 pp., 34 figs. Unpublished Ph. D. thesis, Southern Methodist University.
- , — (1972): Cartilaginous fishes of the Trinity Group and related rocks (Lower Cretaceous) of north central Texas. - *Southeastern Geol.*, 13, 4: 207-227, 14 figs. Durham.
- , — (1974): Lower vertebrate faunas of the Trinity Division in north central Texas. - *Geosci. Man.*, 8: 103-129, 1 pl., 15 figs. Baton Rouge.
- TURNER, S. (1982): Middle Palaeozoic elasmobranch remains from Australia. - *J. Vertebr. Palaeont.* 2, 2: 117-131. Norman.
- , — (1983): Taxonomic note on "*Harpago*". - *J. Vertebr. Palaeont.*, 3, 1: 38.
- TWAY, L. E. & ZIDEK, J. (1983): Catalog of Late Pennsylvanian Ichthyoliths, Part II. - *J. of Vertebr. Palaeont.*, 2, 4: 414-438, 82 figs. Norman.
- WEIDENREICH, F. (1926): Über den Schmelz der Wirbeltiere und seine Beziehungen zum Zahnbein. (Knochenstudien V Teil. - *Z. Anat. Entwicklungsgesch.*, 79: 292-351. Leipzig.
- WILSON, E. (1890): Fossil types in the Bristol Museum. - *Geol. Mag.*, (3) 7: 363-372, 411-416. London.
- WINKLER, T. C. (1880): Description de quelques restes de poissons fossiles des terrains triasiques des environs de Wurzburg. - *Arch. Mus. Teyler*. 5: 109-149, pls. 5-9. Haarlem.
- WOODWARD, A. SMITH (1885): Chapters on fossil sharks and rays. IV. Cestraciontidae. - *Sci. Gossip*, May 1886: 106-109, figs. 71-84. London.
- , — (1887): Notes on some post-Liassic species of *Acrodus*. - *Geol. Mag.* (3) 4: 101-105. London.
- , — (1889): Catalogue of the fossil fishes in the British Museum (Natural History). 1 Elasmobranchii. - XLIV+474 pp., 17 pls. London.
- , — (1890): A synopsis of the Fossil Fishes of the English Lower Oolites. - *Proc. Geol. Ass.* 40, 6: 285-306, figs. 1-5, pl. 3. London.
- , — (1916): The Fossil Fishes of the English Wealden and Purbeck Formations. Part 1. - 1-48, 10 pls. *Mon. Palaeontogr. Soc.* 1916. London.
- ZANGERL, R. (1979): New chondrichthyes from the Mazon Creek Fauna (Pennsylvanian) of Illinois. - In NITCEKI, M. N. (ed.): *Mazon Creek Fossils*, p. 449-500. New York; Academic Press.
- , — (1981): Handbook of Paleoichthyology; vol. 3A. Chondrichthyes 1. - 114 pp., 116 figs. Gustav Fischer Verlag, Stuttgart.

Explanation of Plates

Plate 1

- Fig. 1. Tooth of *Lissodus selachos* (ESTES) from the Maestrichtian (Upper Cretaceous) of Wyoming, U.S.A., UC catalogue number 119288. a, lingual view; b, labial view; c, occlusal view; d, lateral view. Note the strong, upturned labial peg, low coronal profile with lateral cusplet development along the occlusal crest, and vascularisation of the root.
- Fig. 2. Teeth of *Lissodus crenulatus* (PATTERSON) and *Lissodus pustulatus* (PATTERSON) from the Wealden (Lower Cretaceous) of Chilton Chine, Isle of Wight. *L. crenulatus*: a, occlusal view of BM(NH) P. 60729; b, basal view of P. 60767; *L. pustulatus*: c, lingual view of P. 60768; d, lateral view of P. 60768; e, labial view of P. 60769; f, occlusal view of P. 60769; g, lateral view of P. 60769. Note the accessory cusps in *L. pustulatus*.
- Fig. 3. Teeth of *Lissodus striatus* (PATTERSON) from the Weald Clay of Henfield, Sussex. All specimens are housed in the BM(NH). P. 60726: a, occlusal view; b, lateral view; c, lingual view. P. 60727: d, labial view. Note the crenulate occlusal crest, weak labial peg and strong vertical striations.

Plate 2

- Fig. 1. "*Lonchidion rhizion*", an indeterminate fragment of uncertain affinity from the Ashdown Beds (Cliff End Bone Bed; Wealden, Lower Cretaceous) of Cliff End, Sussex, England. BM(NH) P. 47164 in a, ?posterior view; b, oblique posterior view; c, lateral view; d, surface view of the specimen after etching for three seconds in 2n Hydrochloric Acid. Note the lack of enameloid. The surface of the specimen comprises osteodentine.
- Fig. 2. Tooth of *Lissodus babulskii* (CAPPETTA & CASE) from the Upper Campanian (Upper Cretaceous) of Monmouth County, New Jersey, U.S.A. BM(NH) P. 60770 in a, lingual view; b, labial view; c, oblique occlusal view. Note the well developed labial peg and smooth, though very worn, crown.
- Fig. 3. BCM Cc 735, the neotype of *Lissodus minimus* (AGASSIZ) from the Rhaetic Bone Bed basal to the Westbury Beds, Penarth Group, Rhaetian, Upper Triassic of Aust Cliff, Avon, England. a, labial view; b, lingual view; c, occlusal view; d, lateral view.

Plate 3

- Fig. 1. The holotype of *Lissodus africanus* (BROOM) from the Upper Beaufort Series (Lower Triassic) of Becker's Kraal, Orange Free State, South Africa. SAM 1082, a virtually complete fish in left lateral view.
- Fig. 2. The ultrastructure of the enameloid of *Lissodus minimus* (AGASSIZ). a, the enameloid/dentine junction close the occlusal crest in a broken specimen, etched with 2n HCl for 3 seconds; b, radial groups of single apatite crystallites; c, single crystallite enameloid in surface view.

Plate 4

- Fig. 1. Specimen of *Lissodus africanus* (BROOM) from the Upper Beaufort Series (Lower Triassic) of Becker's Kraal, Orange Free State, South Africa. BM(NH) P. 16039, the anterior part of a fish in left lateral view, including the first dorsal fin spine, skull and anterior body outline, and three lateral teeth from the right lower dentition. Scale as for figure 2.
- Fig. 2. *Lissodus africanus* (BROOM), BM(NH) P. 17531 from the Lower Triassic of Becker's Kraal, South Africa. Articulated parts of the dentition are just visible in the top left of the photograph. The mid-body region and presumed second dorsal fin spine are also preserved.
- Fig. 3. An isolated crown of *Lissodus leiodus* (SMITH WOODWARD) from the Great Oolite (Bathonian, Middle Jurassic) of Stonesfield, Oxfordshire, England. BM(NH) P. 2134 in oblique occlusal view.
- Fig. 4. Isolated crown of *Lissodus leiodus* (SMITH WOODWARD); BM(NH) P. 10110 in occlusal view; locality and horizon unknown. Note the crown shape, heavy antemortem wear and coarse vertical striations.
- Fig. 5. Isolated crown of *Lissodus levis* (SMITH WOODWARD) from the Gault (Lower Cretaceous) of Folkestone, Kent, England. BM(NH) P. 11b in labial view. Note the fairly high central cusp and vertical striation development.
- Fig. 6. Isolated tooth of *Lissodus levis* (SMITH WOODWARD) from the Gault Clay (Lower Cretaceous) of Folkestone, Kent. BM(NH) P. 17 in labial view. Note the root vascularisation and reduction in size of the labial peg.

Plate 5

- Fig. 1. Specimens of *Lissodus nodosus* (SEILACHER). All specimens are mesial teeth from the Norian (Upper Triassic) of southern Germany, and housed in the SEILACHER Collection, Staatliches Museum für Naturkunde in Stuttgart. a, 50.211 in lingual view (x 40); b, 50.211 in oblique lingual view (x 50); c, 50.212 in lingual view (x 30); d, 50.212 in oblique basal view (x 28); e, 50.213 in occlusal view (x 45); f, 50.214 in occlusal view (x 32); g, 50.214 in lingual view (x 32); h, 50.214 in labial view (x 33); i, 50.214 in lateral view (x 33).

