

# Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes

Editor: M. STEHMANN

## Part A : Selachii.

No. 1b : Order : Hexanchiformes - Family : Chlamydoselachidae; No. 5 : Order : Heterodontiformes - Family : Heterodontidae; No. 6 : Order : Lamniformes - Families : Cetorhinidae, Megachasmidae; Addendum 1 to No. 3 : Order Squaliformes; Addendum 1 to No. 4 : Order : Orectolobiformes; General Glossary; Summary Part A.

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### Abstract

The morphology of the microteeth of the following taxa is described and illustrated with SEM-photographs in order to elucidate the inter-relationships within the shark orders and families concerned also from an odontological point of view.

**Contribution 1b :** The monotypic single genus of the hexanchiform Chlamydoselachidae. The tooth morphology of *C. anguineus* is compared with that of taxa of the only other hexanchiformes. The dental histology is commented on, and the dental vascular type is re-examined in order to understand the root form. The results are summarized in an odontological diagnosis for the genus. Investigational results on dental morphology, histology and vascularization recommend a reconsideration of the systematic position of the Chlamydoselachidae, which show a closer relation to Orectolobiformes than to Hexanchidae.

**Contribution 5 :** The three genera *Tropidodus*, *Gyropleurodus* and *Heterodontus* of the heterodontiform family Heterodontidae as once proposed by GILL, 1862. The differences in tooth morphology are only of interspecific signification.

**Contribution 6 :** The genera of the monotypic families Cetorhinidae and Megachasmidae. The morphology of the small teeth in both families is characteristic for filter-feeders. *Cetorhinus* exhibits irregular size and shape of its small teeth and a distinct ontogenetic heterodonty in its dentition. *Megachasma*, in contrast, shows small teeth of equal size and shape indicating a relatively recent adaptation to filter-feeding.

**Contribution 3, addendum 1 :** The squalid species *Scymnodon squamulosus* and *Scymnodon obscurus* attributable to the genus *Zameus*, proposed by JORDAN and FOWLER in 1903 and revalidated by TANIUCHI and GARRICK in 1986. Odontological investigations indicate a synonymy of *Zameus* and *Scymnodalatias* with *Scymnodon*.

**Contribution 4, addendum 1 :** The type species of the monotypic orectolobid genus *Sutorectus*. The results are summarized in a dia-

gnosis for the genus and offer hardly any odontological arguments for distinguishing *Sutorectus* from *Orectolobus*.

**Key words :** Elasmobranchii - Selachii - Chlamydoselachidae - Heterodontidae - Cetorhinidae - Megachasmidae - Squalidae - Orectolobidae - Odontology - Systematics.

### Résumé

La morphologie dentaire des taxa suivants est décrite et figurée sur base de clichés MEB, afin d'éclaircir d'un point de vue odontologique les relations au sein des ordres et familles concernés.

**Contribution 1b :** l'unique genre *Chlamydoselachus* de la famille Chlamydoselachidae, toujours considérée comme faisant partie des Hexanchiformes. La morphologie dentaire de *C. anguineus* est comparée avec celles des autres Hexanchiformes. Histologie et vascularisation dentaires sont réexaminées afin de réinterpréter sa structure radulaire. Les données qui résultent de ces observations obligent à reconsidérer la position systématique des Chlamydoselachidae. Ceux-ci présentent odontologiquement plus d'affinités avec les Orectolobiformes qu'avec les Hexanchidae.

**Contribution 5 :** les trois genres *Heterodontus*, *Tropidodus* et *Gyropleurodus* proposés par GILL en 1862 en lieu et place du seul genre *Heterodontus*. Les différences observées relèvent de la seule intraspécificité.

**Contribution 6 :** les genres *Cetorhinus* (Famille Cetorhinidae) et *Megachasma* (Famille Megachasmidae). La morphologie des dents de ces deux genres est caractéristique des requins filtreurs.

**Contribution 3, addendum 1 :** les espèces *Scymnodon squamulosus* et *Scymnodon obscurus* attribuables au genre *Zameus* proposé par JORDAN et FOWLER en 1903 et revalidé par TANIUCHI et GARRICK en 1986. Les observations odontologiques permettent des synonymiser les genres *Zameus* et *Scymnodalatias* avec *Scymnodon*.

**Contribution 4, addendum 1** : l'espèce type du genre *Sutorectus* (*S. tentaculatus*). Les différences odontologiques observées ne permettent pas de distinguer génériquement *Sutorectus* d'*Orectolobus*.

**Mots-clés** : Elasmobranchii - Selachii - Chlamydoselachidae - Heterodontidae - Cetorhinidae - Megachasmidae - Squalidae - Orectolobidae - Odontologie - Systématique.

### Kurzfassung

Die Morphologie der Mikro Zähne der folgenden Taxa wird beschrieben und illustriert mit REM-photos zur Erhellung, auch aus der odontologischen Sicht, der Verwandtschaftsbeziehungen innerhalb der betroffenen Haiordnungen und Familien.

**Beitrag 1b** : die monotypische, einzige Gattung der hexanchiformen Chlamydoselachidae. Die Zahnmorphologie von *C. anguineus* wird verglichen mit derjenigen von Taxa der einzigen anderen hexanchiformen Hexanchidae. Zum besseren Verständnis der Wurzelform wird die Histologie der Zähne kommentiert und das Zahngefäßsystem der Zähne regen zum Überdenken der systematischen Position der Chlamydoselachidae an, die einen näheren Bezug zu Orectolobiformes als zu den Hexanchidae zeigen.

**Beitrag 5** : die drei heterodontiden Gattungen *Heterodontus*, *Tropidodus* und *Gyropleurodus*. Die letzten zwei wurden errichtet von GILL (1862) und gelten gegenwärtig als Synonyme von *Heterodontus*. Die Ergebnisse sind in einer Differentialdiagnose für die drei Gattungen und ihrer Familie dargestellt mit dem Ergebnis, daß die nur geringen odontologischen Unterschiede allenfalls von interspezifischer, aber nicht von intergenerischer Bedeutung sind.

**Beitrag 6** : die monotypischen Gattungen *Cetorhinus* und *Megachasma*. Sie sind in beiden monotypischen lamniformen Familien Cetorhinidae und Megachasmidae charakteristisch für die filtrierende Ernährungsweise ihrer Vertreter.

**Beitrag 3, Addendum 1** : die squalidenarten *Zameus squamulosus* und *Scymnodon obscurus*. Eine odontologische Diagnose der Gattungen *Scymnodon*, *Zameus* und *Scymnodalatis* summiert die Ergebnisse, die eine Synonymie beider letzteren Gattungen mit ersterer andeuten.

**Beitrag 4, Addendum 1** : die orectolobiden Gattung *Sutorectus*. Die odontologische Ergebnisse werden in einer Gattungsdiagnose summiert. Eine kritische Bewertung der Befunde ergibt keine signifikanten Merkmale die *Sutorectus* von *Orectolobus* unterscheiden.

**Schlüsselwörter** : Elasmobranchii - Selachii - Chlamydoselachidae - Heterodontidae - Cetorhinidae - Megachasmidae - Squalidae - Orectolobidae - Odontologie - Systematik.

### General introduction

This fascicle includes the four remaining issues of Part A of this series : 1b, the hexanchiform family Chlamydoselachidae; 5, the heterodontiform family Heterodontidae and 6, the only two lamniform families with micro - teeth : Cetorhinidae and Megachasmidae. Two addenda on previous issues of this series are also presented : Addendum 1, to No. 3 : Order : Squaliformes, genus *Zameus* and to No. 4 : Order : Orectolobiformes, genus *Sutorectus*. A general glossary is included.

### No. 1b : Order : Hexanchiformes Family : Chlamydoselachidae

### Introduction

This issue deals with the hexanchiform family Chlamydoselachidae.

The hexanchiformes comprise only the two families : Chlamydoselachidae and Hexanchidae. The latter has been treated in Part A, No. 1. of this series. The Chlamydoselachidae are monotypic with the monotypic genus *Chlamydoselachus*. The teeth of *C. anguineus* were illustrated and or described before by GUDGER, 1933, SMITH, 1937, BASS, D'AUBREY & KISTNASAMY, 1975, PFEIL, 1983. New considerations of its root structure made it necessary to redescribe and illustrate the teeth of this species and comment on its odontology.

The systematic arrangement of the order is based on COMPAGNO, (1984) and the results of the present study differ from the latter classification. However, the authors will here not draw any nomenclatorially valid conclusions from their odontological results. Being aware of dealing with one complex of characters only, they will present their odontological results and leave it to following revising authors to incorporate also odontological points of view in a full systematic review with possible taxonomic and nomenclatorial changes.

The original literature reference of each specific taxon will be given in the descriptive part, respectively, and not be repeated in the bibliography.

