

Teeth of the fossil shark *Annea* THIES 1983 (Elasmobranchii, Neoselachii) from the Toarcian of Belgium

by

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Abstract: Teeth of the fossil shark *Annea* THIES 1983 (Neoselachii, Orectolobiformes) were discovered in the Toarcian of Belgium. The teeth belong to a new species: *A. maubeugei* sp. nov. *Annea* was previously known only from the Aalenian and Bajocian of NW Germany. The teeth from the Toarcian of Belgium provide further support for the validity of the genus *Annea* and extend its palaeogeographical and stratigraphical range.

Key words: Elasmobranchii - Orectolobiformes - *Annea* - Middle Toarcian - Belgian Lorraine.

Résumé: Des dents du requin fossile *Annea* THIES 1983 (Neoselachii, Orectolobiformes) ont été découvertes dans le Toarcien de Belgique. Les dents appartiennent à une nouvelle espèce: *A. maubeugei* sp. nov. Auparavant, *Annea* était uniquement connue de l'Aalénien et du Bajocien d'Allemagne Nord Occidentale. Les nouveaux spécimens du Toarcien belge confirment à nouveau la validité du genre *Annea* et étendent sa distribution paléogéographique et stratigraphique.

Mots-clefs: Elasmobranchii - Orectolobiformes - *Annea* - Toarcien moyen - Lorraine belge.

Kurzfassung: Zähne der fossilen Haifischgattung *Annea* THIES 1983 (Neoselachii, Orectolobiformes) sind im Toarcium Belgiens entdeckt worden. Die Zähne werden einer neuen Art., *A. maubeugei* sp. nov., zugeordnet. Die Gattung *Annea* war zuvor nur aus dem Aalenium und Bajocium Nordwestdeutschlands bekannt. Die neuen Funde bekräftigen die Gültigkeit der Gattung *Annea*, erweitern ihre paläogeographische Verbreitung und vergrößern ihre stratigraphische Reichweite.

Schlüsselwörter: Elasmobranchii - Orectolobiformes - *Annea* - Mittel Toarcium - Belgische Lothringen.

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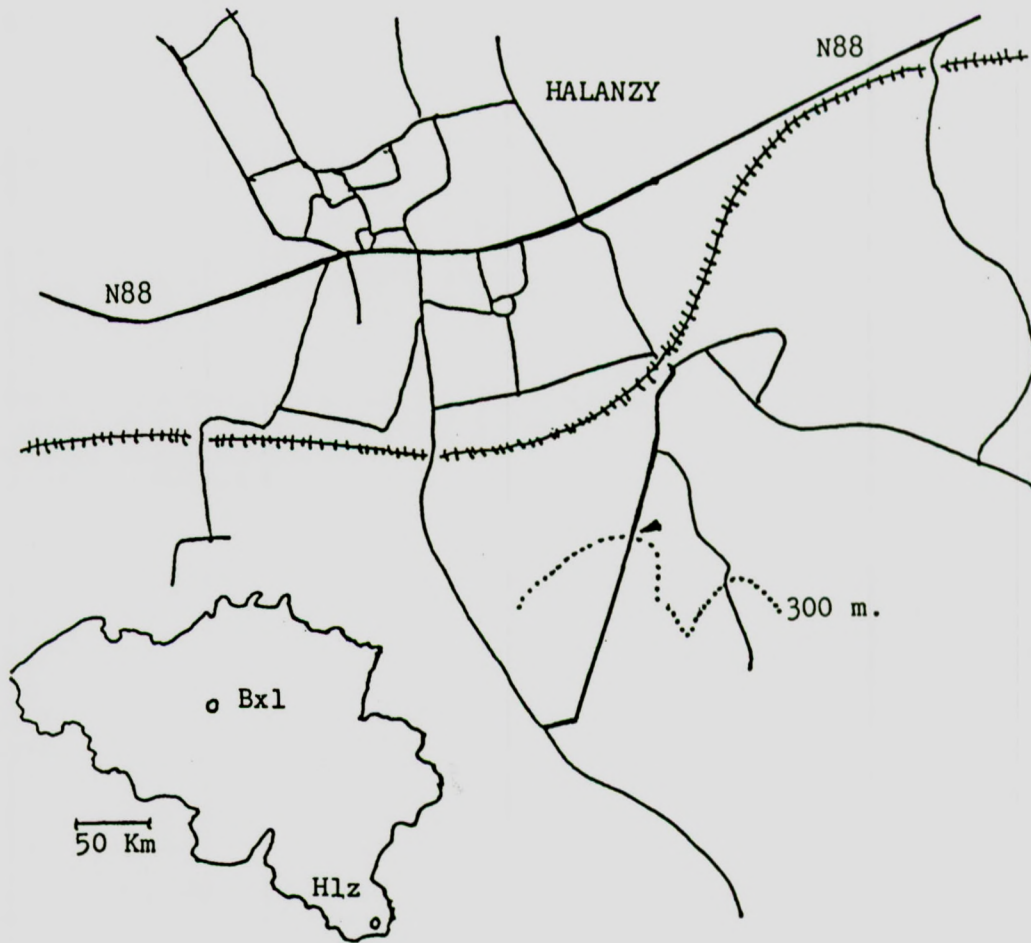
Introduction

The fossil orectolobiform shark *Annea* was first described by THIES (1983) based on a single oral tooth from the Middle Jurassic (Upper Aalenian) of Moorberg near Hannover (NW Germany). The knowledge of *Annea* was subsequently widened on the basis of further material from the Upper Aalenian of Moorberg and Goslar (NW Germany, THIES 1989) and from the Lower Bajocian of Emmerke near Hildesheim (NW Germany, THIES 1993). All the teeth of *Annea* found so far combine the typical dental morphology of orectolobiforms (i.e. development of a multicuspid crown provided with an apron and an uvula, possession of a hemiaulacorhize root) with the presence of a characteristic median vertical keel on the main cusp, extending from the tip of the cusp to the base of the apron. Apart from some fragmentary, specifically indeterminable teeth the German material was attributed to a single species - *Annea carinata* THIES 1983.

Recently, teeth of *Annea* were also discovered in the Toarcian of Belgium. The new material differs morphologically from *A. carinata* and represents a new species. It is the aim of this paper to describe the new material and to discuss its significance in terms of systematics, stratigraphy, and palaeobiogeography.

Locality and stratigraphy

Locality: The material originates from an outcrop SE of the "Rue des Vergers" E of the village of Halanzy (Aubange) in SE Belgium (Textfigure 1). The locality is described as "Sondage 1: 195 mètres au Sud de l'embranchement du chemin montant vers le Sud-Est. Cote approx.: 300 mètres. Prairie en bord de route. (côté Est)" in DELSATE (1990: 17). Grid reference: Carte géologique 1/40.000, feuille de Musson-Aubange; Long. East 5°45'10", Lat. North 49°38'23".



Textfigure 1. Sketch map of the locality.

Stratigraphy: The material was collected from a 15-30 cm thick, brown, conglomeratic horizon rich in phosphates. The horizon occurs at the top of the *Hildoceras bifrons* blue marls and bears the ammonites *Catacoeloceras crassum* and *Haugia variabilis*, the belemnites *Dactyloteuthis* sp. and *Acrocoelites* sp., and the bivalve *Astarte voltzi*. Through the ammonite fauna the horizon is interpreted as a condensed layer comprising the top of the *Hildoceras bifrons* zone (*Zugodactylites braunianum* subzone) and the *Haugia variabilis* zone. The horizon has previously been described from the French and Luxembourg Lorraine by MAUBEUGE (1955, 1958). French scholars (ELMI 1967, POMEROL 1975) subdivide the Toarcian into a lower, middle and upper part with the *Hildoceras bifrons* and *Haugia variabilis* zones forming the Middle Toarcian. By contrast, English (DEAN, DONOVAN & HOWARTH 1961) and German authors (HOFFMANN 1968, SCHLEGELMILCH 1976, BRACHMANN 1989) do not recognize a Middle Toarcian. Instead, they consider the *Haugia variabilis* zone as the base of the Upper Toarcian, which contains the *Haugia variabilis* zone (tc2a), the *Grammoceras*

thouarsense zone (tc2b), and the *Dumortieria levesquei* zone (tc2c)). A detailed description of the locality and the section containing the horizon bearing the teeth of *Annea* is given by DELSATE (1990).

Apart from the Belgian locality of Halanzy, some teeth of *Annea* were also recovered from the French Toarcian locality of Longlaville near Longwy (in the neighbourhood of Halanzy), where the same horizon occurs. However, the Belgian locality of Halanzy has provided better-preserved material.

Methods and material

Methods: The samples were digested in an aqueous solution of liquid soap. Then the sediment was washed and sieved using meshes with mesh widths of 3.0 and 0.3 mm. The carbonate was removed from the residue by applying a 10 % acetic acid solution which was buffered with tricalcic phosphate for one hour. The concentrated residue was washed again, dried, and sorted under a binocular microscope for sharks teeth.