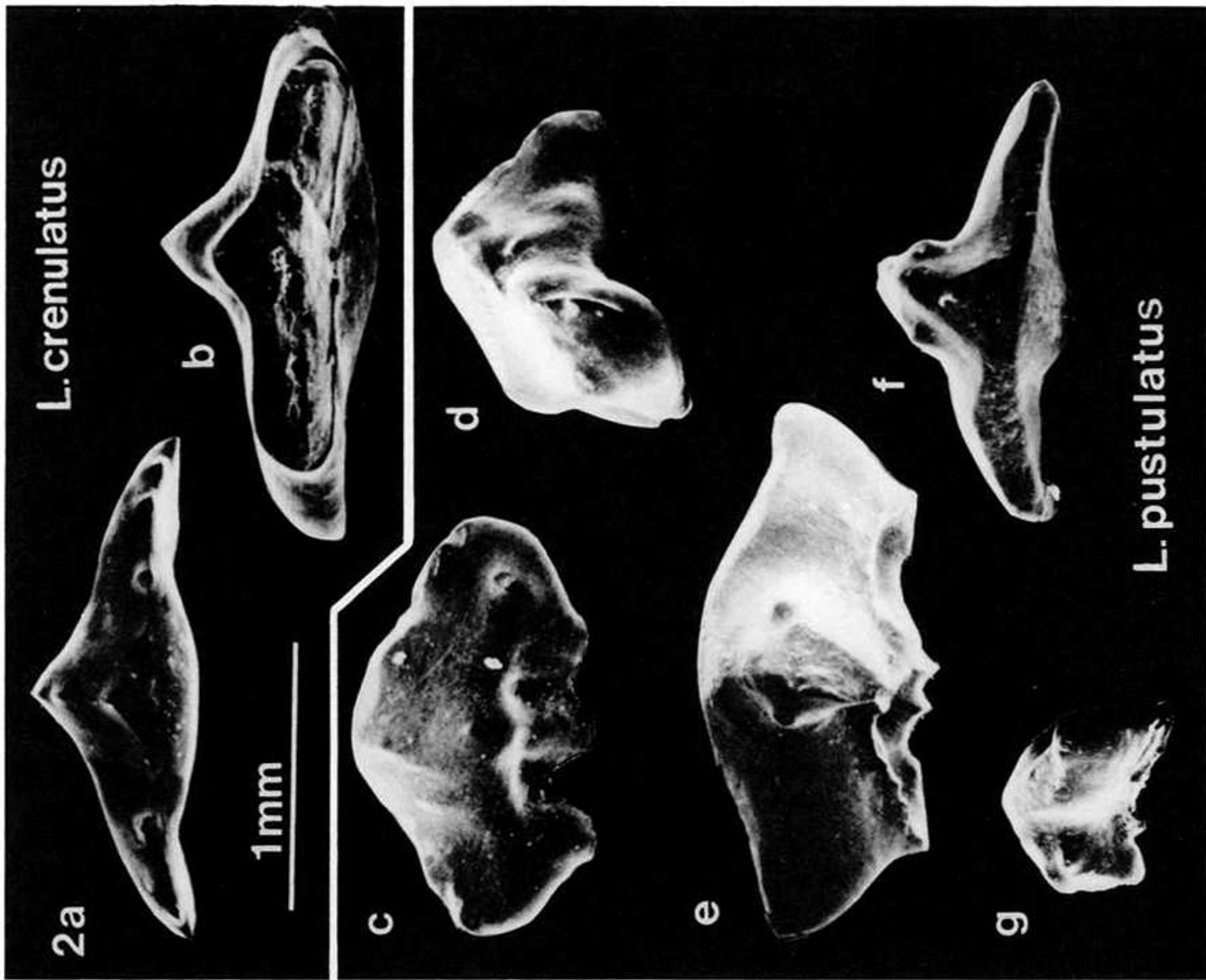
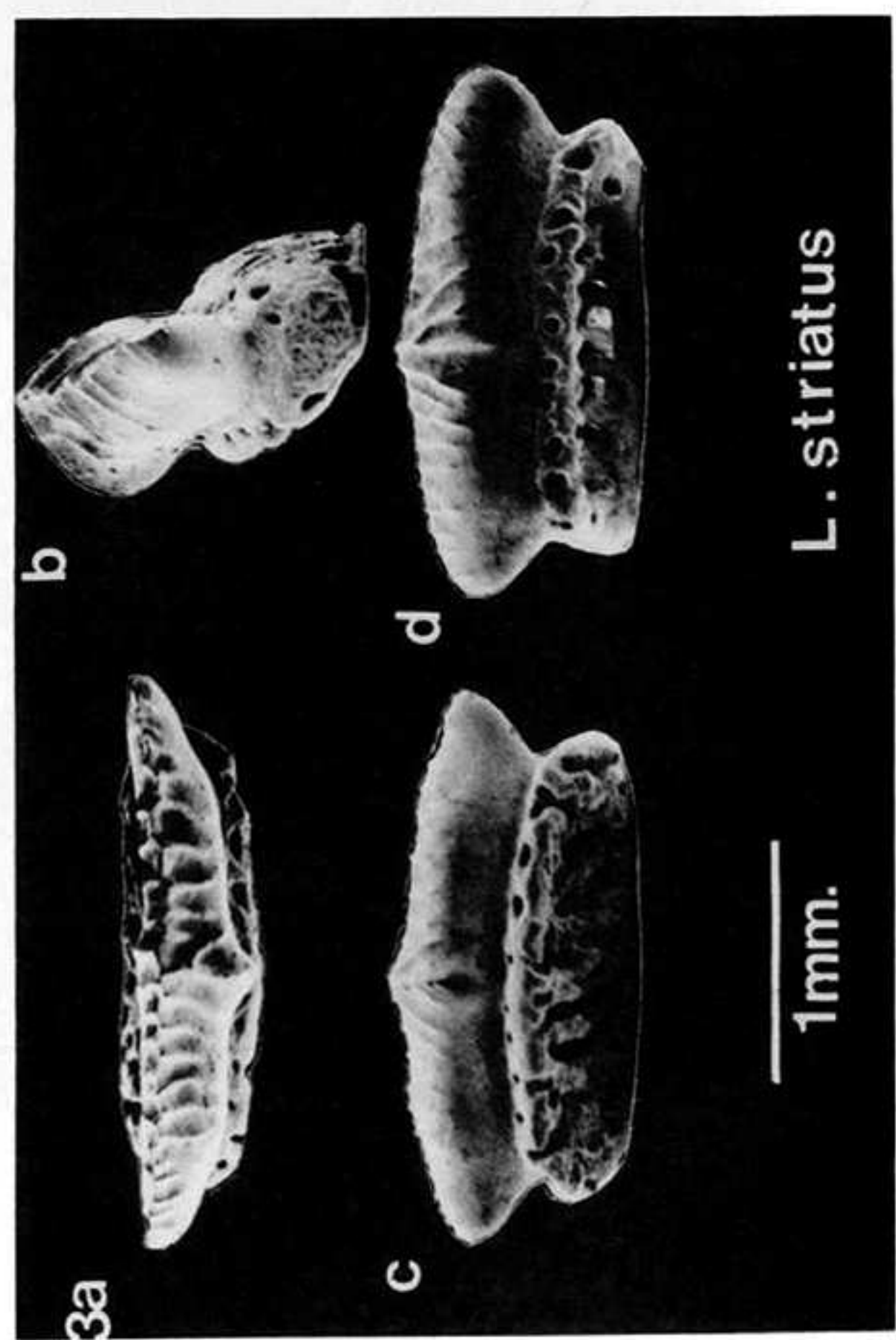
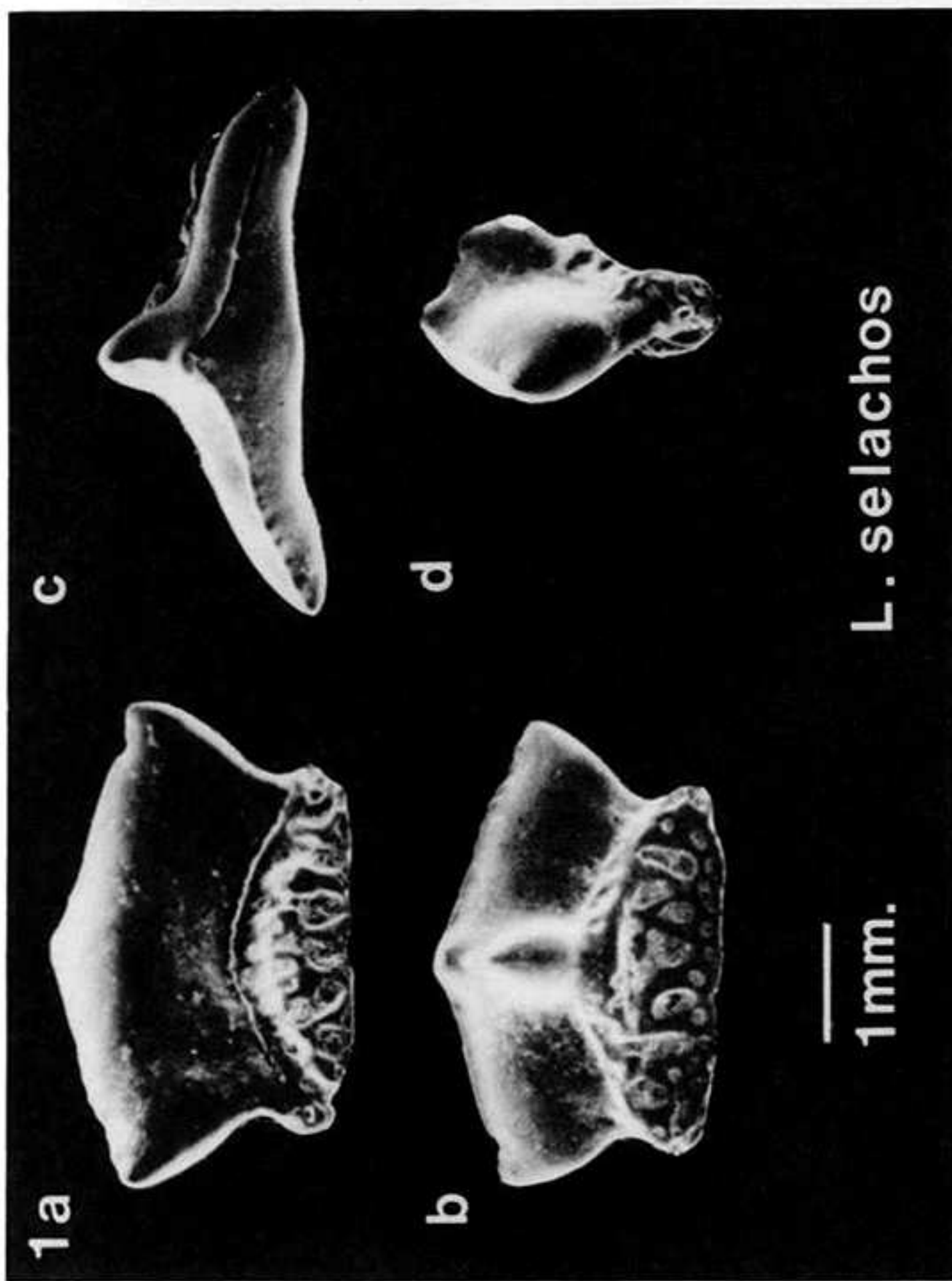
- Fig. 2. Mesial and anterolateral teeth of *Lissodus nodosus* (SEILACHER) from the Norian (Upper Triassic) of southern Germany. All specimens are housed in the SEILACHER Collection, SMNS. a, 50.215 in occlusal view, showing functional wear (x 70); b, 50.216 in lingual view, showing well developed medial wear facet produced by contact with the labial peg of the tooth in the succeeding position in the same tooth row, (x 50); c, 50.216 in basal view (root detached), x 50; d, 50.216 in labial view (x 58); e, 50.216 in lateral view (x 50); f, 50.217 in labial view (x 25); g, 50.217 in oblique basal view (x 45); h, 50.218 in oblique occlusal view (x 26); 50.211 in occlusal view (x 50).