### Systematics and material

#### ORDER : HEXANCHIFORMES sensu COMPAGNO (1984)

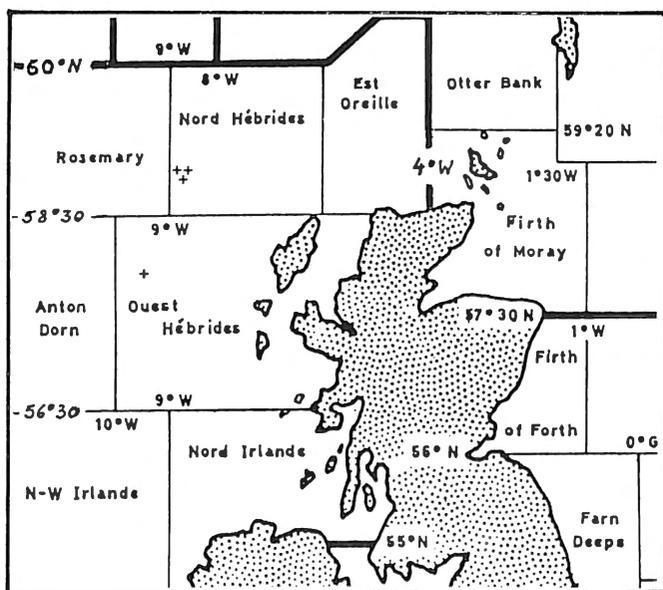
Family : Chlamydoselachidae GARMAN, 1884  
Genus : *Chlamydoselachus* GARMAN, 1884  
Type species : *Chlamydoselachus anguineus*  
GARMAN, 1884

*Chlamydoselachus anguineus* GARMAN, 1884, Bulletin Essex Institute. 16 : 3

The teeth of the following 10 specimens were examined :

Male	Female
110 cm Japan	95 cm Japan
125 cm Japan	131 cm North Atlantic
137 cm North Atlantic	150 cm Japan
138 cm North Atlantic	152 cm Japan
	157 cm North Atlantic
	159 cm North Atlantic

For whom it concerns the localization of the North Atlantic specimens are noted in the map below.



+ : Localization of the North-Atlantic specimens

**South Hebrides, 57°35'N - 09°25'W :**

23 March 1980 (early in the morning), one female of 131 cm (t.l.), on muddy bottom, 920 m depth.

Coll. P. Gueguen.

**North Hebrides, 59°10'N - 08°55'W :**

Night of 15/16th May 1980, one female of 159 cm (t.l.), and two males of 137 and 138 cm (t.l.), on muddy bottom, 680-720 m depth.

Male 137 cm in the Coll. Lab. Biol. Marine, Concarneau; the 2 other specimens Coll. J. Herman.

The precise data concerning the finding of the fifth specimen were lost, but it was a female of 157 cm (t.l.) caught in "the same area and at the same depth", spring 1985.

Coll. A. Bouvry.

## Descriptions of the odontological morphotypes

### HETERODONTY

Chlamydoselachidae are very slightly gradient monognathic heterodont. This is in contrast to the family Hexanchidae. Neither sexual, nor ontogenetic heterodonty has been observed.

*Chlamydoselachus anguineus* GARMAN, 1884  
(Figure 1, plates 1 and 2)

This species exhibits extremely wide interspaces between the tooth rows, which is about two times as broad as the teeth. This interspace is filled by gum tissue, presenting small dermal denticles.

The teeth have three large cusps : a central, distal and mesial one of subequal size. The distal cusp is oblique distally but slightly mesially bent, while the mesial cusp is oblique mesially but slightly bent distally. All three cusps are about equally large and strongly bent inward. A small, well developed cusplet is present at each side of the central cusp, each about one fourth as long as the cusps. All cutting edges are smooth.

The hemiaulacorhizid root is rather flat, and has two parallel lobelike extensions directed inward, which fit into two basal outer depressions of the previous tooth of the row, and provide transversal interlocking.

The teeth are hemicentimetrical in range.

The inner face of the crown is formed by the three strongly convex cusps, which are not merged basally, but separately having their own shape. An uvula and ornamentation are absent. Likewise is the outer face of the crown formed by the three convex cusps also exhibiting their individual face shape.

Poorly developed, short costules are present at the base of each cusp. An apron is absent.

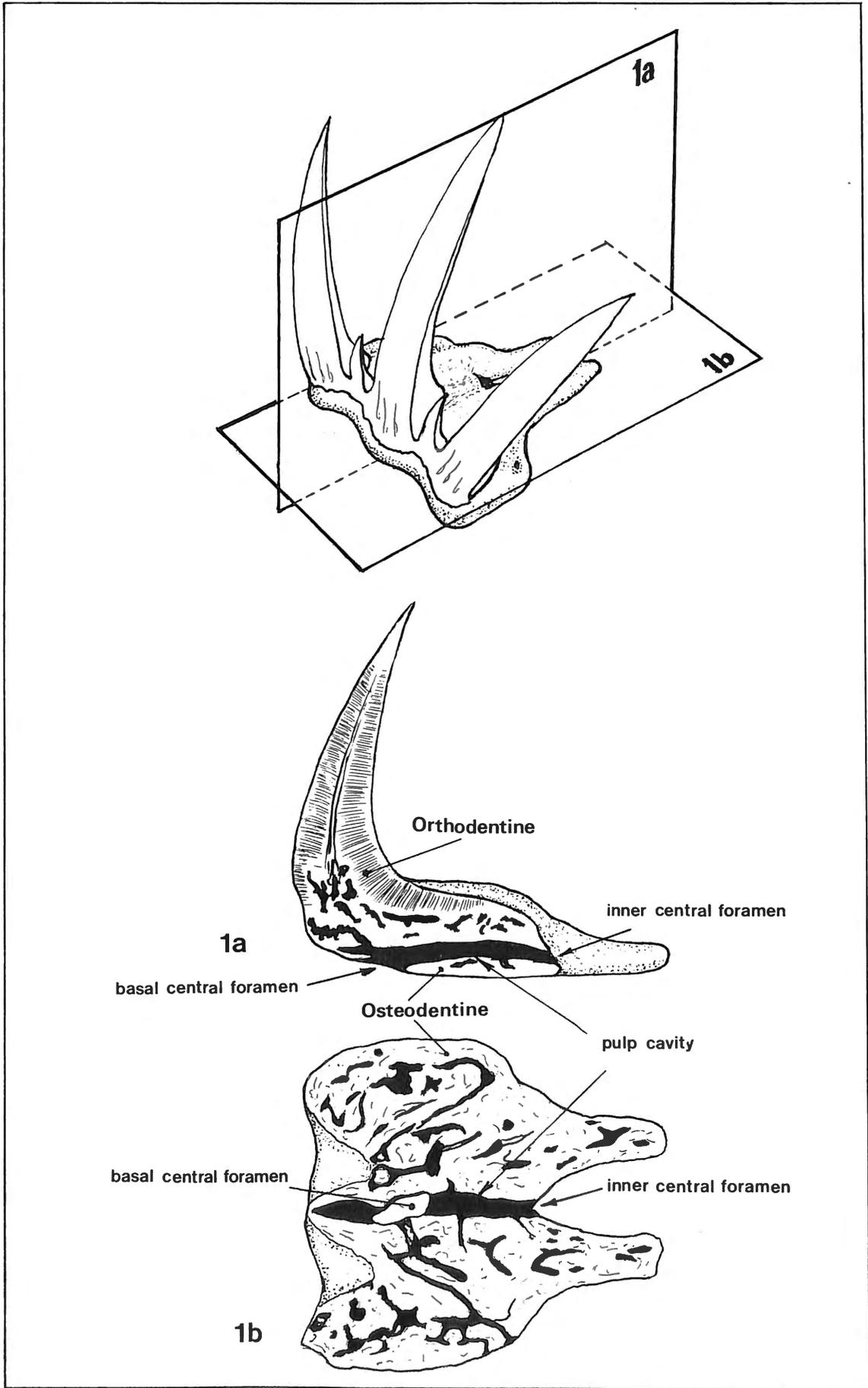
The basal face of the root presents a rather flat and broad root base, which may be divided into two more or less symmetrical mesial and distal parts. Both parts have a depression in the outer section and an elongated, narrow, inner extension.

A large, ovalshaped, central foramen is present on the outer section of the root base, on the junction of both mesial and distal root parts. Except in both mesial and distal depressions, small foramina are randomly scattered over the root base.

The inner face of the root shows a large foramen in the centre of the extensions junction. Some additional smaller foramina are randomly scattered. Both mesial and distal root parts are convex.

The outer face of the root shows only the mesial and distal depressions.

Figure 1. – *Histotype of Chlamydoselachus teeth.*



## DIAGNOSIS

Each tooth shows three large separate cusps, not merging with each other basally, nor with the inner or outer crown base. A cusplet flanks median cusp at each side. Two rows are separated by wide interspaces.

The root has a central pulp cavity (see figure 1), expanding in inner-outer direction, with a large central inner foramen and a large basal foramen. This root type can be considered as an extraordinary kind of hemiaulacorhizy.

The root has a flat base with two inner, parallel extensions. These extensions provide transversal interlocking by fitting into the outer basal depressions of the previous tooth of the row.

## CONCLUSIONS

Three separated (principal) cusps, with a small cusplet in between them, as well as the broad interspaces between the tooth rows indicate a possible ancient development of merging originally three separate tooth rows into one in *Chlamydoselachus anguineus*.

A hemiaulacorhizid root extended inward, with a flat root base and transversal interlocking of rows are all typical features only found in orectolobiform genera.

Six pairs of gill slits remains as most important character shared by Chlamydoselachidae and Hexanchidae, which according to SHIRAI (1992) do not support a monophyly of both hexanchiform families.

Judging from odontological results presented here, Chlamydoselachidae have little in common with Hexanchidae, whereas they show similarity with the Orectolobiformes.