Material: The material comprises 71 teeth of *Annea*. The material is housed in the collection of the Institut Royal des Sciences Naturelles de Belgique (IRSNB) under the catalogue numbers mentioned in the text. Further material is present in the private collection of D. DELSATE.

Systematic Palaeontology

The terminology used in the description of the new material follows CASIER (1947) and CAPPETTA (1987).

Class Chondrichthyes
Subclass Elasmobranchii
Cohort Neoselachii
Superorder Galeomorphii
Order Orectolobiformes
Inc. fam.

Genre *Annea* THIES, 1983

Type species: *A. carinata* THIES 1983 from the Upper Aalenian of NW Germany.

Generic diagnosis: see THIES (1983, 1989).

The new material from the Toarcian of Belgium necessitates a revision of the generic diagnosis with respect to the development of the uvula.

Revised diagnosis (based on oral teeth only): Crown with cusp and one or two pairs of lateral cusplets. Apron and uvula present. Uvula narrow and tongue-shaped or bulbous and bulky. Labial surface of the crown with a prominent vertical keel over cusp and apron. Root hemiaulacorhize.

Differential diagnosis: see THIES (1989).

The teeth of *Annea* were said by THIES (1989) to differ from all other neoselachian teeth due to the presence of a vertical keel extending over the labial surface of the central cusp and apron. This is not correct. WERNER (1989) has shown that a similar keel also occurs in the fossil rajiforms *Onchopristis numidus*, *Baharipristis bastetiae*, *Sechmetia aegyptiaca*, and *Renpetia labiicarinata*, all from the Cenomanian of Egypt. A vertical labial keel is also present in the oral teeth of some other fossil rajiforms such as *Ctenopristis nougareti* (Maestrichtian of Morocco), *Ischirhiza hartenbergeri* (Maestrichtian of Bolivia), and *Sechmetia cruciformis* (= *Onchopristis dunklei*, Cenomanian of the U. S. A.) (CAPPETTA 1987). The teeth of the above rajiforms differ, however, from *Annea* in having a batomorph (i. e. holaulacorhize) root.

Revised differential diagnosis (based on oral teeth only): Presence of a prominent vertical keel on the labial surface of the tooth crown extending over cusp and apron together with a hemiaulacorhize root.

Previously published material:

THIES 1983: pl. 10, fig. 7. Holotype of *Annea carinata* (tooth of 0,85 mm mesiodistal width). Depository: Naturmuseum Senckenberg, Frankfurt-am-Main, cat. no. SMF 7144. Upper Aalenian of Moorberg near Hannover, NW Germany.

THIES 1989: fig. 6-7. *Annea carinata* (2 teeth). Depository: Tooth in fig. 6 - Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover, cat. no. BGR 14063; Upper Aalenian or Lower Bajocian of Goslar, NW Germany. Tooth in fig. 7 - Institut für Geologie und Paläontologie der Universität Hannover, cat. no. IGPH 88-II-6; Upper Aalenian of Moorberg near Hannover, NW Germany.

THIES 1989: fig. 8-10. *Annea* sp. (3 teeth). Depository: Institut für Geologie und Paläontologie der Universität Hannover; cat. no. IGPH 88-II-7, IGPH 88-II-8, IGPH 88-II-9; Upper Aalenian of Moorberg near Hannover, NW Germany.

THIES (1993): fig.1. *Annea carinata* (1 tooth). Depository: Institut für Geologie und Paläontologie der Universität Hannover, cat. no. IGPH 1991-II-1. Early Bajocian of Emmerke near Hildesheim, NW Germany.

The new material from Belgium:

Annea maubeugei sp. nov.

Derivatio nominis: Dedicated to Dr. Sc. P. L. MAUBEUGE (Nancy), in recognition of his work on the Lorraine Jurassic.

Holotype: The specimen in Pl. 1.

Depository: IRSNB, cat. no. P6238.

Type locality: Halanzy (Aubange, Belgian Lorraine), Rue des Vergers.

Type horizon: Conglomeratic marl bed of 15-30 cm thickness, bearing the ammonites *Catacoeloceras crassum* and *Haugia variabilis*.

Lithology: Phosphatic, conglomeratic marls.

Age: Early Jurassic, Middle Toarcian, upper *Hildoceras bifrons* zone (*Zugodactylites braunianus* subzone) and *Haugia variabilis* zone.

Other specimens: Teeth in Pl. 2 to 8 (paratypes 1 to 12, depository: IRSNB, cat. nos. P6239 to 6250), additional specimens in the collection of the IRSNB, cat. nos. P6251 to 6319).

Diagnosis (based on oral teeth only): Teeth of *Annea* having a crown with a central cusp and one pair of lateral denticles only. Uvula narrow, flat, and tongue-shaped. Root hemiaulacorhize.

Small teeth (of presumed younger individuals; teeth measuring less than 0,8 mm apicobasal crown height in labial view): crown of anterior and lateral teeth approximately as wide mesiodistally as high. Anterior vertical keel developed prominently and usually extending over cusp and apron. Apron peg-like and in labial view usually narrower than the basal part of the central cusp is wide mesiodistally. Lingual face of the central cusp bearing two paramedian oblique folds descending from the apex to the beginning of the uvula. Lateral cusplets bearing one to three vertical folds on the labial face and one or two such folds on the lingual face. Lateral cusplets widened mesiodistally, with a pyramidal shape in labial or lingual aspect. Cutting edge well developed over cusp and cusplets.

Large teeth (of presumed older individuals; teeth measuring more than 0,8 mm in apicobasal crown height in labial view): crown of anterior and lateral teeth clearly higher than wide mesiodistally. Vertical keel on labial face of central cusp less clearly developed than in smaller teeth, restricted to the cusp, not extending onto the apron. Apron usually more stubby than in smaller teeth, of semicircular outline and in labial view nearly as wide mesiodistally as the basal part of the central cusp. Ornamentation consisting of occasional vertical folds on the labial faces of cusp and cusplets. Paramedian oblique folds on the lingual face of the central cusp lacking or only weakly developed. Lateral cusplets still widened at their base, but less so than in smaller teeth and thus having a more slender appearance. Cutting edge interrupted or strongly reduced between cusp and lateral cusplets.

Differential diagnosis: The teeth of the new species differ from *A. carinata*, the type species and only other member of the genus, in the following characters: only one pair of lateral cusplets present (one to two in *A. carinata*), lateral cusplets of pyramidal shape in labial or lingual aspect (lateral cusplets much more slender and needle-like in *A. carinata*), uvula flat, narrow, and tongue-shaped (bulbous, bulky and rounded in *A. carinata*).

Description of the teeth:

Holotype (IRSNB P6238; Pl. 1)

The crown is wider than it is high. It has a central cusp, which is slightly inclined distally, and one pair of lateral cusplets. The vertical keel on the labial face is well defined, extending from the apex of the central cusp down to the lower extremity of the apron. The cutting edge is well developed. The apex of the central cusp is damaged. The apron is triangular in outline in labial view. In mesiodistal width it is clearly less wide than the basal part of the central cusp. The lingual face of the central cusp shows two oblique paramedian folds, descending to the beginning of the uvula. The uvula is narrow, flat and tongue shaped.

The lateral cusplets are of pyramidal shape, widened at their base, and have a well-developed cutting edge. The mesial cusplet is wider mesiodistally than the distal one. Each cusplet bears two oblique folds on the labial face. These are spaced more widely on the mesial cusplet. The distal cusplet bears one vertical fold on the lingual face. The mesial one bears two folds on the lingual face. These folds do not reach the apex of the cusplets. The root is hemiaulacorhize. The two root lobes form an angle of approximately 115°. Four small, rounded laterointernal foramina open on the lingual face of the root.

Dimensions: Mesiodistal width of the crown - 0,98 mm, height of the crown (measured from the tip of the apron to the apex of the central cusp) - 0,7 mm.

Position on the jaw: The lateral cusplets, which are of nearly equal size, and the central cusp, which is only slightly inclined distally, indicate an anterior or anterolateral position of the holotype on the jaw.

Paratype 1 (IRSNB P6239; Pl. 2, Fig. 1)

The central cusp is high and nearly straight. On its labial face the vertical keel runs from the apex of the central cusp to the apron. It shows a short interruption at the base of the cusp. The apron is rounded in shape. It is less wide mesiodistally than the central cusp. The distal cusplet is broken off. The labial face of the mesial cusplet is ornamented by one strongly developed oblique fold which is accompanied by two shorter folds. The lingual side of the main cusp shows two oblique paramedian folds running from the apex to the beginning of the uvula. A short median fold is present between the paramedian folds.

The root is hemiaulacorhize. Seven circular laterointernal foramina are present on the lingual side of the root. The mediointernal foramen is partially unroofed lingually.

Dimensions: Mesiodistal width of the crown - 0,76 mm, height of the crown (measured from the base of the apron to the apex of the central cusp) - 0,81 mm.

Position on the jaw: Having a higher central cusp and being smaller in mesiodistal width, paratype 1 presumably had a more anterior (? symphyseal or parasymphyseal) position on the jaw than the holotype.