Plate 6

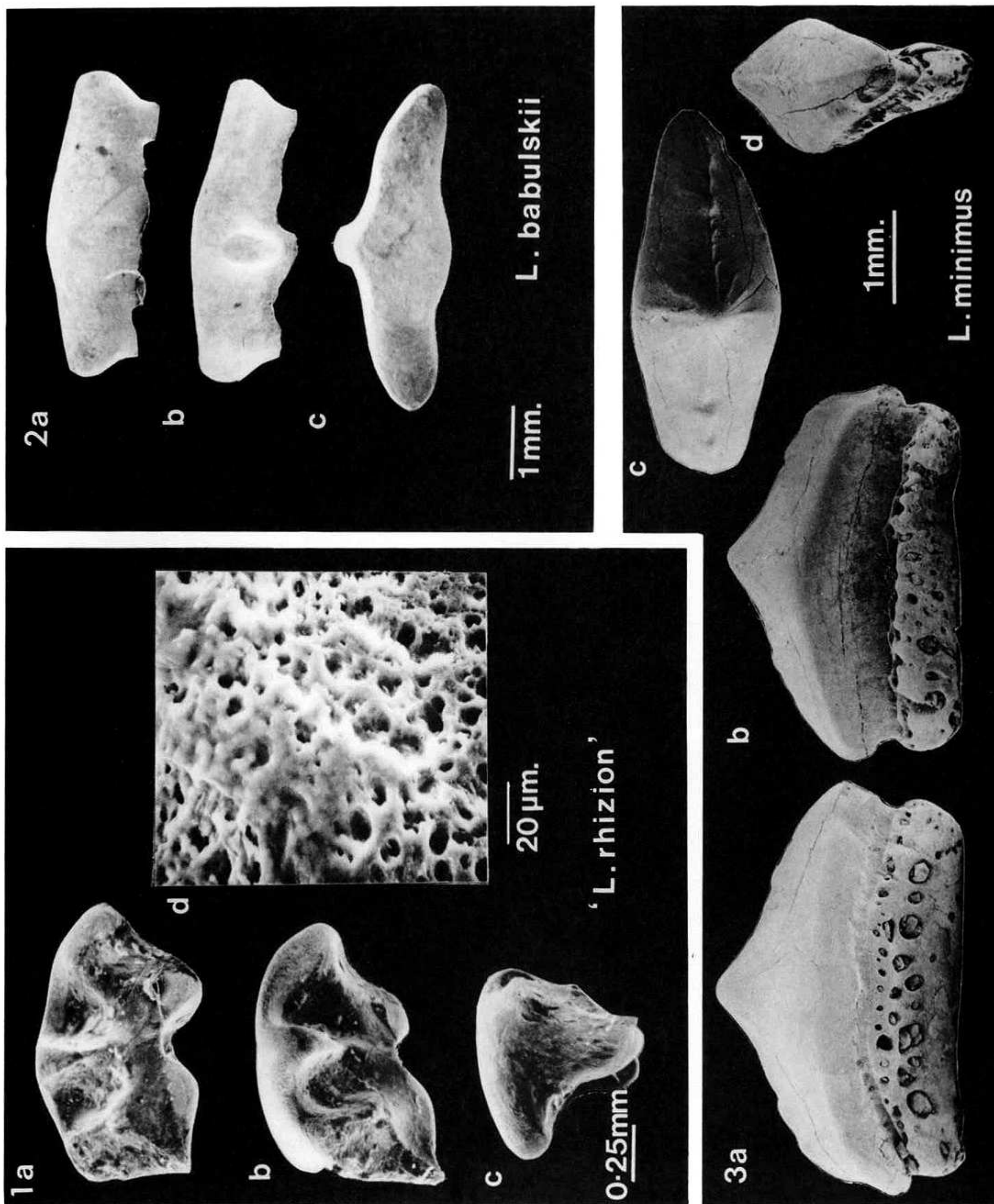
- Fig. 1. Lateral teeth of *Lissodus nodosus* (SEILACHER) from the Norian (Upper Triassic) of southern Germany. All specimens are held in the SEILACHER Collection, SMNS. a, 50.210 in labial view (x 25); b, 50.210 in oblique basal view (x 25); c, 50.206 in labial view (x 25); d, 50.206 in oblique basal view (x 24); e, 50.209 in labial view (x 20); h, 50.209 in occlusal view (23).
- Fig. 2. Tooth of *Lissodus anitae* (THURMOND) from the Paluxy Formation (Albian, Lower Cretaceous) of Butler Farm, Wise County, Texas, U.S.A. SMU-SMP 62146 in a, occlusal view; b, labial view; c, lingual view; d, oblique lateral view; e, basal view. Note the very strong labial peg and smooth, though badly worn crown.
- Fig. 3. Tooth of *Lissodus wardi* n. sp., from the Forest Marble (Bathonian, Middle Jurassic) of Watton Cliff, Dorset, England. BM(NH) 58701 (Holotype) in a, lingual view; b, labial view; c, occlusal view; d, lateral view.