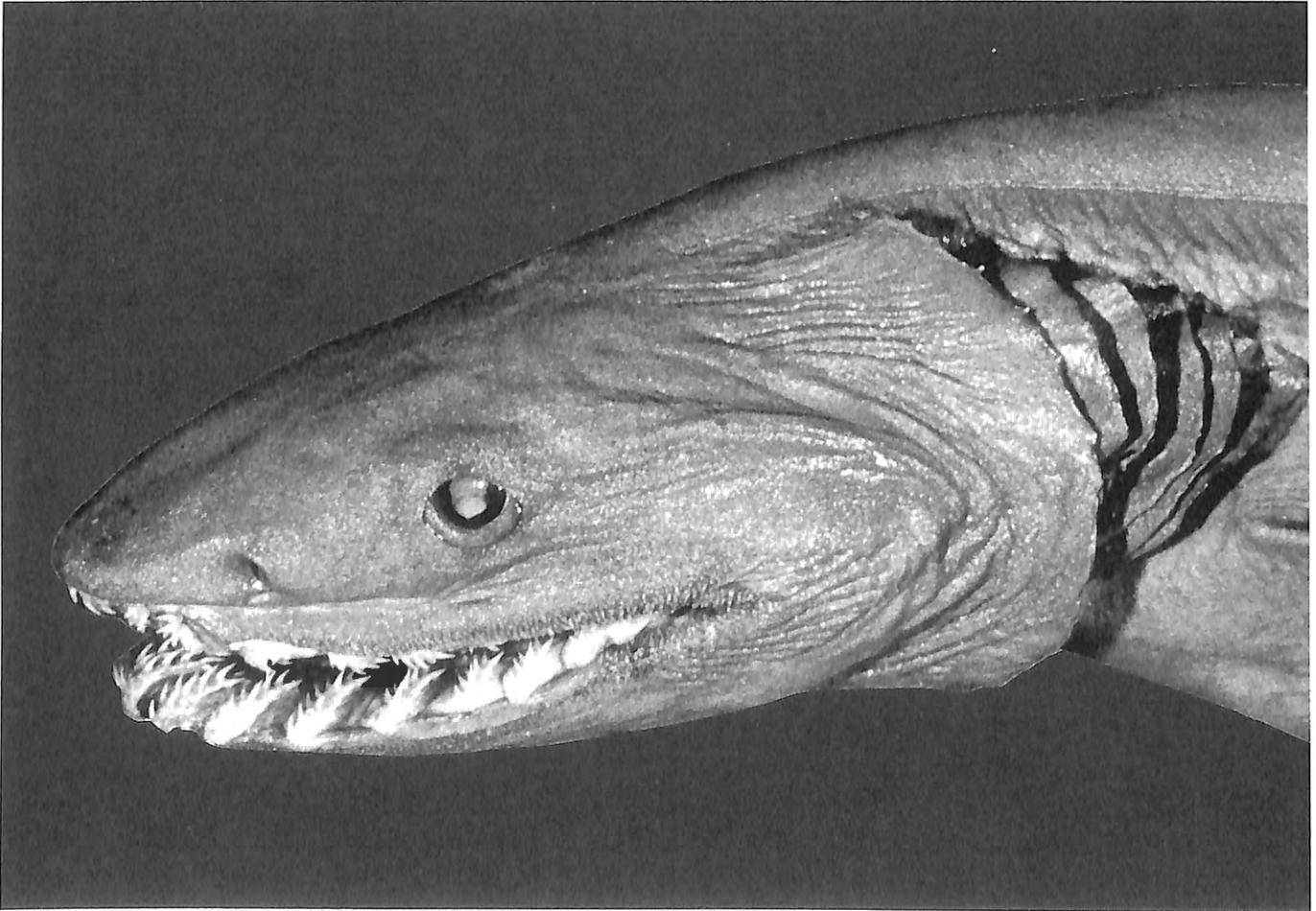


Plate 1. – *Chlamydoselachus anguineus* GARMAN, 1884. Head of a female of 159 cm (t.l.), North Atlantic, caught 15/16 May 1980, 59°10'N-08°55' W, 680-720 m.

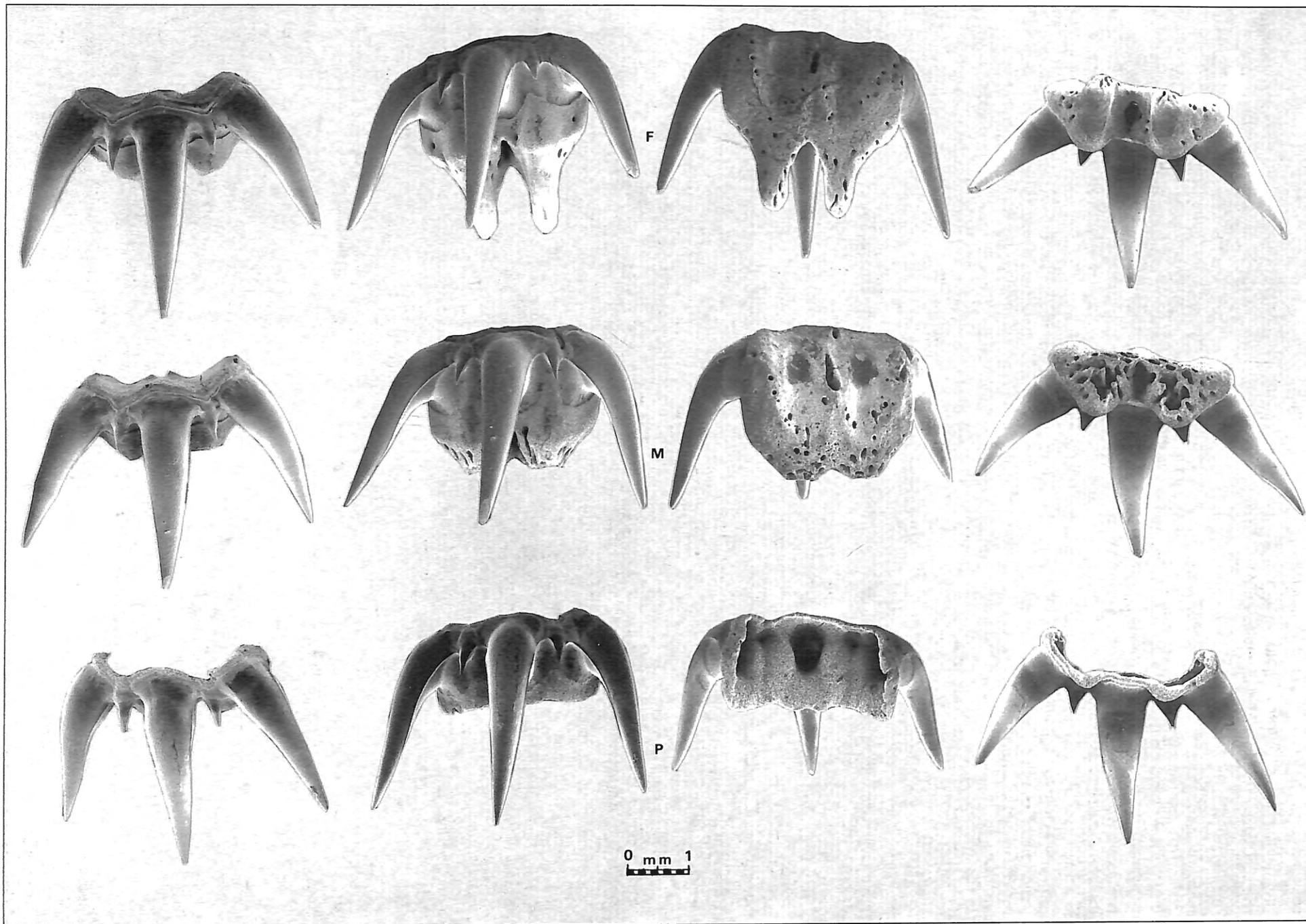


Plate 2. – *Chlamydoselachus anguineus* GARMAN, 1884. Three teeth of the second upper right row in outer, occlusal basal and inner views of a male of 125 cm (t.l.), Japan. F : functional, M : almost developed, P : first stage of development.

No. 5 :  
**Order : Heterodontiformes**  
**Family : Heterodontidae**

### Introduction

After the recent most account by COMPAGNO (1984) are the Heterodontiformes monotypic with only the monotypic family Heterodontidae. Generotype of *Heterodontus* is *H. portusjacksoni* GILL (1862) had assigned *Heterodontus quoyi*, *Heterodontus francisci* and *Heterodontus portusjacksoni* to his new genera *Tropidodus*, *Gyropleurodus* and *Heterodontus* BLAINVILLE, respectively, based on differences in their tooth morphology. Teeth of some species were illustrated by SMITH, 1942 and BASS, D'AUBREY and KISTNASAMY, 1975. Ontogenetic odontology was brilliantly described and illustrated by REIF (1976). The odontological features given remain insufficient for the detailed approach of the present. The tooth morphology of these three species is therefore here illustrated by SEM-photographs in a consistent way and reinvestigated in detail. The classification follows COMPAGNO (1984).