Paratype 2 (IRSNB P6240; Pl. 2, Fig. 2)

The central cusp is reduced in height and is slightly inclined distally. The apex of the central cusp is broken off. On the labial face of the crown a vertical keel extends over the central cusp and the apron. At the base of the cusp the keel bifurcates into two ridges. Only the distal ridge reaches the apron. Paratype 2 agrees with the holotype in the morphology of the apron. It also agrees with the holotype and paratype 1 in the ornamentation on the lingual face of the central cusp. The cusplets are asymmetrical with the mesial one being more massive than the distal one. The labial basal margin of the crown is slightly more concave on the mesial side. A vertical ridge is present on the labial face of each cusplet. No other ornamentation is discernible on the cusplets.

The root is hemiaulacorhize. Six circular laterointernal foramina open on the lingual face of the root. The mediointernal foramen is partially unroofed lingually.

Dimensions: Mesiodistal width of the crown - 0,75 mm, height of the crown (measured from the tip of the apron to the apex of the central cusp) - 0,59 mm

Position: The reduced height of the central cusp, its slight inclination and the asymmetry of the cusplets indicate a lateral position of paratype 2 on the jaw.

Paratype 3 (IRSNB P6241; Pl. 3, Fig. 1)

Paratype 3 agrees with the holotype in the general morphology of the crown, the degree of inclination of the central cusp, the development of the labial vertical keel, the asymmetry of the cusplets, and in the development of the ornamentation on the lingual face of the cusplets. It agrees with the holotype and the paratypes 1 and 2 in the ornamentation of the lingual face of the central cusp. The apron is narrow and of circular shape. The apex of the distal cusplet is broken off. On the labial face of the mesial cusplet a vertical ridge runs from the apex to the base. The mesial part of the labial basal margin of the crown is perpendicular to the apron, its distal part is more obtuse. The root is hemiaulacorhize. Four large rounded laterointernal foramina open on the lingual side of the root. The mediointernal foramen is circular.

Dimensions: Mesiodistal width of the crown - 0,75 mm, height of the crown (measured from the tip of the apron to the apex of the central cusp) - 0,65 mm.

Position on the jaw: The asymmetry of the cusplets indicate a lateral position of paratype 3 on the jaw.

Paratype 4 (IRSNB P6242; Pl. 3, Fig. 2)

The central cusp is inclined distally and slightly displaced from the plane of the apron. On its labial face the vertical keel extends from the apex to the base of the cusp without reaching the apron. The apron is rounded in shape like paratypes 1 and 3. It is less wide mesiodistally than the central cusp, as in the holotype and in the paratypes 1 to 3. The mesial cusplet is wider mesiodistally and higher than the distal one. No ornamentation is visible on the labial face of the cusplets except one small ridge on the distal cusplet. On the lingual face one small subvertical ridge is present on the mesial cusplet and two more are developed on the distal cusplet. The ornamentation on the lingual side of the central cusp of paratype 4 agrees with that of the holotype and paratypes 2 and 3. On the labial side the distal part of the basal crown margin is more concave than the mesial part.

The root is hemiaulacorhize. Four laterointernal foramina are present on the lingual side of the root. The mediointernal foramen is partially unroofed lingually.

Dimensions: Mesiodistal width of the crown - 0,66 mm, height of the crown (measured from the tip of the apron to the apex of the central cusp) - 0,57 mm.

Position on the jaw: The strong asymmetry of the cusplets indicates a lateral or even posterolateral position of paratype 4 on the jaw.

Paratype 5 (IRSNB P6243; Pl. 4, Fig. 1)

Paratype 5 has a very low profile. The tooth is much wider mesiodistally than it is high. The central cusp is inclined distally. On its labial face the vertical keel runs from the apex to the apron. The apron agrees with paratypes 1, 3 and 4 in being rounded in shape. It agrees with the apron of the holotype and that of the paratypes 1 to 4 in being less wide mesiodistally than the central cusp. The ornamentation of the lingual face of the central cusp is the same as in paratype 1. The two cusplets are approximately of equal dimensions. Each cusplet possesses one strong vertical fold on the labial face. There is no ornamentation on the lingual face of the crown.

The root is hemiaulacorhize. Two laterointernal foramina open on the lingual face of the root. The mediointernal foramen is partially unroofed lingually. The root lobes form an angle of 125° and are more divergent than in the holotype and the previously described paratypes.

Dimensions: Mesiodistal width of the crown - 0,77 mm, height of the crown (measured from the tip of the apron to the apex of the central cusp) - 0,51 mm.

Position on the jaw: The asymmetry and the low profile of the crown suggest a posterolateral position of paratype 5 on the jaw.

Paratype 6 (IRSNB P6244; Pl. 4, Fig. 2)

Paratype 6 has an even lower profile than paratype 5. The central cusp is stout and low. The development of the labial keel on the central cusp agrees with that of the holotype and paratypes 1,3,4 and 5. The apron is narrow and rounded in shape. *Paratype 6* agrees with the holotype and paratypes 2 to 4 in the ornamentation on the lingual face of the central cusp. It also shows a strong asymmetry of the cusplets. A vertical ridge is present on the labial face of each cusplet, with that on the distal cusplet being more pronounced.

The root is hemiaulacorhize. Five rounded laterointernal foramina open on the lingual face of the root. The mediointernal foramen is partially unroofed lingually.

Dimensions: Mesiodistal width of the crown - 0,59 mm, height of the crown (measured from the tip of the apron to the apex of the central cusp) - 0,36 mm.

Position on the jaw: The tiny central cusp and the strong asymmetry of the cusplets suggest a posterolateral position of paratype 6 on the jaw.

Paratype 7 (IRSNB P6245; Pl. 5, Fig. 1)

Paratype 7 differs from the holotype and paratypes 2 to 6 in bearing a very high central cusp, making the crown as high as wide mesiodistally, as in paratype 1. It differs from the holotype and paratypes 1 to 6 in that the labial vertical keel does not reach the apron basally. The apron is relatively wider than in the teeth described above, and is approximately as wide as the central cusp. Paratype 7 agrees with the holotype in the slight distal inclination of the central cusp and in the development of the ornamentation on the lingual face of the central cusp. The distal cusplet is more inclined and a little smaller than the mesial one. Both bear a labial vertical ridge. The base of the cusplets is relatively narrower than in the teeth described above, and thus gives them a more slender appearance. The root is damaged.

Dimensions: Mesiodistal width of the crown - 0,62 mm, height of the crown (measured from the tip of the apron to the apex of the central cusp) - 0,66 mm.

Position on the jaw: The slight distal inclination of the central cusp and the weak asymmetry of the cusplets suggest an anterolateral position of paratype 7 on the jaw.

Paratype 8 (IRSNB P6246; Pl. 5, Fig. 2)

Paratype 8 agrees with paratype 7 in being as high as it is wide mesiodistally and in the incomplete development of the labial keel on the central cusp not reaching the apron. It differs from paratype 7 in having a more asymmetrical crown and in having a more triangular and relatively narrower apron. The ornamentation of the lingual face of the central cusp is the same as in the holotype and in paratypes 2,3,4,6, and 7. The mesial cusplet is higher and wider mesiodistally than the distal one; both carry a vertical ridge on the labial face. The lingual face of the mesial cusplet shows a weakly developed vertical fold. On the labial side the basal margin of the crown is more obtuse mesially.

The root is hemiaulacorrhize. Four large, circular laterointernal foramina open on the lingual face of the root. There are two mediointernal foramina of uneven size. The smaller one is adjacent to the lingual extremity of the uvula. The larger one opens on the lingual protuberance of the root mesially to the smaller mediointernal foramen. It is partially unroofed.

Dimensions: Mesiodistal width of the crown - 0,80 mm, height of the crown (measured from the tip of the apron to the apex of the central cusp) - 0,80 mm.

Position on the jaw: Because of its asymmetrical crown paratype 8 presumably had a more lateral position on the jaw than paratype 7.

Paratype 9 (IRSNB P6247; Pl. 6)

Paratype 9 differs from the holotype and paratypes 1 to 8 in the development of the central cusp, which is very high and slender, and in the absence of the paramedian oblique folds on the lingual face of the central cusp. Paratype 9 is similar to paratypes 7 and 8 in the extent of the vertical keel being restricted to the labial face of the central cusp and in the formation of a relatively wide, tongue-shaped apron. The apron is almost as wide as the base of the central cusp. The central cusp has well developed cutting edges. The lateral cusplets are broken off.

The root is hemiaulacorrhize. Six large, oval foramina are present on the lingual face of the root. The mediointernal foramen is partially unroofed lingually.

Dimensions: Mesiodistal width of the crown - not measurable due to the loss of lateral cusplets, height of the crown (measured from the tip of the apron to the apex of the central cusp) - 1,29 mm.

Position on the jaw: As the central cusp is only slightly inclined, this indicates an anterior position of paratype 9 on the jaw.

Paratype 10 (IRSNB P6248; Pl. 7)

The central cusp of the crown is high, slender, and dagger-shaped in labial aspect. It is inclined distally. The median keel is restricted to the labial face of the central cusp and does not extend onto the apron basally. The cutting edge is well developed on the central cusp. The apron is of semicircular outline in labial view. Its width equals the width of the basal part of the central cusp. The uvula is flat and tongue shaped. Only the mesial cusplet is preserved, having a more slender appearance than in the holotype or in paratypes 1 to 8.