Plate 7

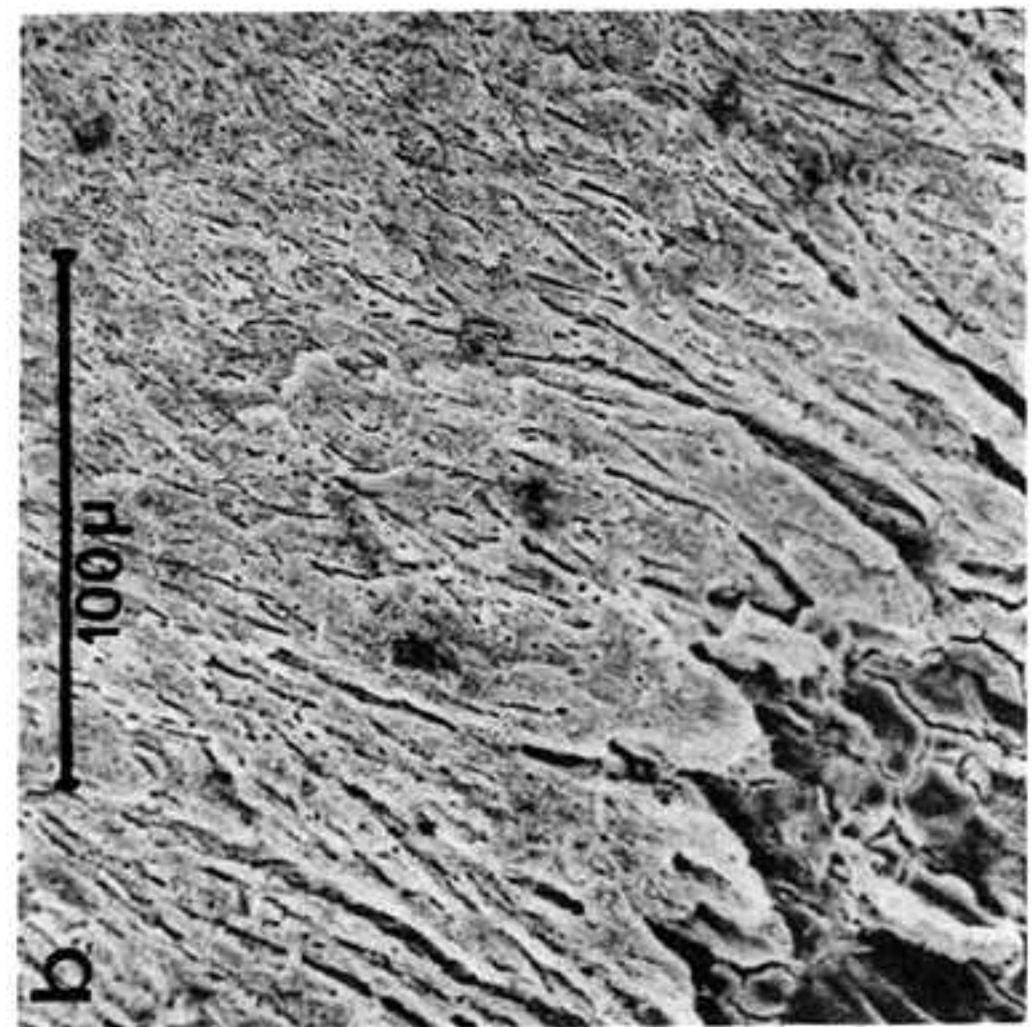
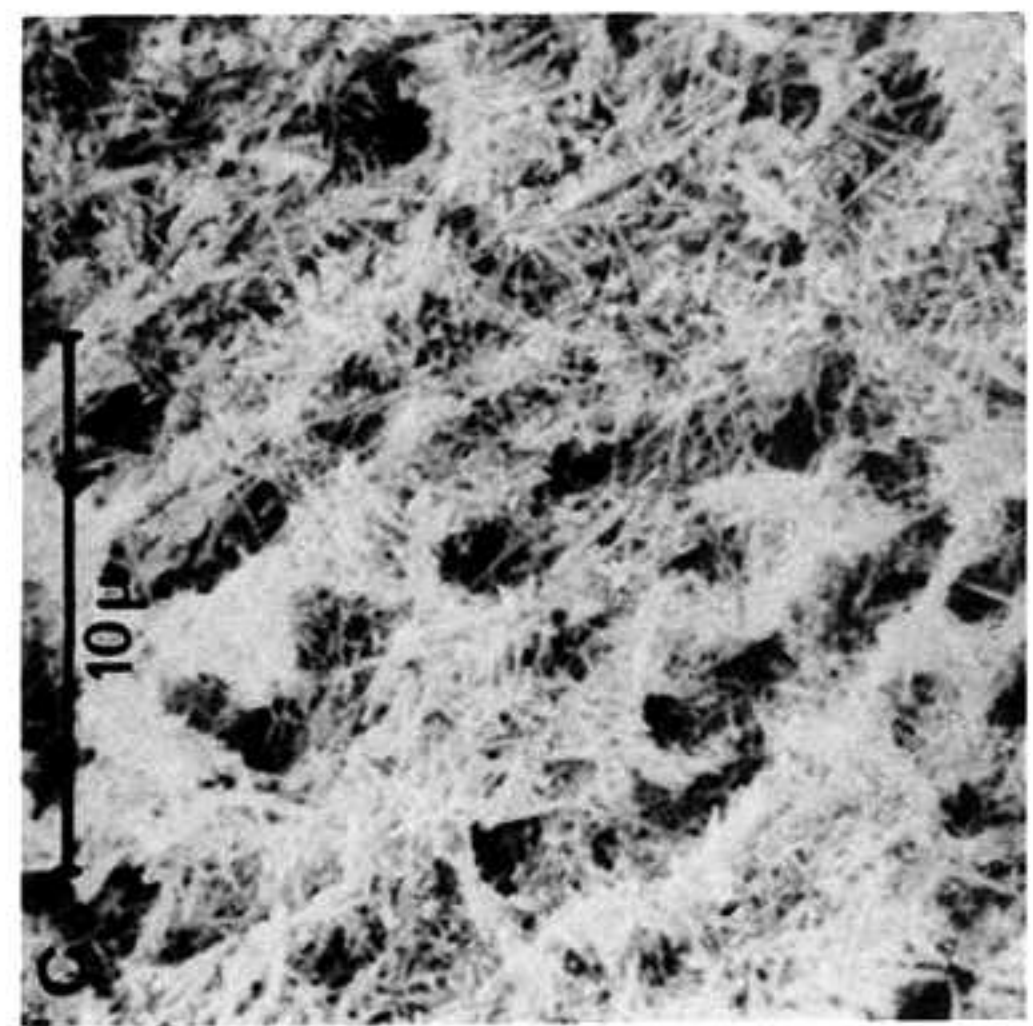
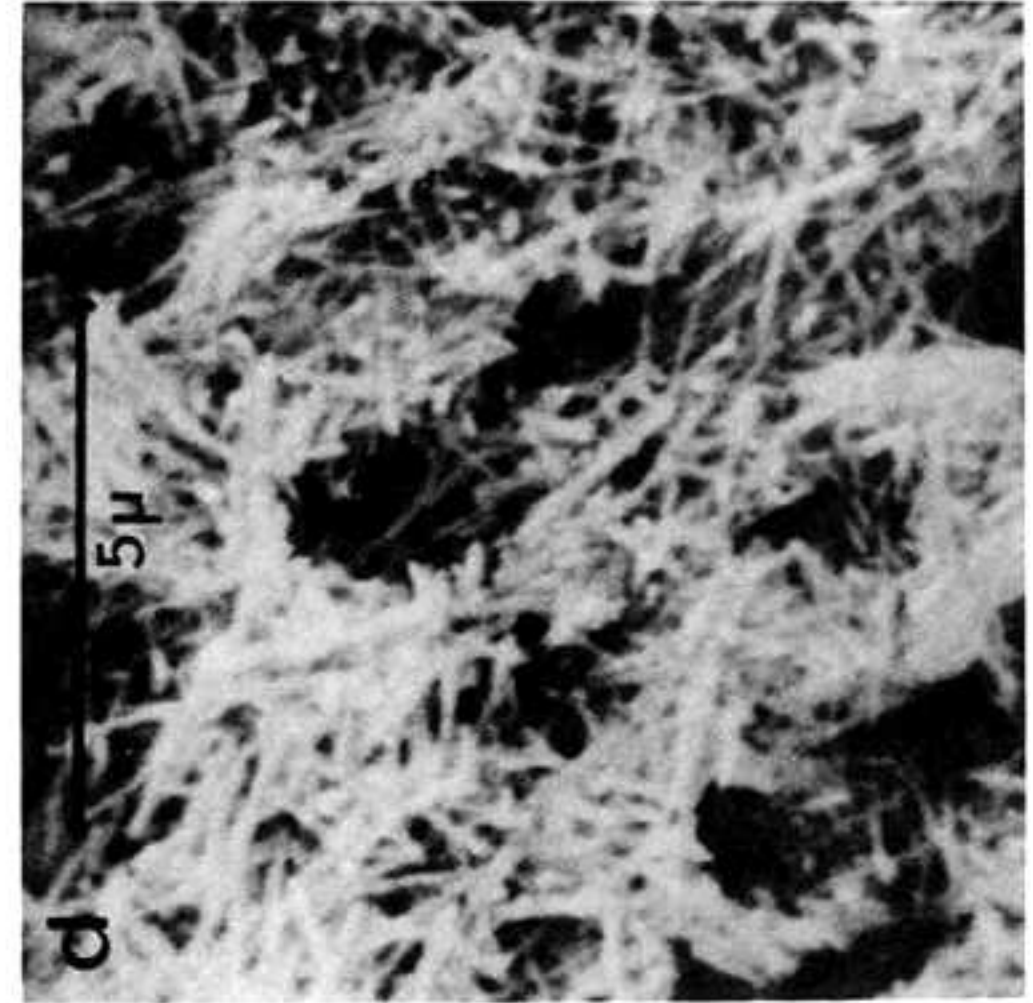
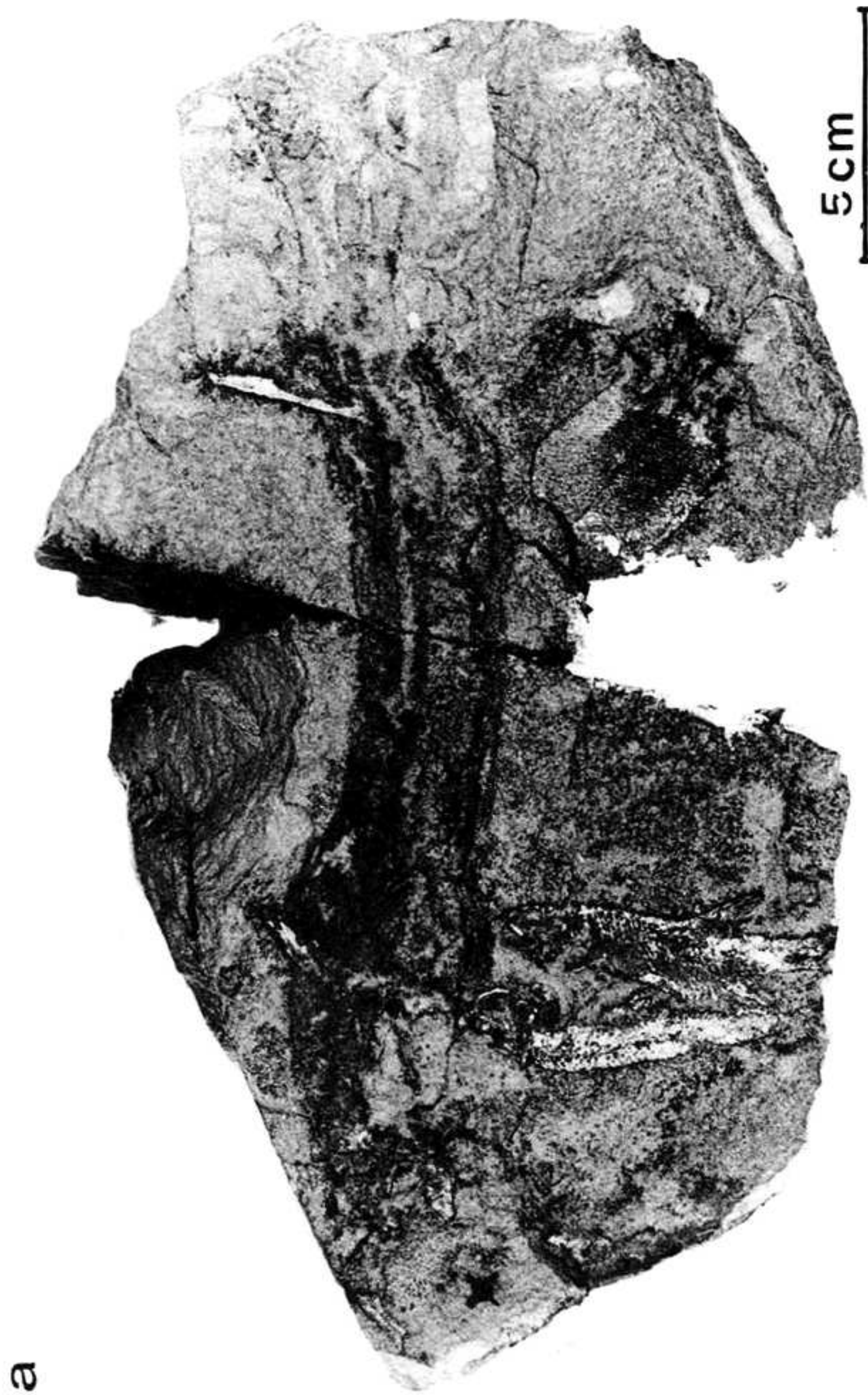
- Fig. 1. Teeth of *Lissodus pattersoni* n. sp., from the Forest Marble (Bathonian, Middle Jurassic) of Watton Cliff, Dorset, England. All specimens housed in BM(NH). a, Holotype (P. 58698), a mesial tooth, in lateral view; b, P. 58698 in lingual view; c, holotype in basal view; d, holotype in oblique lateral view; e, P. 58699 in labial view; f, P. 58699 in lingual view; g, P. 58699 in occlusal view; h, P. 58699 in lateral view; i, P. 60734 in labial view; j, same specimen in basal view; k, same specimen in occlusal view. Note the well developed lateral cusplets, labial nodes and low labial peg supported by the upper labial root face in mesial teeth.
- Fig. 2. Teeth of *Lissodus weltoni* n. sp., from the Cenomanian (Upper Cretaceous) of Suplee, Crook County, Oregon, U.S.A. Figures a-d, P. 60775; a, occlusal view; b, labial view; c, lingual view; d, lateral view. Figures e-h, P. 60772 (Holotype); e, lingual view; f, occlusal view; g, labial view; h, lateral view. Figures i-k, P. 60774; i, occlusal view; j, lingual view; k, lateral view. All specimens are held in the BM(NH).