### Systematics and material

ORDER : HETERODONTIFORMES  
 sensu COMPAGNO (1984)

Family : Heterodontidae, GRAY, 1851  
 Genus : *Heterodontus*, BLAINVILLE, 1816  
 Type species : *Heterodontus portusjacksoni*

The teeth of 22 specimens of four species were examined :

<i>Heterodontus francisci</i>	4 males	4 females
<i>Heterodontus mexicanus</i>	3 males	3 females
<i>Heterodontus portusjacksoni</i>	6 males	1 female
<i>Heterodontus quoyi</i>	1 male	

### Descriptions of the odontological morphotypes

#### HETERODONTY

Heterodontidae have a disjunct monognathic heterodonty due to the shape of their jaws. The dentition of upper and lower jaws of adult specimens can be roughly subdivided into about four to six anterior and about four to six lateral tooth rows depending on the age of the individual. The anterior teeth are transversally short, exhibit cuspidity and shows arched roots in basal view. The lateral and posterior teeth are transversally

long, don't show true cuspidity and almost straight roots in basal view. This kind of dentition and individual tooth morphology is so far only known in Heterodontidae and is understood as an ancient development, which exists already for a very long period (CAPPETTA, 1987).

A strong ontogenetic heterodonty is documented by gradient monognathic heterodonty in juveniles, with strong cuspidity of the crown, becoming less distinct in lateral teeth.

The principal cusp is flanked by two cusplets at each side in juveniles, adults have only one cusplet at each side. Juveniles also have less tooth rows than adults.

Sexual heterodonty was not observed.

Due to the disjunct monognathic heterodonty it was necessary to describe anterior and lateral teeth separately.

Genus : *Heterodontus* BLAINVILLE, 1816

This genus comprises eight species : *H. francisci*, *H. galeatus*, *H. japonicus*, *H. mexicanus*, *H. portusjacksoni* (type species), *H. quoyi*, *H. ramalheira* and *H. zebra*. *H. francisci* and *H. quoyi* are the type species of the generic synonyms *Tropidodus* and *Gyropleurodus*, respectively.

*Heterodontus portusjacksoni* (MEYER, 1793)  
 (Plates 3 to 22)

*Squalus portusjacksoni* MEYER, 1793, Systematisch summarische Übersicht der neuesten zoologischen Entdeckungen in Neuholland und Afrika : 71.

The anterior teeth of both upper and lower jaws have a broad, relatively short and erect principal cusp flanked at each side by a relatively short and erect cusplet of which the cutting edges at the distal and mesial tooth parts are merged with the outer crown base. The principal cusp as well as the mesial cusplet become more oblique on teeth close to the lateral ones.

The anaulacorhizid root is transversally compressed. The teeth are plurimillimetrical in range.

The inner face of the principal cusp is strongly convex. A small uvula is present at the central crown base. Basal ornamentation and costules or striae are absent.

The outer face of the principal cusp is slightly convex. An extremely broad apron, occupying the entire crown base overhangs the crown root junction. A weak reticulated basal ornamentation is present on the apron on teeth close to the lateral ones.

The root is arched, almost v-shaped in basal view, but not lobated.

The inner face of the root is strongly convex and shows a central protuberation, with a well developed foramen. A mesial and distal depression of equal size, each with a central foramen, are present at both sides of the protuberation in teeth close to the symphysis. The distal depression becomes larger than the mesial one in teeth closer to the lateral ones and has up to three foramina. The outer face of the root is strongly concave and shows a large central foramen. One or two smaller foramina are present near the crown-root junction at the mesial and distal root parts.

The lateral and posterior teeth of both upper and lower jaws are relatively flat, and inner and outer parts of the crown are divided by a rounded median keel. This keel is still bent as a relic of a cusplet in teeth close to the anterior ones, which are transversally long, becoming shorter toward the commissure. In occlusal view the inner part of the crown is slightly broader than the outer part in inner-outer direction, while the inner part is strongly distally directed in contrast to the outer part, which is strongly mesially directed. The root in basal view is narrow in inner-outer direction, transversally long and still slightly arched in teeth close to the anterior ones, but almost straight in teeth toward the commissure.

The teeth are plurimillimetrical to hemicentimetrical in range.

Both inner and outer parts of the crown are strongly convex, and show a well developed coarse reticulated ornamentation all over, which becomes slightly coarser toward the median keel. Another finer reticulation is present within the less coarse ornamentation toward the crown root junction.

Both inner and outer faces of the root show a series of about 20 foramina, of which often a central one of is slightly enlarged.

*Heterodontus francisci* (GIRARD, 1854)  
(Plates 23 to 30)

*Cestracion francisci* GIRARD, 1854, Proceeding of the Academy of Natural Science Philadelphia, 7(6) : 196.

The anterior teeth of both upper and lower jaws have a broad, relatively short and erect principal cusp flanked at each side by a relatively short, poorly developed cusplet. The cutting edges at the distal and mesial tooth parts are merged with the outer crown base. The principal cusp, as well as the mesial cusplet become more oblique and lower on teeth close to the lateral ones.

The anulacorhizid root is longitudinally compressed. The teeth are plurimillimetrical in range.

The inner face of the principal cusp is strongly convex. A small uvula is present at the central crown base. Basal ornamentation and costules or striae are absent.

The outer face of the principal cusp is slightly convex. An extremely broad apron, occupying the entire crown base, overhangs the crown root junction. A reticulated basal ornamentation is present on the apron on teeth close to the lateral ones.

The root is arched, almost v-shaped in basal view, but not lobated.

The inner face of the root is strongly convex, shows a central protuberation, and has a well developed foramen. A mesial and distal depression of equal size, each with a central foramen are present at both sides of the protuberation in teeth close to the symphysis. The distal depression becomes larger than the mesial one in teeth closer to the lateral ones and has up to three foramina. The outer face of the root is strongly concave, and shows a large central foramen. One or two smaller foramina are present near the crown-root junction at the mesial and distal root parts.

The lateral and posterior teeth of both upper and lower jaws are relatively flat, transversally long, becoming shorter toward the commissure. In occlusal view, the inner part of the crown is slightly broader than the outer part in inner-outer direction and the inner part is strongly distally directed in contrast to the outer part, which is strongly mesially directed. Both, inner and outer parts of the crown are divided by a rounded median keel. This keel shows a blunt relic of a cusp and sometimes even remains of a distal and mesial cusplet.

The root in basal view is narrow in inner-outer direction, transversally long, and still slightly arched in teeth close to the anterior ones, but almost straight in teeth toward the commissure.

The teeth are plurimillimetrical to hemicentimetrical in range.

Both, inner and outer parts of the crown are strongly convex, and show a well developed, coarse, reticulated ornamentation all over, which becomes slightly coarser toward the median keel. Another finer reticulation is present within the less coarse ornamentation toward the crown root junction.

Both inner and outer faces of the root show a series of about 20 foramina, of which often a central one is slightly enlarged.

*Heterodontus quoyi* (FREMENVILLE, 1840)  
(Plates 31 to 38)

*Cestracion quoyi* FREMENVILLE, 1840, Magazine of the zoological series. 2(2) : 1-3, pl. 3.

The anterior teeth of both upper and lower jaws have a broad, relatively short and erect principal cusp, flanked on each side by a relatively short and erect cusplet of which the cutting edges at the distal and mesial tooth

parts are merged with the outer crown base. The principal cusp, as well as the mesial cusplet becomes more oblique on teeth close to the lateral ones.

The anaulacorhizid root is transversally compressed. The teeth are plurimillimetrical in range.

The inner face of the principal cusp is strongly convex. A small uvula is present at the central crown base. Basal ornamentation and costules or striae are absent.

The outer face of the principal cusp is slightly convex. An extremely broad apron, occupying the entire crown base, overhangs the crown root junction. Weak, irregular, basal costules are present on the apron on teeth close to the lateral ones.

The root is arched, almost v-shaped in basal view, but not lobated.

The inner face of the root is strongly convex, and shows a central protuberation, with a well developed foramen. A mesial and distal depression of equal size, each with a central foramen, are present at both sides of the protuberation, in teeth close to the symphysis. The distal depression becomes larger than the mesial one in teeth closer to the lateral ones, and has up to three foramina.

The outer face of the root is strongly concave, and shows a large central foramen. One or two smaller foramina are present near the crown-root junction at the mesial and distal root parts.

The lateral and posterior teeth of both upper and lower jaws are relatively flat, and inner and outer part of the crown are divided by a rounded median keel. This keel is still bent as a relic of a cusplet in teeth close to the anterior ones, which are transversally long, becoming shorter toward the commissure. In occlusal view the inner part of the crown is slightly broader than the outer part in inner-outer direction, and the inner part is strongly distally directed in contrast to the outer part, which is strongly mesially directed.

The root in basal view, is narrow in inner-outer direction transversally long, and still slightly arched in teeth close to the anterior ones, but almost straight in teeth toward the commissure.

The teeth are plurimillimetrical to hemicentimetrical in range.

Both, inner and outer parts of the crown are strongly convex, and show a poorly developed, coarse, more or less reticulated ornamentation, which becomes slightly coarser toward the median keel.

Both, inner and outer faces of the root show a series of about 20 foramina, of which often a central one is slightly enlarged.

#### DIAGNOSIS

The following odontological differences were found between *Heterodontus francisci*, *Heterodontus portusjacksoni* and *Heterodontus quoyi* :

– Anterior teeth with poorly developed cusplets, and lateral teeth with a median keel, bearing a relic of a cusp and even cusplets in *Heterodontus francisci*, mostly missing in *Heterodontus portusjacksoni* and *Heterodontus quoyi*.