The ornamentation consists of an oblique fold on the labial face of the cusplet and of two weakly developed paramedian folds on the lingual side of the central cusp.

The root is hemiaulacorhize and bilobated. It has a flat basal face. The lingual face of the root shows nine laterointernal foramina. Four of these (two on each lobe) are enlarged and slot-like. The other five are small and circular in outline. The mediointernal foramen opens below the uvula of the crown. The number of lateroexternal foramina remains obscure.

Dimensions: Mesiodistal width of the crown - approximately 1 mm (the loss of left the cusplet prevents exact measurement), height of the crown (measured from the tip of the apron to the apex of the central cusp) - 1,31 mm.

Position on the jaw: The asymmetry of the tooth, with the central cusp being inclined distally and the labial basal margin of the crown being strongly notched between the apron and the distal cusplet, suggests an anterolateral or lateral position of paratype 10 on the jaw.

Paratype 11 (IRSNB P6249; Pl. 8, Fig. 1)

Paratype 11 is similar to paratypes 7 to 10 in having the labial vertical keel restricted to the central cusp and in having a wide apron. It agrees with paratypes 7 and 8 in possessing a crown which is as high as it is wide mesiodistally. It differs from the holotype and the other paratypes by its cusplets being developed in a hook-like manner. The central cusp is strongly inclined distally. Its cutting edges are well developed. The vertical keel on the labial face of the central cusp is accompanied distally by a fold. The lateral cusplets are devoid of ornamentation. The apron is of semicircular outline. It is slightly narrower than the base of the central cusp.

The root is poorly preserved. It is hemiaulacorhize and bilobated. Three laterointernal foramina are discernible on the lingual face of the distal root lobe. Two more are present on the mesial lobe. The mediointernal foramen is circular and opens below the uvula.

Dimensions: Mesiodistal width of the crown - 0,9 mm, height of the crown (measured from the tip of the apron to the apex of the central cusp) - 0,91 mm.

Position on the jaw: The asymmetrical crown suggests a lateral or posterolateral position of paratype 11 on the jaw.

Paratype 12 (IRSNB P6250; Pl. 8, Fig. 2)

Paratype 12 shows a massive and hypertrophic distal cusplet and an apron which is quadratic in outline. The central cusp is very low and slightly inclined distally. As in paratypes 1 to 6, the labial vertical keel extends from the apex of the central cusp onto the apron. The lateral cusplets are smooth. As in paratypes 9 and 11 there are no oblique paramedian folds on the lingual face of the central cusp. The labial basal margin of the crown is notched between the apron and the distal cusplet.

The root is hemiaulacorhize.

Dimensions: Mesiodistal width of the crown - 0,71 mm, height of the crown (measured from the tip of the apron to the apex of the central cusp) - 0,65 mm.

Discussion: The morphology of paratype 12 is unique among our material. The hypertrophied distal cusplet and the quadratic shape of the apron distinguish this tooth from all other teeth attributed to *Annea maubeugei* n. sp. With regard to the development of other characters such as the presence of a vertical keel on the labial face of central cusp and apron, the presence of only a single pair of lateral cusplets, and the formation of a narrow, tongue-like uvula, paratype 12 agrees well with the holotype and the other paratypes of *A. maubeugei* n. sp. We therefore consider paratype 12 as a pathological tooth of *A. maubeugei*. Its formation could have been caused by hard or spiny food particles which may have injured some tooth anlagen. Injuries to tooth anlagen caused by fin spines of prey fishes and subsequent formation of anomalous dental morphologies are common among Recent neoselachians (SCHWEIZER 1964) and are also known from fossil sharks (LIENAU 1985).

Remark: The holotype and paratypes 1 to 8 and 12 are considerably smaller than paratypes 9 to 11. As discussed below, we consider all the types as belonging to the same species. The holotype and paratypes 1 to 8 and 12 seem to be teeth of younger individuals. Due to their larger size paratypes 9 to 10 appear to represent older individuals.

Discussion and conclusions

Systematic

The most conspicuous characteristic of the teeth described above from the Toarcian of Belgium is the development of a prominent vertical keel on the labial face of the crown extending over the central cusp and apron in smaller teeth. Additionally, all of the teeth from Belgium have a hemiaulacorhize root. The presence of a vertical labial keel on the crown together with a hemiaulacorhize root is characteristic of the fossil neoselachian genus *Annea* THIES 1983. We therefore attribute the Belgian teeth to this genus.

Only one species of *Annea* has been known so far: *A. carinata* THIES 1983 from the Middle Jurassic (Aalenian and Bajocian) of North Germany (THIES 1983, 1989, 1993). The teeth from the Toarcian of Belgium differ from the species *carinata* in the development of the uvula which is massive, bulbous and bulky in *A. carinata*, but narrow and tongue-shaped in the Belgian teeth. Another difference is developed in the apron. In teeth of comparable size (i. e. all the known teeth of *A. carinata*, holotype and paratypes 1 to 6 of the new species from Belgium) the apron is prominent (or even very prominent), peg-like and of semi-oval shape in labial aspect with a blunt basal end in *A. carinata*, but is often less prominent, of triangular shape in labial view, and more pointed basally in the Belgian teeth. The lateral cusplets of *A. carinata* are pointed and needle-like in labial or lingual aspect. Also, in addition to the pair of lateral cusplets there is a vestigial second lateral cusplet on the mesial side of the crown in *A. carinata*. In the teeth from the Belgian Toarcian, however, the lateral cusplets are widened mesiodistally at the base to show a roughly triangular outline in labial or lingual view. This is most evident in the holotype and paratypes 1 to 8. In general, the Belgian teeth have a crown more widened mesiodistally than the crown of *A. carinata*. A vestigial second mesial cusplet is constantly absent in the teeth from Belgium. A further difference is discernible in the ornamentation. Whereas the lingual face of the crown is smooth in *A. carinata*, it has two paramedian oblique folds on the central cusp in the Belgian teeth. Because of the morphological differences between the teeth of *A. carinata* and the teeth from the Toarcian of Belgium we consider the Belgian teeth as belonging to a new species of *Annea*, for which we propose the name *Annea maubeugei* n. sp.

Heterodonty

The teeth described here as *Annea maubeugei* n. sp. show a considerable morphological variation. Comparison of the holotype (Pl. 1) and paratype 10 (Pl. 7) reveals an enormous morphological gap between the two teeth demonstrated best by the crown. The differences include the development of the median keel, which is prominent and extends over the entire cusp and apron in the holotype, but is much less prominent and does not reach the apron basally in paratype 10. Also the central cusp appears as stout and low in the holotype, but is slender, high and needle-like in paratype 10. In the holotype the lateral cusplets are widened mesiodistally to such an extent that they are nearly as wide as they are high. In paratype 10 the lateral cusplets are nearly twice as high as they are wide. The apron is more delicate and of roughly triangular shape in the holotype. In paratype 10 it is more massive and of semicircular outline in labial view. In the holotype (and in all the smaller teeth) the apron does not reach the mesiodistal width of the central cusp above. In paratype 10 the apron is as wide mesiodistally as the central cusp is at its base. The central cusp is stout in the holotype whereas it is high, slender, and dagger-shaped in paratype 10. The different relative height of the central cusp in the holotype and in paratype 10 becomes most evident when it is compared to the height of the lateral cusplets. The central cusp of the holotype is less than twice as high as the accompanying lateral cusplets. In paratype 10 the central cusp is more than twice as high as the lateral cusplets. Finally, paratype 10 is twice as large as the holotype (regarding the apicobasal diameter from the basal extremity of the apron to the tip of the central cusp). Considering only the holotype and paratype 10, most workers on fossil selachian teeth would probably not hesitate to attribute them to different species. For the following reasons we believe, however, that our material represents only a single species.

1. There are transitional dental morphologies present in our material which link paratype 10 to the holotype. These are demonstrated by paratypes 7 and 8 (Pl. 5, Figs. 1-2). Paratype 7 agrees with the holotype in that the crown is widened mesiodistally. Like paratype 10 it has a high and slender central cusp, an apron as wide as the central cusp, and a median keel not reaching the apron basally. The same applies to paratype 8.

2. The smaller teeth outnumber the larger ones by far. This parallels the frequency of age groups in a species population decreasing as the individuals grow older. In Recent sharks, as far as is known, litter sizes range between one (*Carcharhinus sealei*, COMPAGNO 1984b) and 82 young (*Galeocerdo cuvier*, COMPAGNO 1984b, ELLIS 1978; *Notorynchus cepedianus*, COMPAGNO 1984a). In Recent orectolobiforms, numbers of young are reported to be as high as 37 in *Orectolobus maculatus*. *Hemiscyllium ocellatum* was even observed to lay about 50 eggs annually (LAST & STEVENS 1994). These data certainly reflect different ways of adaptation, but they also indicate that in many species of Recent sharks young individuals are many times more numerous than the old ones. One should expect this to be mirrored in the fossil record of an extinct neoselachian species by the numerical relation of its teeth of different sizes, with the smaller ones being more frequent than the larger ones.