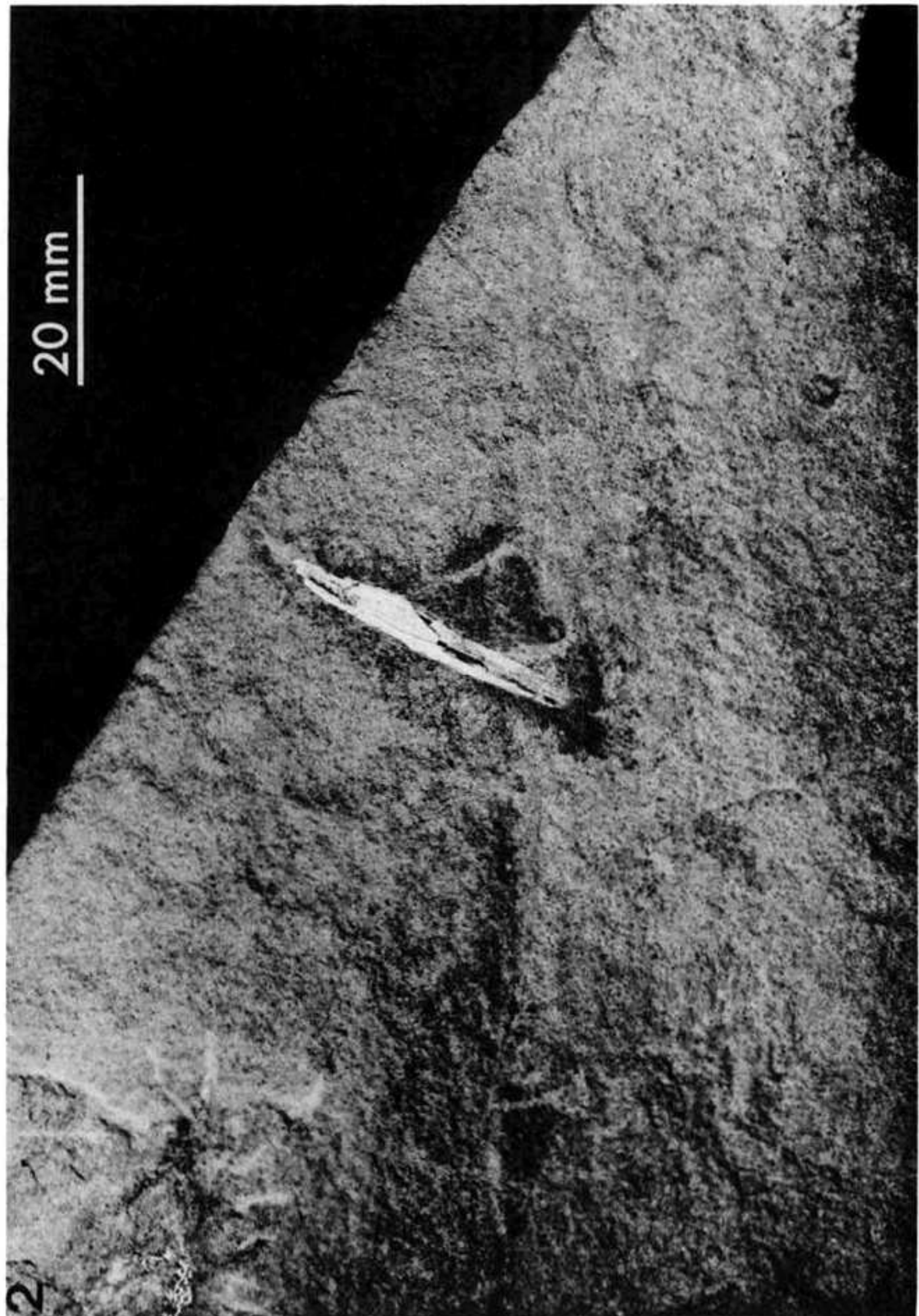
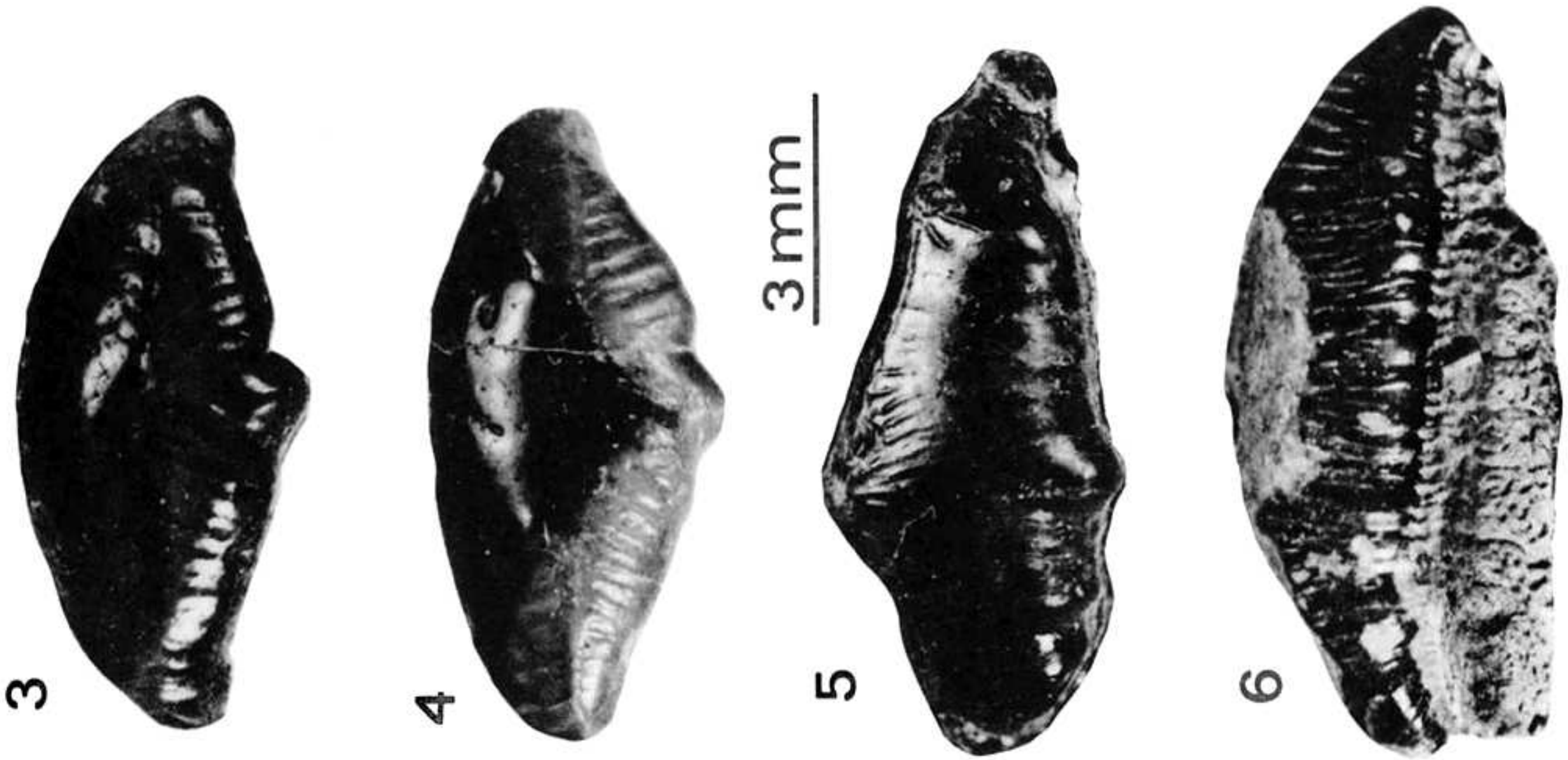
C. J. Duffin: Revision of the hybodont Selachian: Genus *Lissodus* BROUGH (1935).