– Lateral teeth of *Heterodontus quoyi* with poorly developed ornamentation, in contrast to a well developed ornamentation in both *Heterodontus portusjacksoni* and *Heterodontus francisci*.

#### CONCLUSIONS

There are only slight odontological differences between the three species *Heterodontus francisci*, *Heterodontus portusjacksoni* and *Heterodontus quoyi* : namely in distinctness of cusplets in anterior teeth, and outer basal ornamentation; also regarding the variations of the median keel in lateral and posterior teeth, and distinctness of the inner and outer ornamentation on lateral teeth. All these are comparatively insignificant on the generic level, but may be used for interspecific distinctions. GILL's (1862) proposal is thus not supported by odontological arguments.

#### The following material was borrowed for this study :

Plates 3-6	<i>Heterodontus portusjacksoni</i>	AMS IB-6521
Plates 7-15	<i>Heterodontus portusjacksoni</i>	WAM P5185-001
Plates 16-23	<i>Heterodontus portusjacksoni</i>	WAM P24545-001
Plates 24-33	<i>Heterodontus francisci</i>	LACM W59-5
Plates 34-39	<i>Heterodontus quoyi</i>	LACM 44006-3

#### Legend for Heterodontidae

Considering the unique heterodonty of the Heterodontidae, the authors chose to use a numerical system on their illustrations to explain the relative position of the selected teeth illustrated of both jaws. The consistent system is the following : number 1 shows the parasymphysial; the following numbers illustrate the anteriors and the laterals, and the last number equals the posterior.

No. 6 :  
 Order : Lamniformes  
 Families : Cetorhinidae, Megachasmidae

### Introduction

Only the teeth of two out of seven lamniform families are considered to be micro-teeth and will be dealt with in this series, namely of the monotypic cetorhinid genus *Cetorhinus* and the monotypic megachasmid genus *Megachasma*. The teeth of Cetorhinidae were described and illustrated earlier by HERMAN (1979) and VAN DEN BOSCH (1984). Only a single tooth of *Megachasma pelagios* was illustrated by TAYLOR, COMPAGNO & STRUHSAKER, 1983. However, the illustrations and descriptions by these authors were insufficient for these series and not comparable with its other contributions and will therefore commented on in the way and with the terminology used in this series.

The systematic arrangement of the orders mentioned is based on COMPAGNO, 1984.

The original literature reference of each specific taxon will be given in the descriptive part, respectively, and not be repeated in the bibliography.

### Systematics and material

ORDER : LAMNIFORMES  
 sensu COMPAGNO (1984)

The order comprises 7 families : Alopiidae, Cetorhinidae, Megachasmidae, Mitsukurinidae, Lamnidae, Odontaspidae and Pseudocarcharinidae.

Only two families possess micro-teeth and are relevant for this series :

Family : Cetorhinidae GILL, 1862  
 Genus : *Cetorhinus* BLAINVILLE, 1816  
 Type species : *Cetorhinus maximus*

Family : Megachasmidae  
 TAYLOR, COMPAGNO & STRUHSAKER, 1983  
 Genus : *Megachasma*  
 TAYLOR, COMPAGNO & STRUHSAKER, 1983  
 Type species : *Megachasma pelagios*

The teeth of seven specimens of the two species were examined :

<i>Cetorhinus maximus</i>	4 males	2 females
<i>Megachasma pelagios</i>	1 male	

### Descriptions of the odontological morphotypes

Family : Cetorhinidae GILL, 1862

#### HETERODONTY

Due to adaptation to filter-feeding, the teeth of Cetorhinidae are rudimentary remains, which results in irregular shapes. The Cetorhinidae are gradient monognathic heterodont. Sexual heterodonty has not been observed. However a strong ontogenetic heterodonty is present. Therefore teeth of both juvenile and adult specimens will be described and illustrated.

Genus : *Cetorhinus* BLAINVILLE, 1816

This genus is monotypic with the type species *Cetorhinus maximus*.

*Cetorhinus maximus* (GUNNERUS, 1765)  
 (Plates 39 to 44)

*Squalus maximus* GUNNERUS, 1765, K.-norske Vidensk-Selsk. Skr. Trondheim : 33, pl. 2.

The teeth of juvenile specimens have an oval-shaped, principal cusp, which is strongly directed inward. Cusplets are absent.

The unlobated root is osteodont, and more or less bulb-shaped.

The inner face of the crown is very low and slightly convex, and ornamented by fine, irregularly shaped costules. An uvula is absent.

The outer face of the crown is rather convex. The crown base slightly overhangs the crown-root junction. Strongly developed, irregularly shaped protuberances are present at the crown base, forming a pseudo-collar. Well developed and irregularly shaped, coarse costules are present also on these protuberances. Finer, longer, more regularly shaped costules run more or less parallel from the pseudo-collar toward the crown-root junction.

Fine, short, more or less irregularly arranged costules run from the pseudo-collar toward the apex of the crown. An apron is absent.

The root is more or less oval-shaped, and strongly convex in inner and outer view, and shows numerous scattered foramina. In basal view, the root is more or less circular and convex. The teeth of adult specimens have an oval-shaped, elongated principal cusp, which is directed inward and often twisted in its vertical axis. Cusplets are absent.

The osteodont root of anterior teeth is more or less circular in inner and outer view, broader and slightly arched also in lateral teeth.

The inner face of the crown is convex. A basal ornamentation is sometimes shown by very fine, short, irregularly shaped costules. An uvula is absent.

The outer face of the crown is convex. The crown base does not overhang the crown-root junction. Poorly developed, irregularly shaped protuberances are present at the crown base; short well developed costules run more or less irregularly from these protuberances half way to the crown's apex. The pseudo-collar and apron are absent.

The inner and outer faces of the root are strongly convex and show numerous scattered foramina. An uvula is absent.

Family : Megachasmidae

TAYLOR, COMPAGNO & STRUHSAKER, 1983

HETERODONTY

Although adapting filter feeding the tooth shapes are stable. Its heterodonty is to be considered gradient monognathic heterodont, however, there is an extremely wider symphysial interspace, which is larger in upper than in lower jaw. This results in a slight difference of the gradient heterodonty in upper and lower jaws.

Genus : *Megachasma*

TAYLOR, COMPAGNO & STRUHSAKER, 1983

The genus is monotypic with the type species *Megachasma pelagios*.

*Megachasma pelagios*

TAYLOR, COMPAGNO & STRUHSAKER, 1983  
(Plates 45 to 48)

*Megachasma pelagios*, TAYLOR, COMPAGNO & STRUHSAKER, 1983. Proceedings of the Californian Academy Science; (4) 43(8) : 87.

The teeth of this species have a broad based, elongated principal cusp. Because the cutting edges are poorly developed or even absent, the inner and outer faces are not clearly separated. The crown of anterior teeth is twice as long as the base, which changes in anterior and posterior teeth to a broader crown base and a lower principal cusp. A distal cusplet, also without cutting edges is present on the lower posterior teeth.

The osteodont root has randomly scattered, rather large foramina. The teeth are hemicentimetrical in range.

The inner face of the crown is strongly convex. An ornamentation or uvula are absent.

The outer face of the crown is convex, showing fine, poorly developed costules on the lateral and posterior teeth. An apron is absent.

The inner face of the root is extremely protuberated and strongly convex. Randomly scattered foramina are present all over the inner root face, plus one or two larger, central foramina.

The outer face of the root shows a rather large central depression with randomly scattered foramina.

Anterior teeth sometimes show a lot of foramina, lined up on the crown root junction.

The basal face of the root is slightly convex and presents an outer, central depression joining the central depression of the outer face. An inner pseudo-median groove with some larger foramina is also present.

DIAGNOSIS

The dentition of *Cetorhinus maximus* is rather unique. A strong ontogenetic heterodonty has been observed, as well as an irregularity of tooth shape and size. The root is strictly osteodont.

The dentition of *Megachasma pelagios* is also rather unique, in that the teeth are of equal shape although this species has also adapted to filter-feeding. The root is osteodont however has one or sometimes two pseudo-median grooves. These grooves include the main foramina for the vascularization canals, which do not lead to a pulp cavity, as in the holaulacorhizid type of root.

CONCLUSIONS

*Cetorhinidae*

The shape of the teeth is irregular.

Ontogenetic heterodonty is documented by a strongly developed ornamentation in juveniles. These ontogenetic differences may be obscured in older specimens by the irregular tooth shape.

*Megachasmidae*

Teeth are of equal size and shape. This may indicate, that the adaption to their filter-feeding habit is still in progress.

All filter-feeding sharks share some odontological characteristics : their teeth become smaller to even rudimentary, have rather massive roots, strongly protuberated inner faces, and the principal cusp is strongly curving inward.

**The following material was borrowed for this study :**

Plates 45 to 48

*Megachasma pelagios*

LACM 43745-1

### Addendum 1 to Contribution No. 3

ORDER : SQUALIFORMES

Family : Squalidae - Genus *Zameus*

#### Introduction

Specimens of the squaliform species *Zameus squamulosus* and *Scymnodon obscurus* have become available for examination.

The generic distinction of the taxa *Scymnodon*, *Scymnodalarias* and *Zameus* have recently been in discussion as well as a possible synonymy of *Zameus squamulosus* and *Scymnodon obscurus*. TANIUCHI and GARRICK (1986) resurrected the generic taxon *Zameus* JORDAN and FOWLER, 1903 and simultaneously synonymized *Scymnodon obscurus* (VAILLANT, 1888) with its type species *Z. squamulosus* (GÜNTHER, 1877) formerly also considered as a species of *Scymnodon*.