3. Intraspecific heterodonty is not uncommon in neoselachians. Many Recent neoselachians show an ontogenetic and/or a sexual and/or a dignathic heterodonty. Among orectolobiform sharks a fine example is provided by the Recent *Stegostoma fasciatum* (HERMANN, 1783). When comparing the teeth of a 105 cm t. l. female with those of a 210 cm t. l. male, apart from the different height of the teeth, one immediately notices the different development of features such as the shape of the apron, relative height of the lateral cusplets, and the shape of the central cusp and cusplets (HERMAN, HOVESTADT-EULER & HOVESTADT 1992: pls. 28 and 31). In the 105 cm female of *S. fasciatum* the apron shows a double indentation, the lateral cusplets reach up to approximately half the height of the central cusp, and the central cusp and lateral cusplets are narrow, slender and dagger-shaped in labial view. In contrast, in the teeth of the 210 cm male there is no well-developed apron. Instead, the labial basal margin of the crown shows only one broad and shallow indentation below the central cusp. The lateral cusplets reach up only to one quarter to one third of the height of the central cusp, and, due to the mesiodistal expansion of the crown in the 210 cm male, all the cusps appear to be much stouter and do not show a dagger-shaped outline in labial view.

We therefore consider all the teeth described here as belonging to a single species and explain the different dental morphologies present in our material by ontogenetic (and possibly also by sexual) heterodonty.

Stratigraphical and palaeobiogeographical range of *Annea*

Annea was previously known only from the early Middle Jurassic (Aalenian, Bajocian) of North Germany. The new material from Belgium extends the stratigraphic and palaeobiogeographical range of the genus into the late Early Jurassic (Toarcian) of Belgium. (Unpublished material in the collection of D. THIES shows that *Annea* also occurs in the Upper Toarcian of South Germany. The material was recovered from the *thouarsense*-zone and is therefore only slightly younger than the Belgian teeth, which are from the *bifrons*-/*variabilis*-zones. The South German material comprises some fragmentary teeth of *Annea*, among which is a specimen of *A. maubeugei* n. sp. and possible specimens of *A. carinata*.)

Accompanying Elasmobranches

The following elasmobranch taxa identified by their teeth are also present in the *Annea*-bearing horizon (DELSATE, HERMAN & LEPAGE 1989; DELSATE & LEPAGE 1990; THIES 1993, and DELSATE pers. observation):

Euselachii

Lissodus sp.
Hybodus sp.

Neoselachii

Galeomorphii

Synechodontiformes
Sphenodus sp.
Synechodus sp.

Heterodontiformes

Heterodontus sarstedtensis THIES 1983

Orectolobiformes

Palaeobrachaelurus cf. *alisonae* THIES 1983
Palaeobrachaelurus sp.

Chiloscyllium sp.
Incerti ordinis
Jurobatos cappettai THIES, 1983
Squalomorphii
Protospinax sp.
Batomorphii
Rhinobatidae gen. et spec. indet.

From this list it is evident that the orectolobiforms are dominant in the elasmobranch fauna in the *Annea*-bearing horizon.

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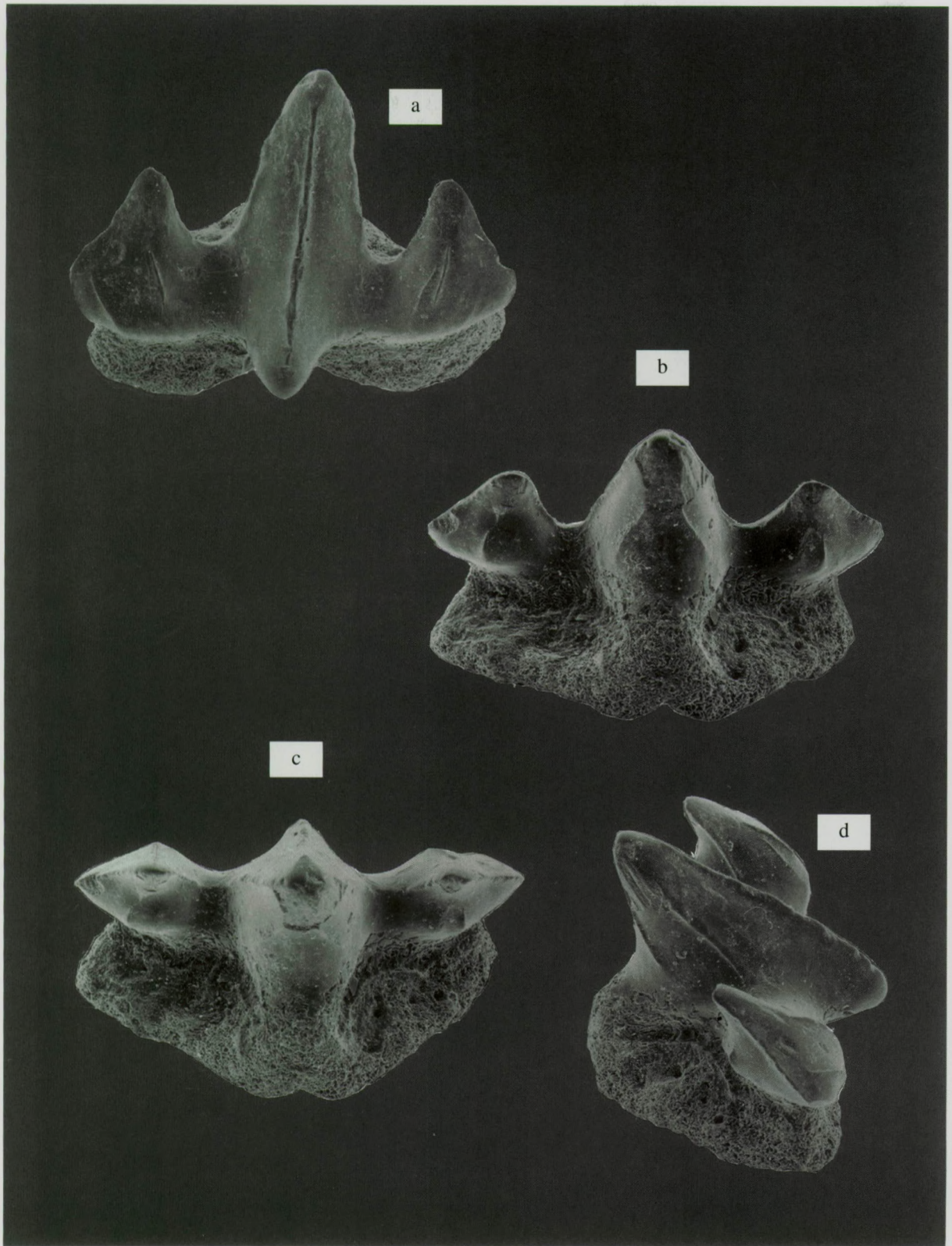


Plate 1. *Annea maubeugei* n. sp.: Holotype (IRSNB P6238); anterior or anterolateral oral tooth in **a**: labial, **b**: lingual, **c**: occlusal, and **d**: lateral view (x 80).