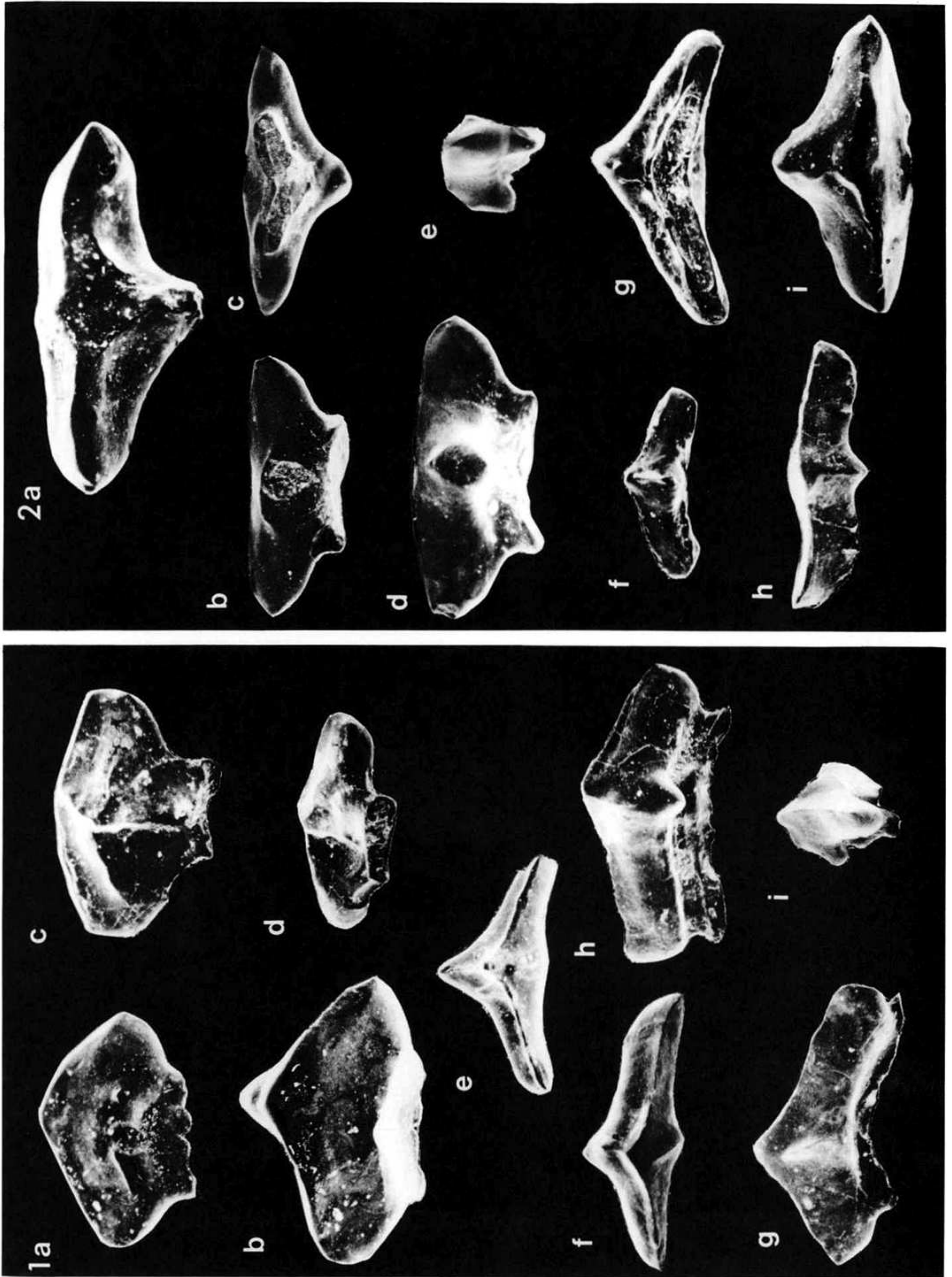
C. J. Duffin: Revision of the hybodont Selachian: Genus *Lissodus* BROUGH (1935).



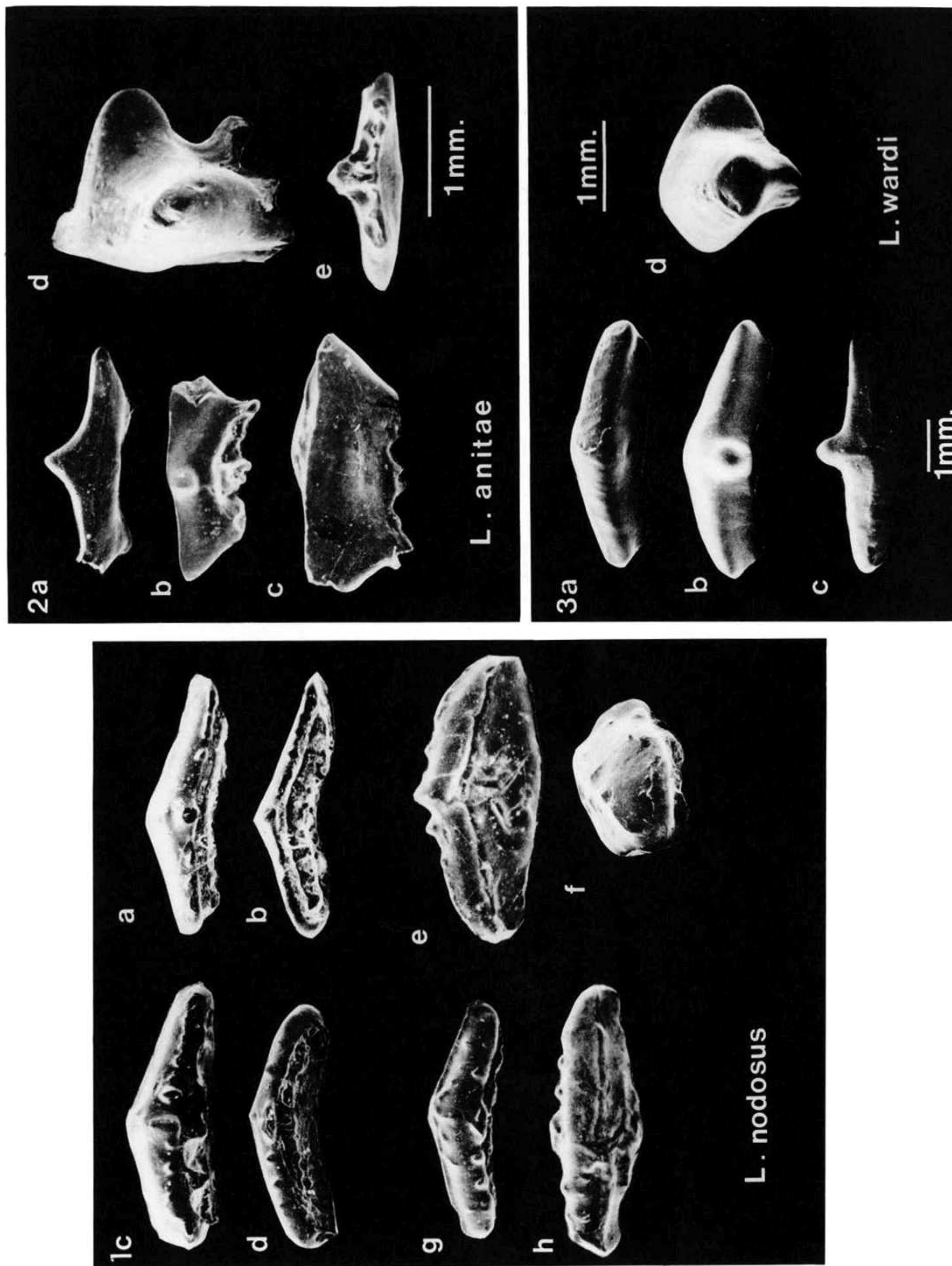
C. J. Duffin: Revision of the hybodont Selachian: Genus *Lissodus* BROUGH (1935).