The tooth morphology of the species mentioned above will be commented on. They will also be described and illustrated. Teeth of *Scymnodon ringens*, *Scymnodalarias albicauda* were dealt with in part A No. 3 of this series.

#### Material

The teeth of 5 specimens of two species were examined in addition to those of 49 individuals of *Scymnodalarias albicauda* (1 female) and *Scymnodon ringens* (18 males, 30 females) published in Part A : No. 3 of this series :

<i>Scymnodon obscurus</i>	2 males	2 females
<i>Zameus squamulosus</i>	1 male	

#### Description of the odontological morphotypes

*Scymnodon squamulosus* (GÜNTHER, 1877)  
(Text plate 1, plate 49)

*Centrophorus squamulosus* GÜNTHER, 1877. Annual Magazine of natural History. (4), 20 (119) : 433.

This species shows a strong dignathic heterodonty and a weak gradient monognathic heterodonty. The tooth root is anaulacorhizid. The upper teeth are hemicentrometrical in range.

##### Upper jaw

The teeth have an elongated, narrow principal cusp, which has a slight constriction near the crown base. Cusplets are absent. The mesial and distal cutting edges are slightly sigmoidal. The root is bilobated in anterior

and lateral teeth, becoming quadrangular toward the commissure. The principal cusp is inclined toward the commissure in latero-posterior teeth.

The inner face of the crown is convex. An uvula is absent, as well as an inner ornamentation.

The outer face of the crown is slightly convex. An apron is absent. The crown base is depressed, with a mesial and distal, vertical ridge. An outer ornamentation is absent.

The inner face of the root joins the crown surface in an angle. A central foramen is present on the crown-root junction. A short, narrow and shallow, basal sulcus is present.

The outer face of the root has a central root depression. A few randomly scattered foramina may be present on latero-posterior and commissural teeth.

##### Lower teeth

The teeth are strongly compressed. The height of the triangular crown is slightly higher than the crown base width.

The principal cusp is inclined toward the commissure, joining the distal blade in a notch. The rectangular root is narrowing from below the crown-root junction downward, becoming more oblique toward the commissure.

The inner face of the crown is flat to very weakly convex. The basal part is slightly depressed. A well developed uvula is absent.

The outer face of the crown is also weakly convex. A relatively broad, subquadrangularly shaped apron not overhanging the root but keeping level with its surface, is present.

The inner face of the root is strongly convex near the crown-root junction, forming a longitudinal ridge. A central and mesial aperture is situated on the ridge. A rather long basal sulcus is present.

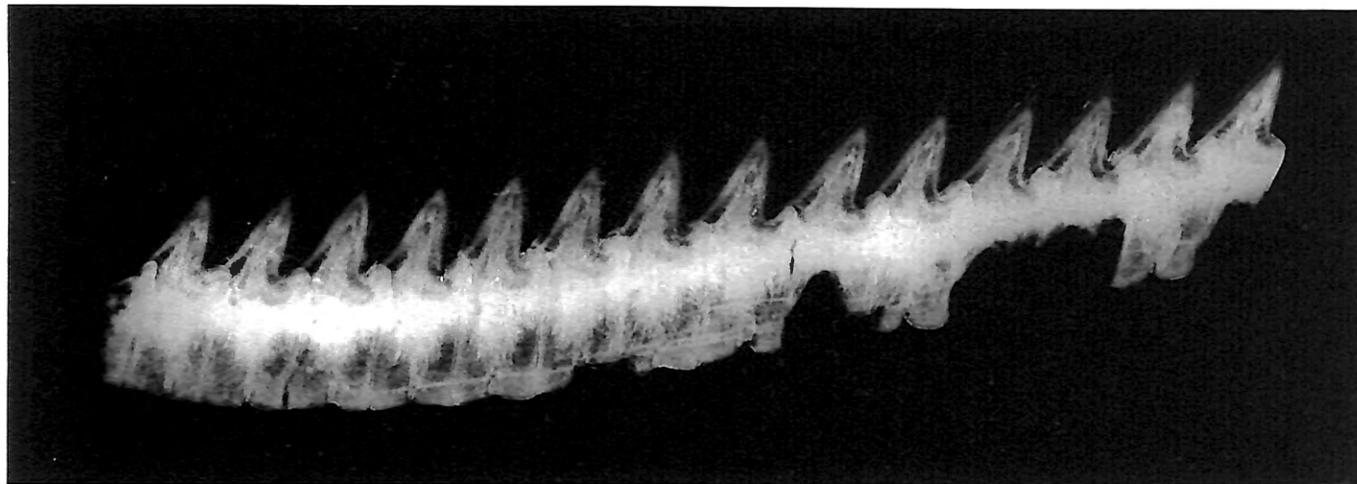
A distal depression, as result of longitudinally interlocking of the tooth rows, is poorly developed.

The outer face of the root shows one or two mesial and distal apertures at both sides of the apron. These are more or less vertically arranged and horizontally expanded. Basal foramina are absent. The mesial depression is poorly developed.

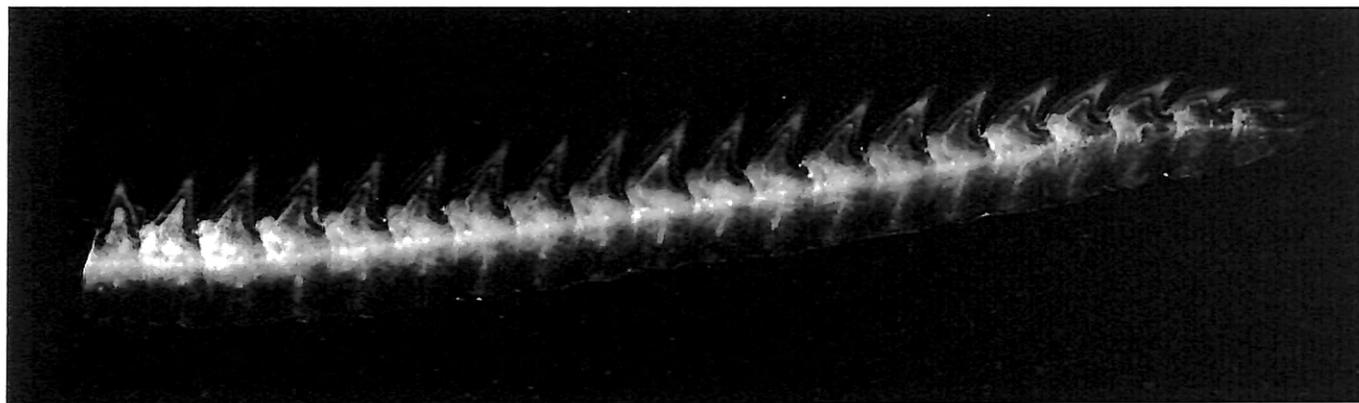
*Scymnodon obscurus* (VAILLANT, 1888)  
(Text plate 2, plate 50)

*Centroscymnus obscurus* VAILLANT, 1888. Expédition Scientifique du "Travailleur" et "Talisman", 1880-1883, Paris, Poissons : 67.

This species shows a strong dignathic heterodonty as well as a weak gradient monognathic heterodonty. The tooth roots are anaulacorhizid.



Text plate 1. – *Scymnodon squamulosus* (GÜNTHER, 1877). Male 49 cm (t.l.), Japan. Diagraphy of lower teeth (formerly *Zameus*).



Text plate 2. – *Scymnodon obscurus* (VAILLANT, 1888). Male 41 cm (t.l.), Senegal. Diagraphy of lower teeth..

*Upper jaw*

The teeth have an elongated, narrow principal cusp with a slight constriction near the crown base. Cusplets are absent. The mesial and distal cutting edges are strongly sigmoidal. The root is bilobated on anterior and lateral teeth becoming quadrangular in teeth toward the commissure. The principal cusp is inclined toward the commissure in latero-posterior teeth.

The inner face of the crown is convex. An uvula is absent, as well as an inner ornamentation.

The outer face of the crown is slightly convex. An apron is absent. The crown base is depressed, with a mesial and distal, vertical ridge. An outer ornamentation is absent. The inner face of the root joins the crown surface in an angle. A central foramen is present on crown-root junction. A short, narrow, shallow, basal sulcus is present.

The outer face of the root has a central root depression. A few randomly scattered foramina may be present on latero-posterior and commissural teeth.

*Lower jaw*

The teeth are strongly compressed. The height of the triangular crown equals the crown base width.

The slightly arched principal cusp is inclined toward the commissure, joining the distal blade in a notch. The rectangular root is narrowing from below the crown-root junction downward becoming more oblique toward the commissure.

The inner face of the crown is flat to very weakly convex. The basal part is slightly depressed. A well developed uvula is absent.

The outer face of the crown is also weakly convex. A relatively broad, subquadrangularly shaped apron not overhanging the root but keeping level with its surface. The inner face of the root is strongly convex near the crown-root junction, forming a longitudinal ridge. A central and mesial aperture is situated on the ridge. A rather long basal sulcus is present.

A distal depression, as result of longitudinally interlocking of the tooth rows, is poorly developed.

The outer face of the root shows three to four mesial apertures at both sides of the apron. These apertures are more or less vertically arranged and horizontally expanded. Three to four small, horizontally arranged basal foramina may also be present. The mesial depression is poorly developed.