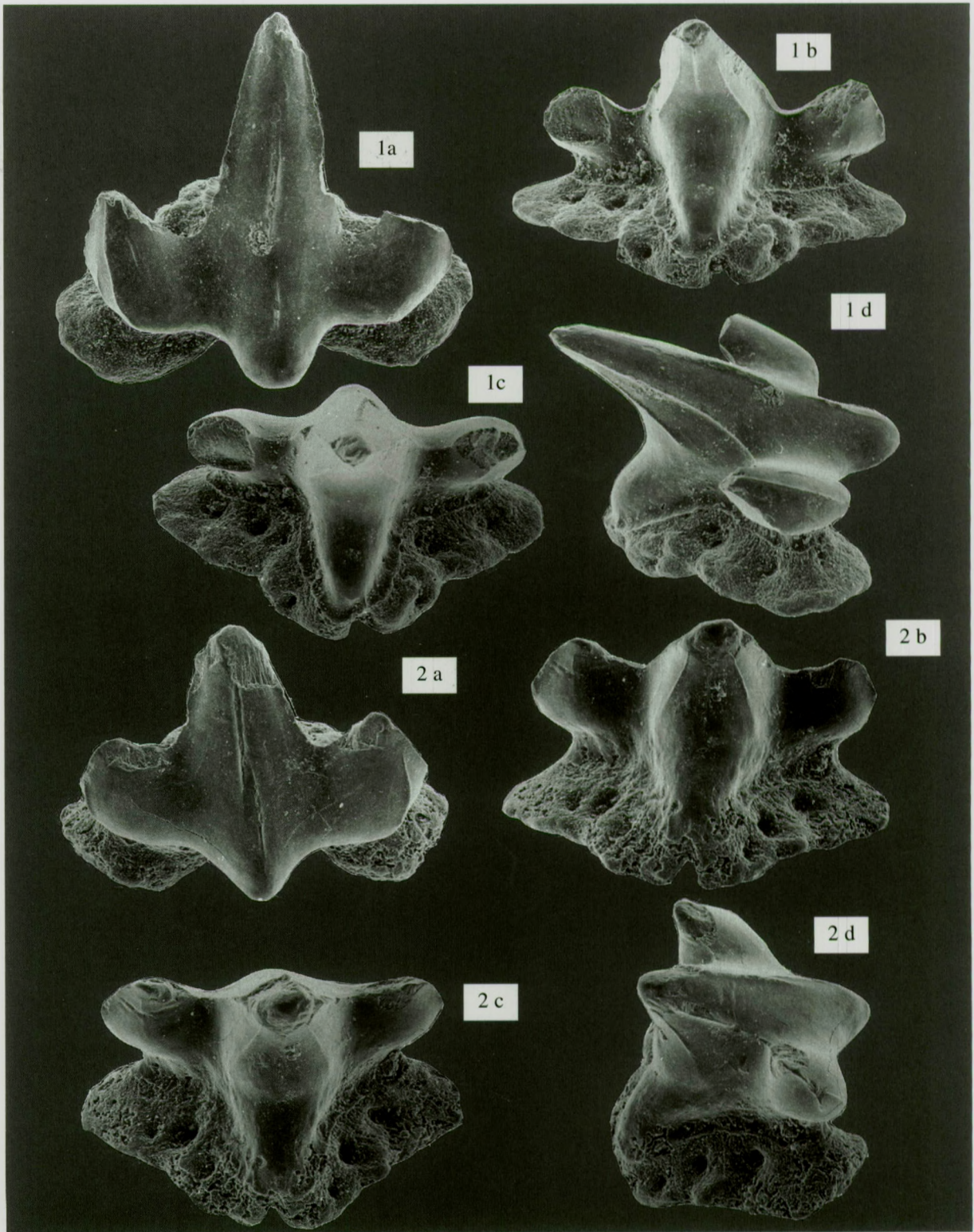


Plate 2. *Annea maubeugei* n. sp.: 1. Paratype 1 (IRSNB P6239); anterior (symphyseal or parasymphyseal) tooth in **a**: labial, **b**: lingual, **c**: occlusal, and **d**: lateral view. 2. Paratype 2 (IRSNB P6240); lateral tooth in **a**: labial, **b**: lingual, **c**: occlusal, and **d**: lateral view (x 80).

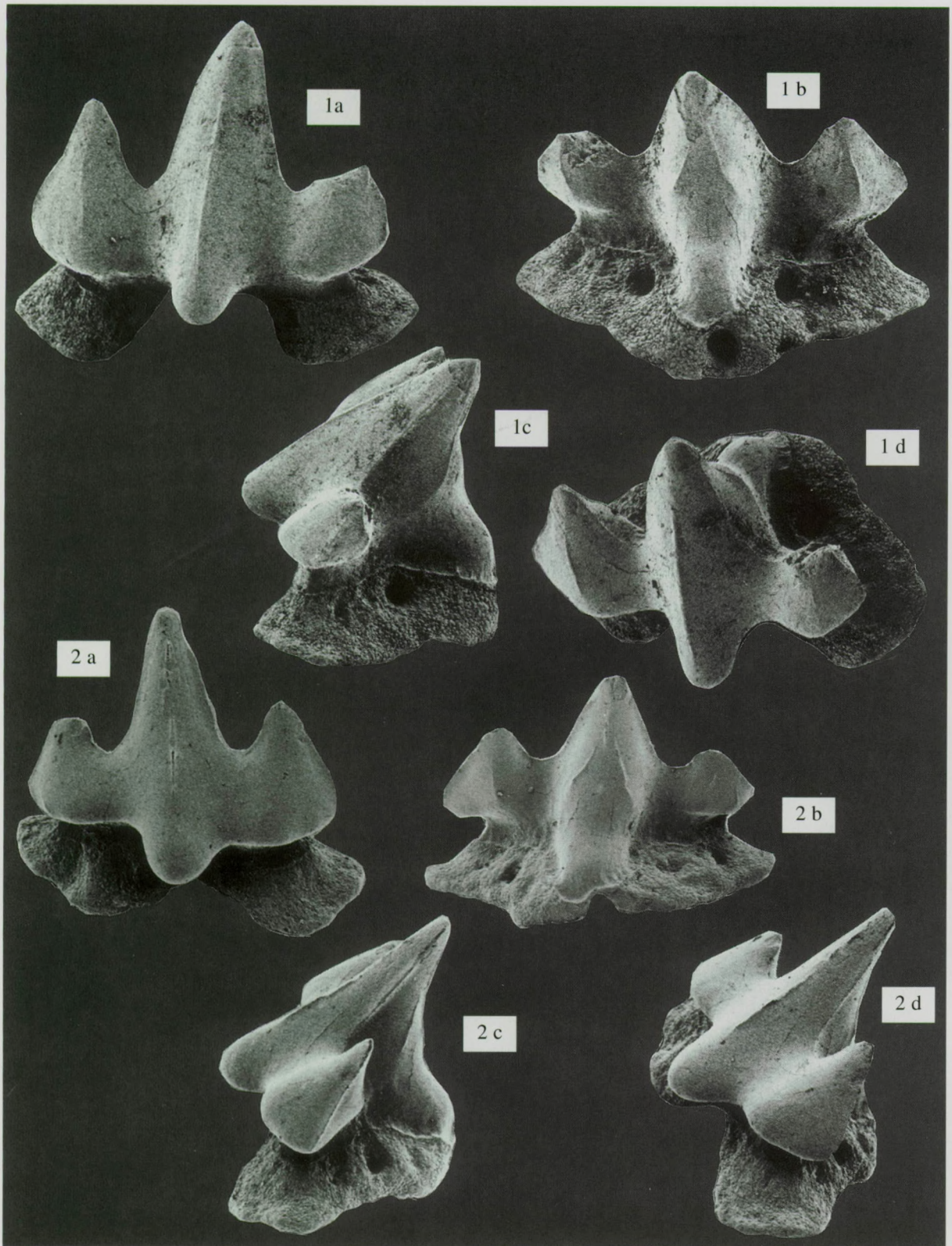


Plate 3. *Annea maubeugei* n. sp.: 1. Paratype 3 (IRSNB P6241); lateral tooth in **a**: labial, **b**: lingual, **c**: lateral, and **d**: oblique-occlusal view. 2. Paratype 4 (IRSNB P6242); lateral or posterolateral tooth in **a**: labial, **b**: lingual, **c**: lateral, and **d**: oblique-lateral view (x 80).