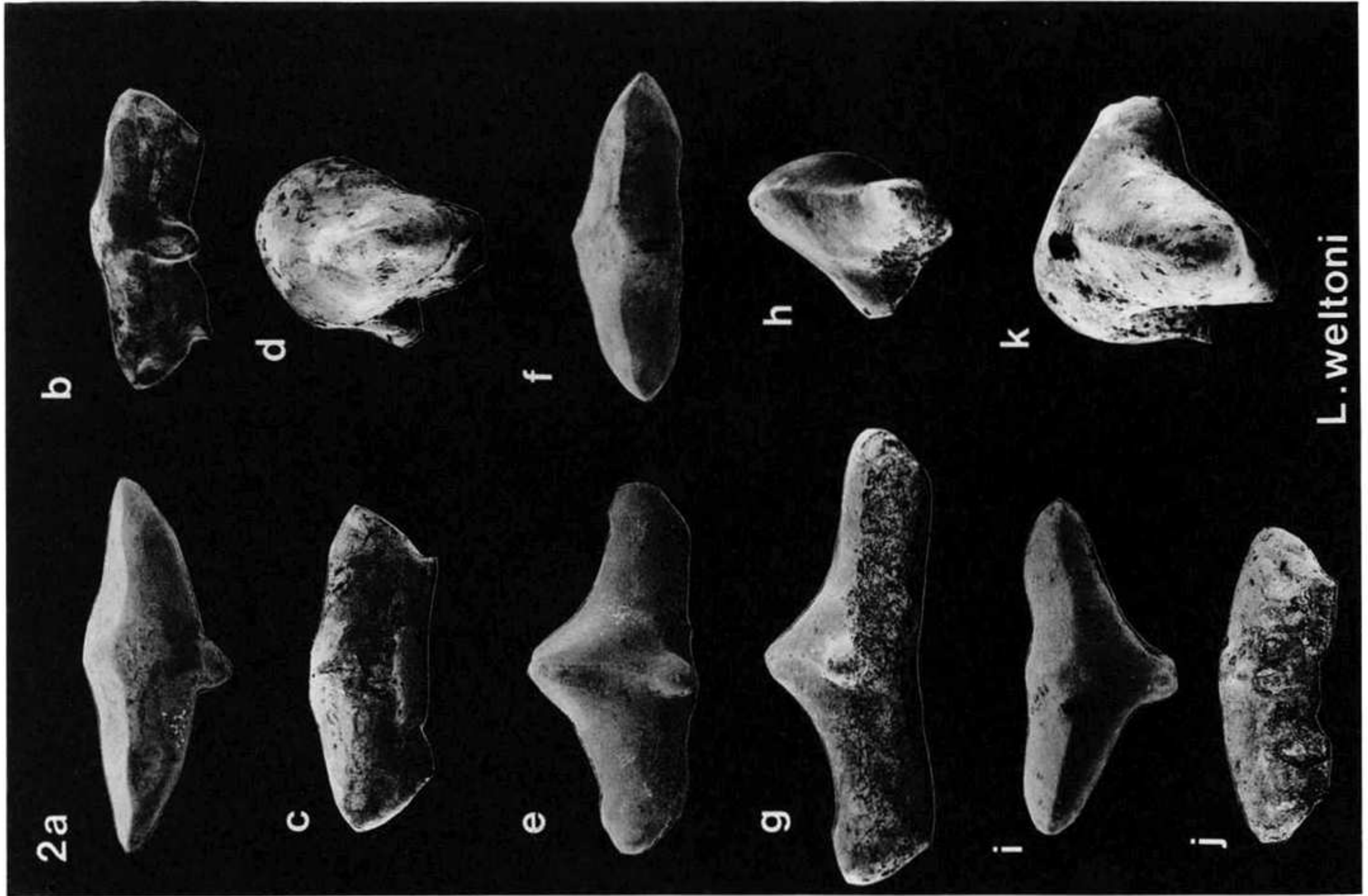
C. J. Duffin: Revision of the hyodont Selachian: Genus *Lissodus* BROUGH (1935).



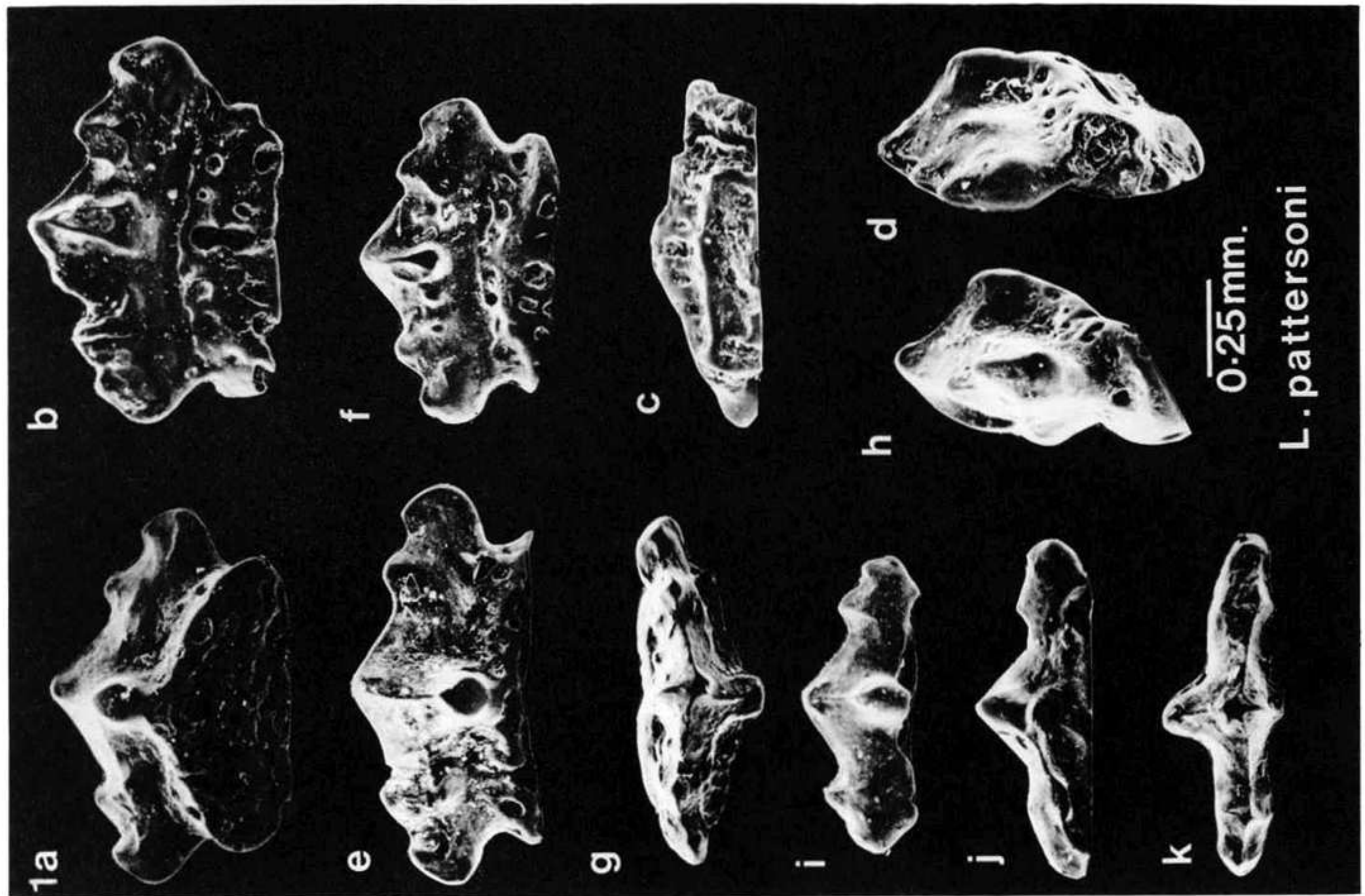
C. J. Duffin: Revision of the hybodont Selachian: Genus *Lissodus* BROUGH (1935).



C. J. Duffin: Revision of the hybodont Selachian: Genus *Lissodus* BROUGH (1935).



L. weltoni



L. pattersoni

C. J. Duffin: Revision of the hybodont Selachian: Genus *Lissodus* BROUGH (1935).