## DIAGNOSIS

The following odontological differences have been observed :

<i>Scymnodon squamulosus</i>	<i>Scymnodon obscurus</i>
– Principal cusp of the upper teeth slightly sigmoidal.	Principal cusp of the upper teeth strongly sigmoidal.
– Crown height of the lower teeth equals the crown width, and is slightly arched.	Crown height of the lower teeth slightly higher than crown width.
– The outer face of the root with three to four mesial and distal, horizontally expanded apertures, as also up to four horizontally arranged basal foramina.	The outer face of the root with one or two mesial and distal, horizontally expanded apertures, basal foramina lacking.

The odontological differences between *Scymnodon ringens* and both *Scymnodon squamulosus* and *Zameus obscurus* are more significant :

The upper teeth of *Scymnodon ringens* have no bilobated root but is always quadrangular. The lower teeth have a shorter root and apron.

However *Scymnodalarias albicauda* shares, apart from costules on the lower part of its apron, most of the odontological characters of *Zameus squamulosus* and *Zameus obscurus*.

(see Part A. No. 3 of this series)

## CONCLUSIONS

The odontological differences between *Scymnodon obscurus* and *Scymnodon squamulosus* are minimal, which supports their specific synonymy and assigning both to the same genus.

The odontological characters of both species differ slightly from *Scymnodon ringens*, but are quite similar with *Scymnodalarias albicauda*. However, despite these interspecific differences rather, the general odontological characters of the four species are very similar and therefore the genera *Scymnodon* and *Scymnodalarias* might well be congeneric as well as both with *Zameus*.

**Addendum 1 to Part A : Contribution No. 4**

ORDER : ORECTOLOBIFORMES

Family : Orectolobidae - Genus *Sutorectus***Introduction**

Specimens of the orectolobid species *Sutorectus tentaculatus*, still lacking when the studies for Part A, No. 4 of this series were undertaken, became available for examination and allow this addendum and the comparison of *Sutorectus* with other orectolobid genera treated before in Part A, No. 4 of this series.

The odontological results will be presented as an aid for following revising authors to incorporate also these odontological points of view in a systematic revision with possible taxonomic and nomenclatorial changes.

**Material**

The teeth of two specimens were examined :  
*Sutorectus tentaculatus* 1 male 1 female (embryo)

**Description of the odontological morphotype**Genus *Sutorectus* WHITLEY, 1939

## HETERODONTY

The type species of this monotypic genus is strongly monognathic heterodont. Neither sexual, nor ontogenetic heterodonty could be examined, because the female embryo did not yet have developed teeth. The lower jaw halves are separated by a large symphyseal tooth.

*Sutorectus tentaculatus* (PETERS, 1864)  
(Plates 51 to 54)

*Crossorhinus tentaculatus* PETERS, 1864. Monatsberichte Akademie der Wissenschaften. Berlin, 123.

The anterior teeth of this species have a broad based, extremely elongated, erect principal cusp, which has extended, almost horizontal cutting edges, curving toward the crown base. The lateral teeth have a lower, slightly oblique principal cusp, but more extended cutting edges. The smooth cutting edges are as long as one third of the crown height at anterior, and as long as the crown height at lateral teeth. Cuspets are absent.

The hemiaulacorhizid root has two broad, flattened root lobes that are angled at the root base.

The teeth are pluricentimetric in range.

The outer face of the principal cusp is rather convex. A narrow apron at the crown base overhangs the crown root junction. Basal ornamentation is presented by well developed basal costules, which are even stronger developed in lateral and posterior teeth.

The inner face of the principal cusp is strongly convex. A narrow uvula is present at the central crown base, supported by a central root protuberation. Basal ornamentation or costules or striae are absent.

The outer face of the root shows both root lobes. Foramina are absent.

The inner face of the root shows a strongly developed central protuberation, with a well developed foramen. On the crown-root junction up to three foramina at anterior, and up to five at lateral teeth are present at both sides of the protuberation.

The flat, triangular shaped basal part of the root displays a large outer, central depression. Up to four large foramina are present in the depression. Numerous small foramina are scattered all over the slightly curved root lobes.

## DIAGNOSIS

*Sutorectus tentaculatus* differs from the other orectolobid taxa (cf. Part A, 4 of this series) only by having outer basal costules on lateral and posterior teeth, and an extremely large lower symphyseal tooth.

## CONCLUSIONS

The tooth morphology of *Sutorectus tentaculatus* is very similar to the other orectolobid taxa, which supports assignment to the Orectolobidae.

**The following material was borrowed for this study :**

Plates 51 to 54

*Sutorectus tentaculatus*

SAMA F7089

*Sutorectus tentaculatus*

SAMA F1956

### General glossary

(Applying to all previous issues of this series).

#### CONCERNING THE JAW

Anterior	Tooth position close to junction of left and right jaw parts halves.
Commissural	Tooth position near the end of jaw.
Dignathic	Heterodont by having different tooth morphology in upper and lower jaws.
File	Tooth row from symphysis toward end of jaw.
Heterodonty	Different tooth morphology within a tooth file. There are two types of heterodonty : dignathic and monognathic.
Homodonty	Uniform tooth morphology within a tooth file.
Lateral	Tooth positions half way along the jaw.
Longitudinal	Symphysial/commissural direction of a tooth file.
Monognathic	Heterodonty within one jaw only. (this can appear as gradient or disjunct)
Parasymphysial	First anterior tooth row, if a symphysial tooth row is absent.
Posterior	Tooth positions toward the angle of jaw.
Pseudosymphysial	One of the parasymphysial tooth rows placed in the position of the symphysial tooth row (symmetry).
Row	Tooth row from inner face to outer face of jaw.
Symphysial	Teeth at junction of both halves of a jaw.
Transversal	Outer/inner direction of a row.

#### CONCERNING THE TOOTH

An-, Hemi-, Hol- and Polyaulacorhizid	Concerning their vascularization, E. CASIER (1947) recognised and described 4 phylogenetically significant root types within the orthodont histotypes of elasmobranch teeth.
Anaulacorhizid	Vascularization through scattered foramina of equal size on both outer and inner faces, (e.g. Hexanchidae).

Hemiaulacorhizid	Vascularization through a median groove and 1 or 2 lateral foramina on inner face, (like in Squatinidae and Orectolobidae)
Holaulacorhizid	Vascularization through many small foramina concentrated in a median groove running from outer to inner face, (e.g. Rajidae)
Polyaulacorhizid	Vascularization through many small foramina concentrated in several grooves running parallel from outer to inner face, (e.g. Myliobatidae)
Apron	Expansion of the central part of the outer crown base.
Basal	Bottom face concerned.
Costules	Short, vertical ridges sometimes present on inner and/or outer crown base.
Crown	Enamelled tooth part.
Distal	Tooth edge or part toward angle of jaws.
Histotype	Type of internal tooth vascularization.
Inner face	Viewed from inside the mouth.
Longitudinally	Apicobasally directed structuring on a tooth.
Median groove	Groove running from the inner root base to the inner crown-root junction, dividing a holaulacorhizid type of root into two root lobes. It includes the main foramina of the vascularization system.
Median keel	Transverse ridge dividing the crown into inner and outer face.
Mesial	Tooth edge or part toward junction (symphysis) of left and right jaw halves.
Neo-holaulacorhizid	Modification of the holaulacorhizid type of root, combining a shallow median groove and an extremely expanded pulp cavity.
Orthodont	Histotype of vascularization, by which a tooth is supplied primarily by an internal pulp cavity radiating into numerous tiny canals penetrating the orthodentine layer.
Osteodont	Histotype of vascularization, by which a tooth is supplied without any pulp cavity by scattered tiny cavities and canals penetrating the osteodentine layer of the root and the internal crown material.
Outer face	Viewed from outside the mouth.

Pseudo-apron	Apron-like vertical ridges that appear sometimes on lateral and posterior teeth.
Pseudo-osteodont	The former pulp cavity of an originally orthodont histotype of tooth being filled secondarily with osteodentine.
Pulp cavity	Cavity inside the tooth from which the vascularization is spread via canaliculi.
Root	Non-enamelled tooth part, that forms the junction with the jaw and provides vascularization of the tooth.
Striae	Vertical ridges running from crown base toward apex.
Secondarily anaulacorhizid	Median groove of a holaulacorhizid type of root totally overgrown to form a closed tube internally connected or merged with the pulp cavity
Secondarily hemiaulacorhizid	Median groove of holaulacorhizid type of root overgrown to various extent, but terminally groove or pores still open.
Sulcus	Groove developed by the primary vascularization canals leading from root base to the main foramina in anaulacorhizid root type. It differs from the median groove in which several foramina are concentrated of the holaulacorhizid root type and the parallel grooves of the poly-aulacorhizid root type, respectively, in that a sulcus lacks foramina.
Transversal Uvula	Mesio-distally directed. Lobate extension of the inner crown base.

### Summary

The micro-teeth of almost all supraspecific taxa of Selachii were examined (with the exception of *Heteroscyllium*, *Miroscyllium*, *Mollisquama* and *Trigonognathus*), resulting in the following recommendations for chondrichthyan systematics. They are presented here to encourage revising authors to incorporate also these odontological points of view in a systematic revision with possible taxonomic and nomenclatorial changes.