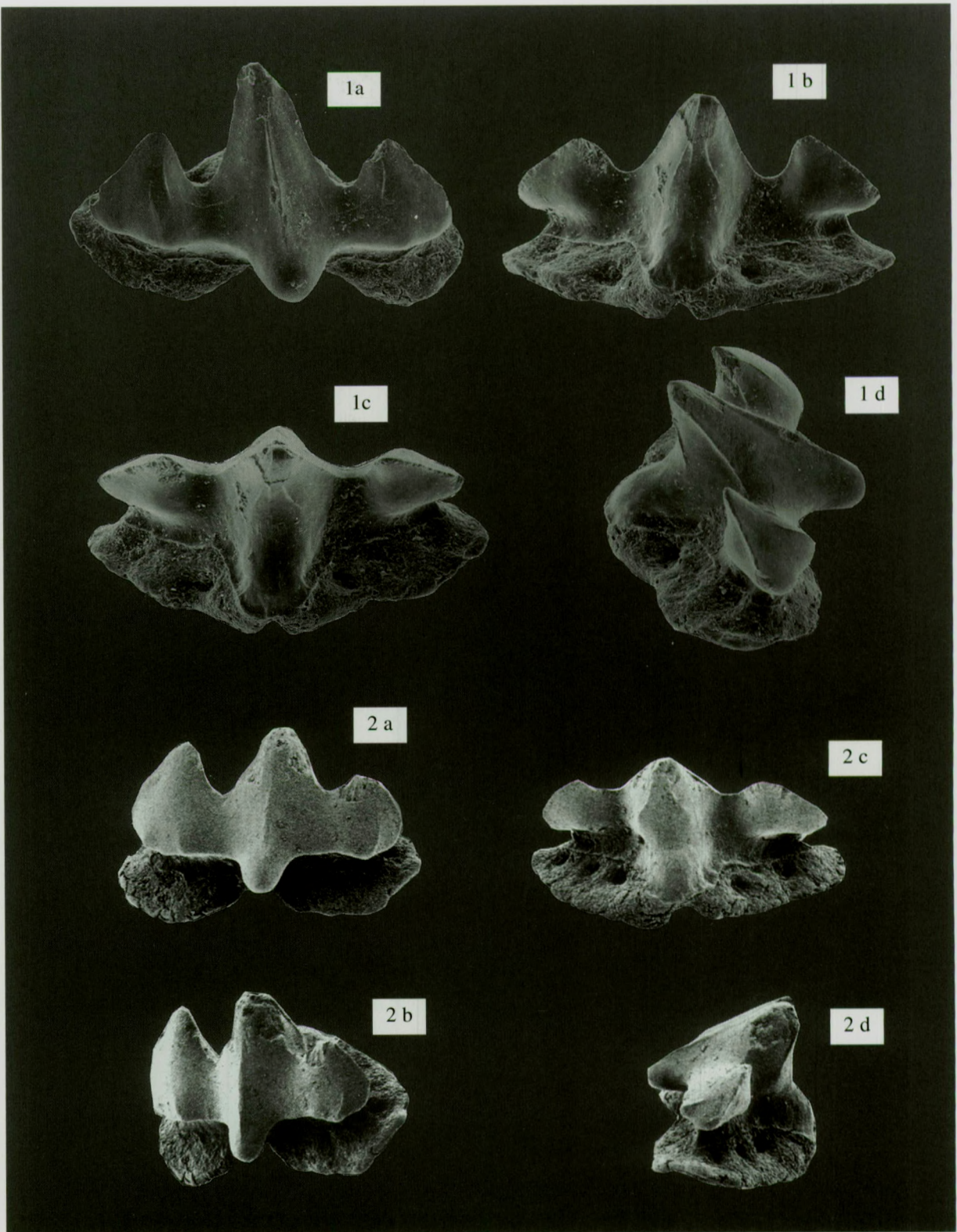


Plate 4. *Annea maubeugei* n. sp.: **1.** Paratype 5 (IRSNB P6243); posterolateral tooth in **a:** labial, **b:** lingual, **c:** occlusal, and **d:** lateral view. **2.** Paratype 6 (IRSNB P6244); posterolateral tooth in **a** and **b:** labial, **c:** lingual, and **d:** lateral view (x 80).

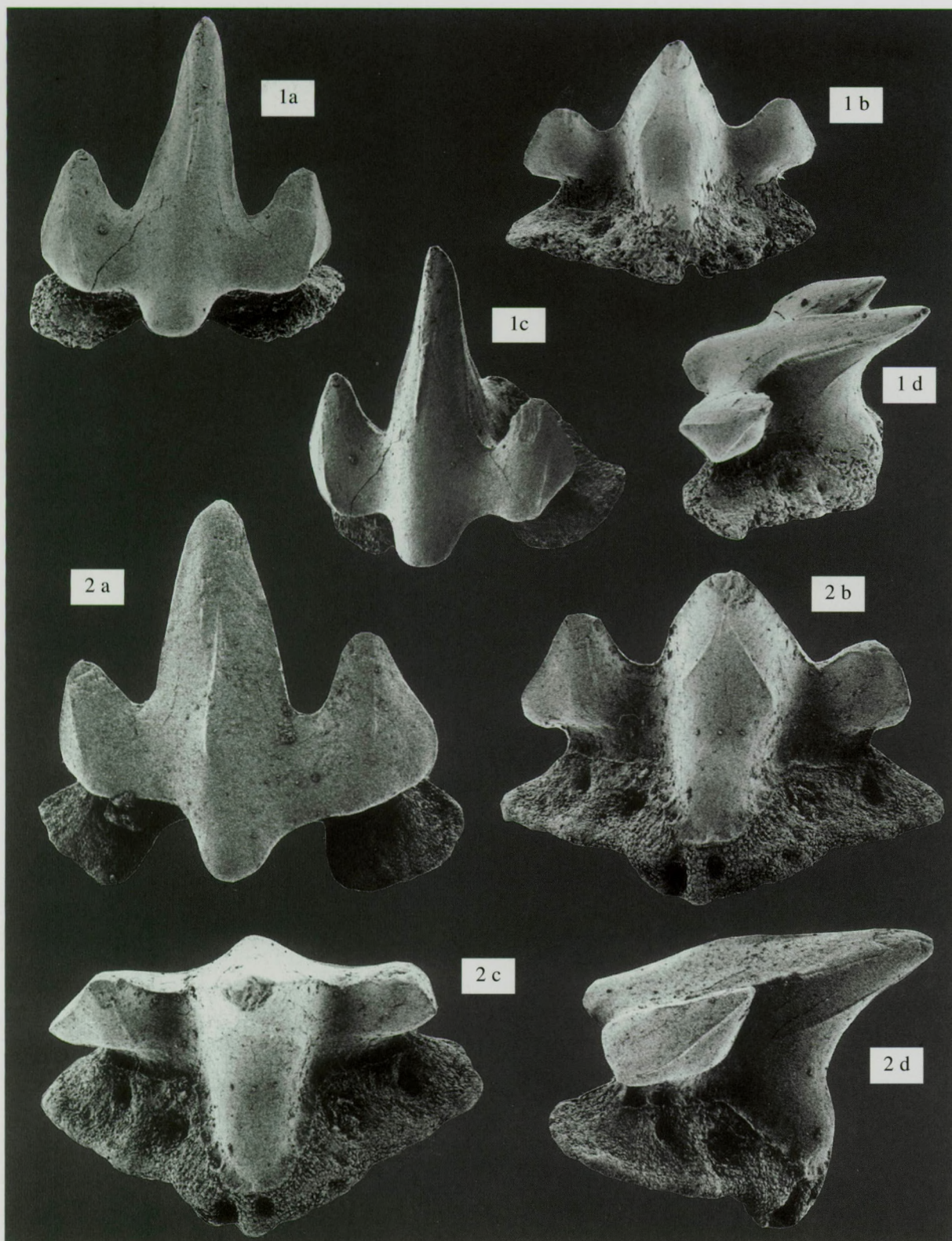


Plate 5. *Annea maubeugei* n. sp.: 1. Paratype 7 (IRSNB P6245); anterolateral tooth in **a**: labial, **b**: lingual, **c**: oblique-labial, and **d**: lateral view. 2. Paratype 8 (IRSNB P6246); lateral tooth in **a**: labial, **b**: lingual, **c**: occlusal, and **d**: lateral view (x 80).

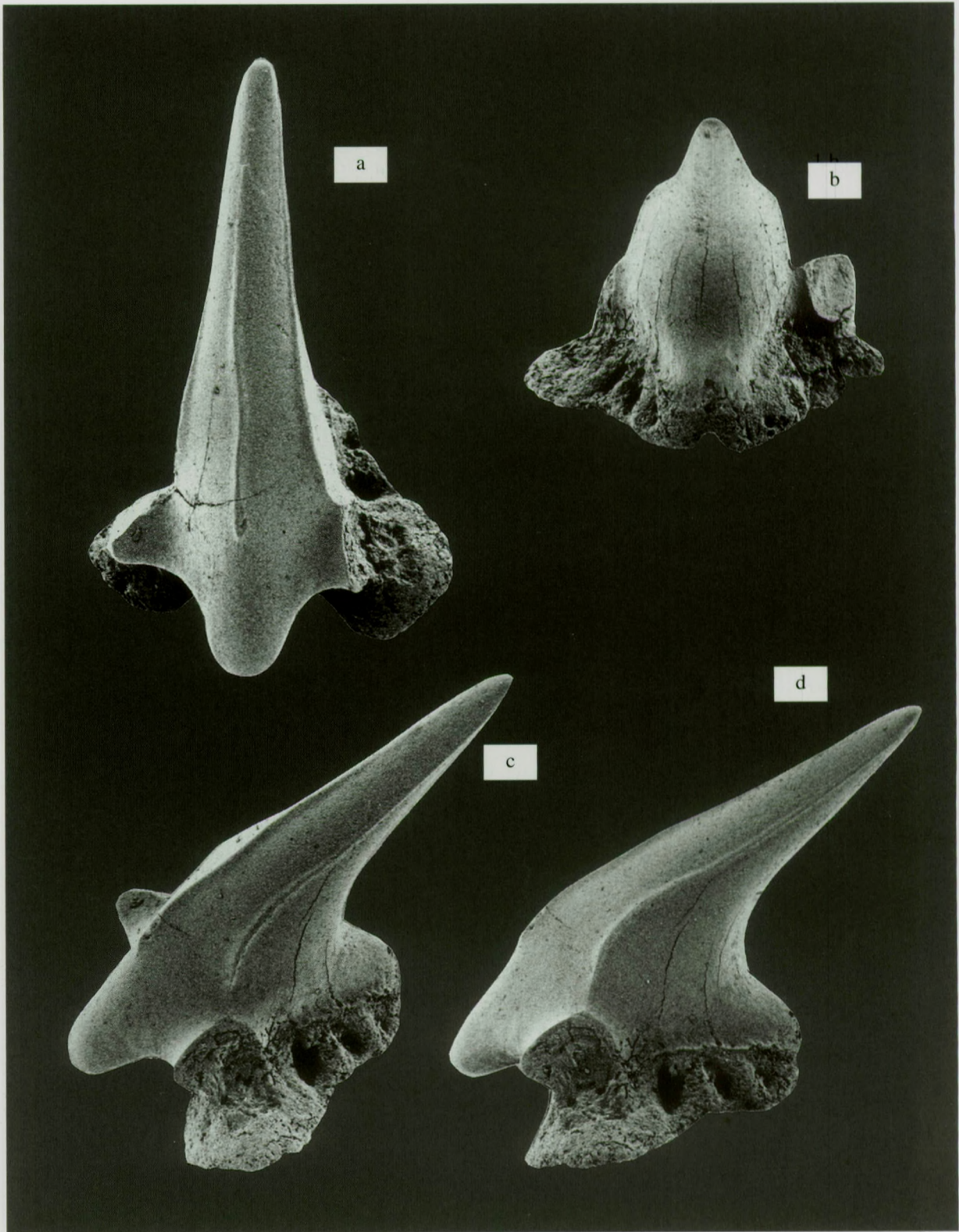


Plate 6. *Annea maubeugei* n. sp.: Paratype 9 (IRSNB P6247); anterior tooth in a: labial, b: lingual, c: lateral, and d: oblique-lateral view (x 80).

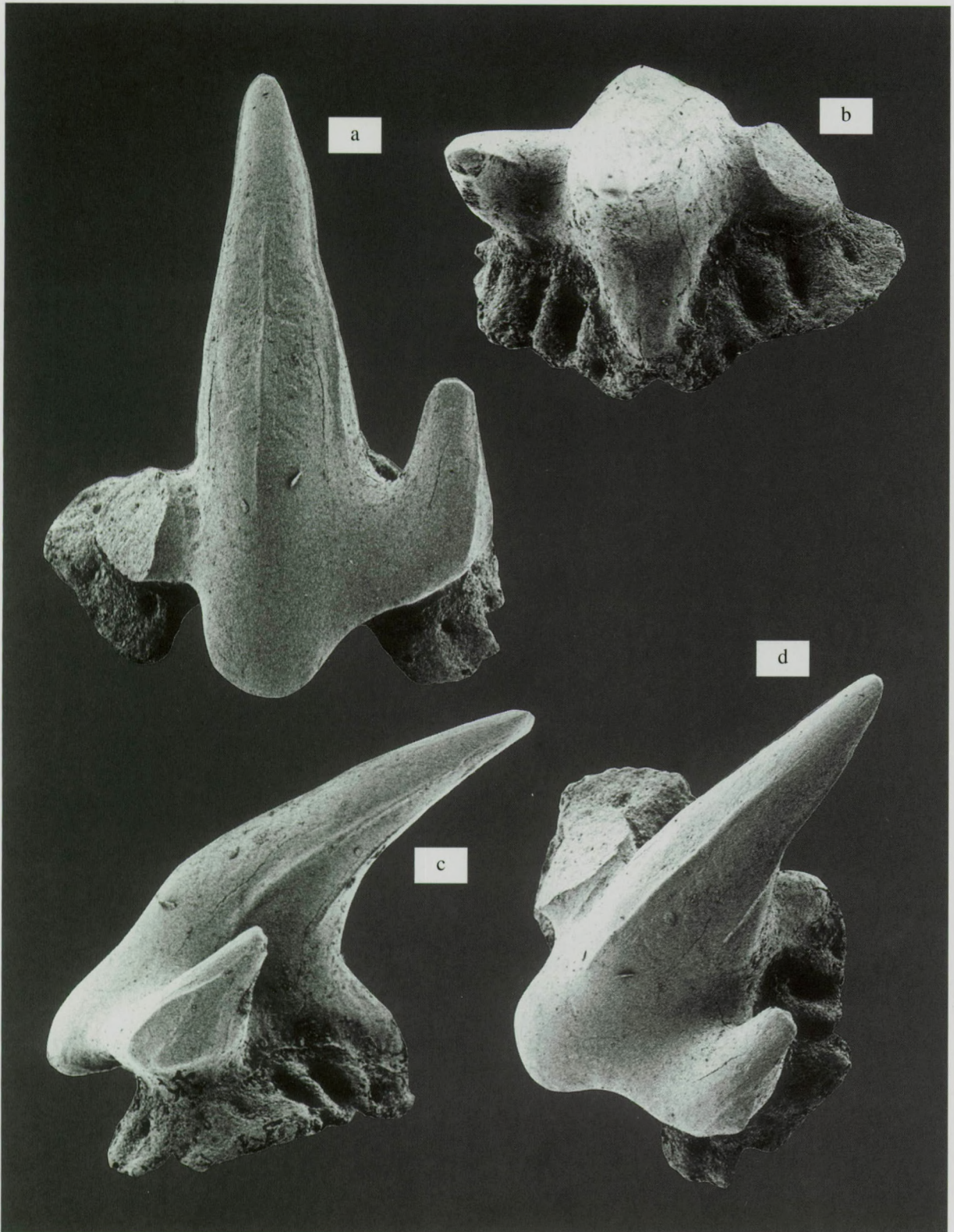


Plate 7. *Annea maubeugei* n. sp.: Paratype 10 (IRSNB P6248); anterolateral or lateral tooth in **a**: labial, **b**: lingual, **c**: lateral, and **d**: oblique-lateral view (x 80).

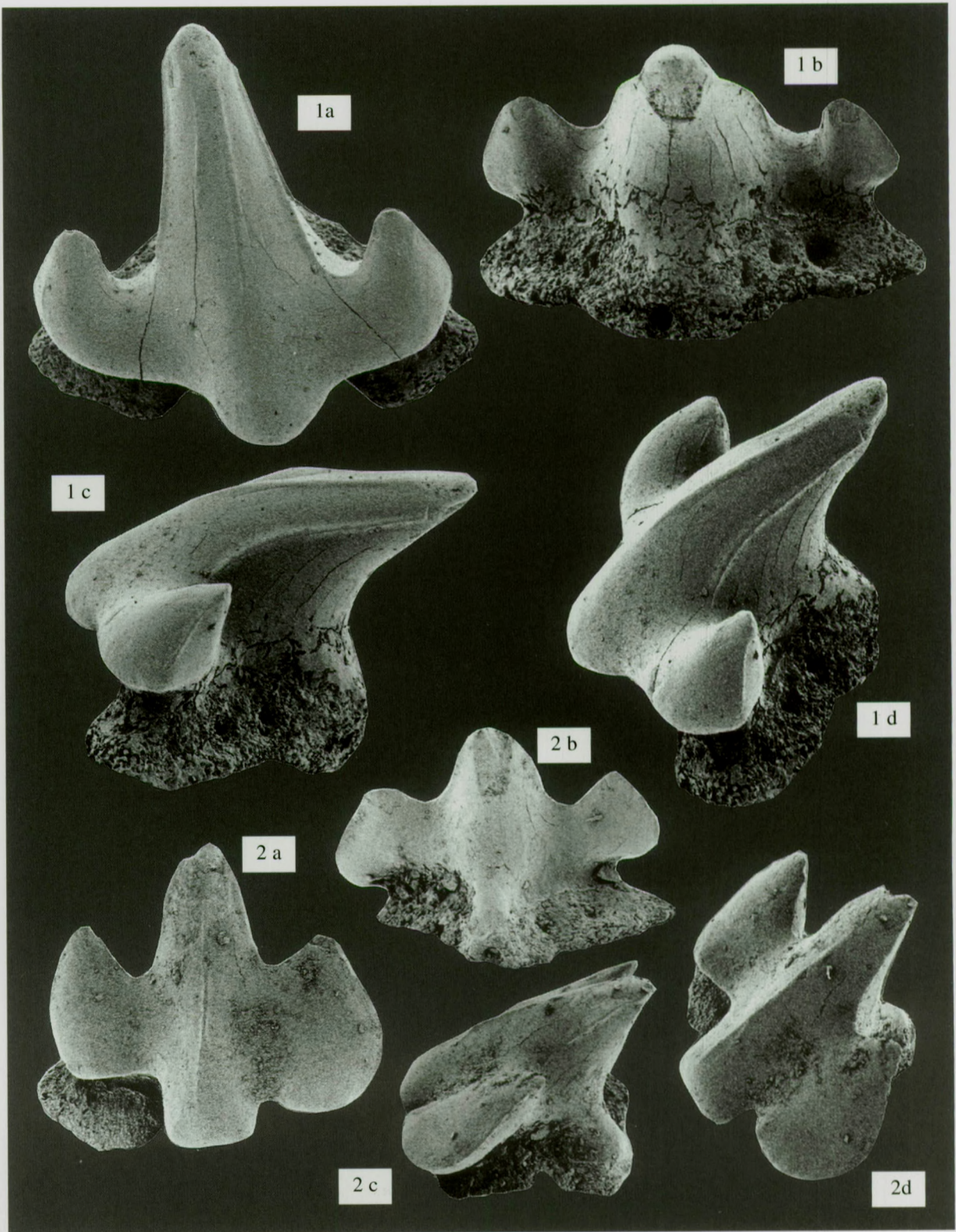


Plate 8. *Annea maubeugei* n. sp.: 1. Paratype 11 (IRSNB P 6249); lateral or posterolateral tooth in **a**: labial, **b**: lingual, **c**: lateral, and **d**: oblique-lateral view. 2. Paratype 12 (IRNSB P.6250); pathological tooth in **a**: labial, **b**: lingual, **c**: lateral, and **d**: oblique-labial view (x 80).