### SQUALIFORMES

- Exclusion of Echinorhinidae from Squaliformes to form an order of its own (Part A No. 3).
- Lumping of Oxynotidae and Squalidae (Part A No. 3).
- Splitting of Squalidae into 8 families (Part A No. 3).
- Lumping the genera *Squalus* and *Cirrhigaleus* as well as the genera *Euprotomicrus*, *Squaliolus* and *Heteroscymnoides* (Part A No. 3).
- Lumping the genera *Scymnodon*, *Scymnodalarias* as also *Zameus* (Part A No. 3).
- Splitting the genus *Somniosus* into two subgenera (Part A No. 3).
- Revalidation of the genus *Centroselachus* (Part A No. 3).

### CARCHARHINIFORMES

- Splitting the Carcharhiniformes into 3 suborders (Part A No. 2c).
- Reallocation of *Furgaleus* from Triakidae to Hemigaleidae (Part A No. 2c).
- Splitting the genus *Triakis* into two subgenera (Part A No. 2c).
- Revalidation of the genus *Rhinotriacis* (Part A No. 2c).
- Synonymizing of *Hypogaleus* with *Galeorhinus* (Part A No. 2a).
- Splitting the family Scyliorhinidae into six subfamilies including also *Pseudotriakis* (Part A No. 2c).
- Lumping the families Proscylliidae with Scyliorhinidae with *Ctenacis* as seventh subfamily of the latter family (Part A No. 2c).
- Elevation of the genus *Triaenodon* to a carcharhinid subfamily (Part A No. 2c).
- Synonymizing of *Loxodon* with *Rhizoprionodon* (Part A No. 2c).

### ORECTOLOBIFORMES

- Lumping the families Hemiscylliidae and Stegostomatidae (Part A No. 4).
- Lumping the families Brachaeluridae and Ginglymostomatidae (Part A No. 4).
- Including the Squatinidae into the Orectolobidae (Part A No. 4).

### HEXANCHIFORMES

- Exclusion of Chlamydoselachidae from Hexanchiformes to form an order of its own (Part A No. 1b).

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## Bibliography

- BASS, A.J., D'AUBREY, J.D. and KISTNASAMY, N., 1975. Sharks of the east coast of southern Africa. IV. The families Odontaspidae, Scapanorhynchidae, Isuridae, Cetorhinidae, Alopiidae, Orectolobidae and Rhiniodontidae. *South African Association for marine biological Research, Oceanographic Research Institute, Durban. Investigational Report*, (39) : 1-102.
- BASS, A.J., D'AUBREY, J.D. and KISTNASAMY, N., 1975. Sharks of the east coast of southern Africa. V. The families Hexanchidae, Chlamydoselachidae, Heterodontidae, Pristiophoridae, Squatinidae and Sphyrnidae. *South African Association for marine biological Research, Oceanographic Research Institute, Durban, Investigational Report*, (43) : 1-50.
- BOSCH VAN DEN, M., 1984. Oligocene to recent Cetorhinidae (Vertebrata, Basking sharks); Problematical finds of teeth, dermal scales and gill-rakers. *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, 21(4) : 205-232.
- COMPAGNO, L.J.V., 1984. FAO species catalogue Vol. 4 Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. FAO Fisheries Synopsis (125), 4 (2) : 251-655.
- DINGERKUS, G. and DE FINNO, T.C., 1983. A Revision of the orectolobiform shark family Hemiscylliidae (Chondrichthyes, Selachii). *Bulletin of the American Museum of Natural History*, 176 (1), 93 p. New York.
- GILL, T., 1862. Analytical synopsis of the Order of Squali and revision of the nomenclature of the genera : Squalorum Generum Novorum Descriptiones Diagnostica. *Annals Lyceum Natural History*, New York, 7 (32) : 367-413.
- HERMAN, J., 1977. Additions to the Eocene fish fauna of Belgium. 3. Revision of the Orectolobiforms. *Tertiary Research*, London, 1 (4) : 127-138.
- HERMAN, J., 1979. Réflexions sur la systématique des galeoidei et sur les affinités du genre *Cetorhinus* à l'occasion de la découverte d'éléments de la denture d'un exemplaire fossile dans les Sables du Kattendijk à Kallo (Pliocène inférieur), Belgique. *Annales de la Société Géologique de Belgique* 102 : 357-377.
- HERMAN, J., HOVESTADT-EULER, M. and HOVESTADT, D.C., 1987. Order : Hexanchiformes, family : Hexanchidae. In : Contributions to the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes, Part A : Selachii No. 1. Ed. Stehmann, M. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie*, 57 : 43-56, Bruxelles.
- HERMAN, J., HOVESTADT-EULER, M. and HOVESTADT, D.C., 1988. Order : Carcharhiniformes, family : Triakidae. In : Contributions to the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes. Part A : Selachii No. 2a. Ed. Stehmann, M. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie*, 58 : 99-126, Bruxelles.
- HERMAN, J., HOVESTADT-EULER, M. and HOVESTADT, D.C., 1990. Order : Squaliformes, families : Echinorhinidae, Oxynotidae and Squalidae. In : Contributions to the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes, Part A : Selachii No. 3. Ed. Stehmann, M. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie*, 59 : 101-157, Bruxelles.
- HERMAN, J., HOVESTADT-EULER, M. and HOVESTADT, D.C., 1991. Order : Carcharhiniformes, family : Scyliorhinidae. In : Contributions to the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes, Part A : No. 2b. Ed. Stehmann, M. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie*, 60 : 181-230, Bruxelles.
- HERMAN, J., HOVESTADT-EULER, M. and HOVESTADT, D.C., 1991. Order : Carcharhiniformes, families : Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae and Carcharhinidae In : Contributions to the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes, Part A : No. 2c. Ed. Stehmann, M. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie*, 61 : 73-120, Bruxelles.
- HERMAN, J., HOVESTADT-EULER, M. and HOVESTADT, D.C., 1992. Order : Orectolobiformes, families : Brachaeluridae, Ginglymostomatidae, Hemiscylliidae, Orectolobidae, Parascylliidae, Rhiniodontidae, Stegostomatidae. Order : Pristiophoriformes, family : Pristiophoridae. Order : Squatiniformes, family : Squatinidae In : Contributions to the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes, Part A : No. 4. Ed. Stehmann, M. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie*, 62 : 193-254, Bruxelles.
- HERMAN, J., HOVESTADT-EULER, M. and HOVESTADT, D.C., 1993. General Glossary; No. 1b : Order : Hexanchiformes - Family : Chlamydoselachidae; No. 5 : Order : Heterodontiformes - Family : Heterodontidae; No. 6 : Order : Lamniformes - Families : Cetorhinidae, Megachasmidae; Addendum 1 to No.

3 : Order Squaliformes; Addendum 1 to No. 4 : Order : Orectolobiformes; Summary Part A. In : Contributions to the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes, Part A : (Selachii). Ed. Stehmann, M., *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie*, 63 : 185-256, Bruxelles.

PFEIL, F.H., 1983. Zahnmorphologische Untersuchungen an rezenten und fossilen Haien der Ordnungen Chlamydoselachiformes und Echinorhiniformes. *Palaeoichthyologica*, München, 1 : 1-316.

REIF, W.E., 1976. Morphogenesis, Pattern Formation and Function of the Dentition of *Heterodontus* (Selachii). *Zoomorphologie*, Springer Verlag, 83 : 1-47.

SHIRAI, S., 1992. Identity of Extra Branchial Arches of Hexanchiformes (Pisces, Elasmobranchii). *Bulletin Faculty Fisheries*. Hokkaido Univ., 43(1) : 24-32.

SMITH, B.G., 1937. The anatomy of the frilled shark *Chlamydoselachus anguineus* Garman. In : Gudger E.W. (Ed.). The Bashford Dean Memorial Volume, Archaic Fishes. Article VI (pp. 331-505) *The American Museum of Natural History*. New York.

SMITH, B.G., 1942. The heterodontid sharks : their natural history, and the external development of *Heterodontus japonicus* based on notes and drawings by Bashford Dean. The Bashford Dean Memorial Volume, Archaic Fishes. Article VI (pp. 649-770). *The American Museum of Natural History*, New York.

TANIUCHI, T. & GARRICK, J.A.F., 1986. A new species of Scymnodalarias from the Southern Oceans, and comments on other squaliform sharks. *Japanese Journal of Ichthyology*, 33(2) : 119-134.

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### Composition of the plates

Generally, the plates have a consistent composition : upper teeth are always presented with the crown downwards, and the lower teeth with the crown upwards.

Sometimes, the plate shows upper teeth as well as lower teeth; otherwise the plate shows either the upper or the lower teeth.

The choice of left or right jaw halves depends on the preservation quality of the specimen's tooth files only.

### General legend

- ps = parasymphysial position
- s = symphysial position
- a = anterior position
- la = latero-anterior position
- l = lateral position
- lp = latero-posterior position
- p = posterior position
- c = commissural position

Plate 1 shows a side view of the head of one of the rare North Atlantic European *Chlamydoselachus anguineus*.

Plate 2 illustrates only three growing stages of a single upper row of *Chlamydoselachus anguineus*, because this species is only slightly gradient heterodont.

The plates 3, 4, 5 and 6 illustrate the teeth of a juvenile male of *H. portusjacksoni* with mixed diverse views. All the following plates, concerning the Heterodontidae (7 to 38), show only upper or lower teeth with a consistent presentation.

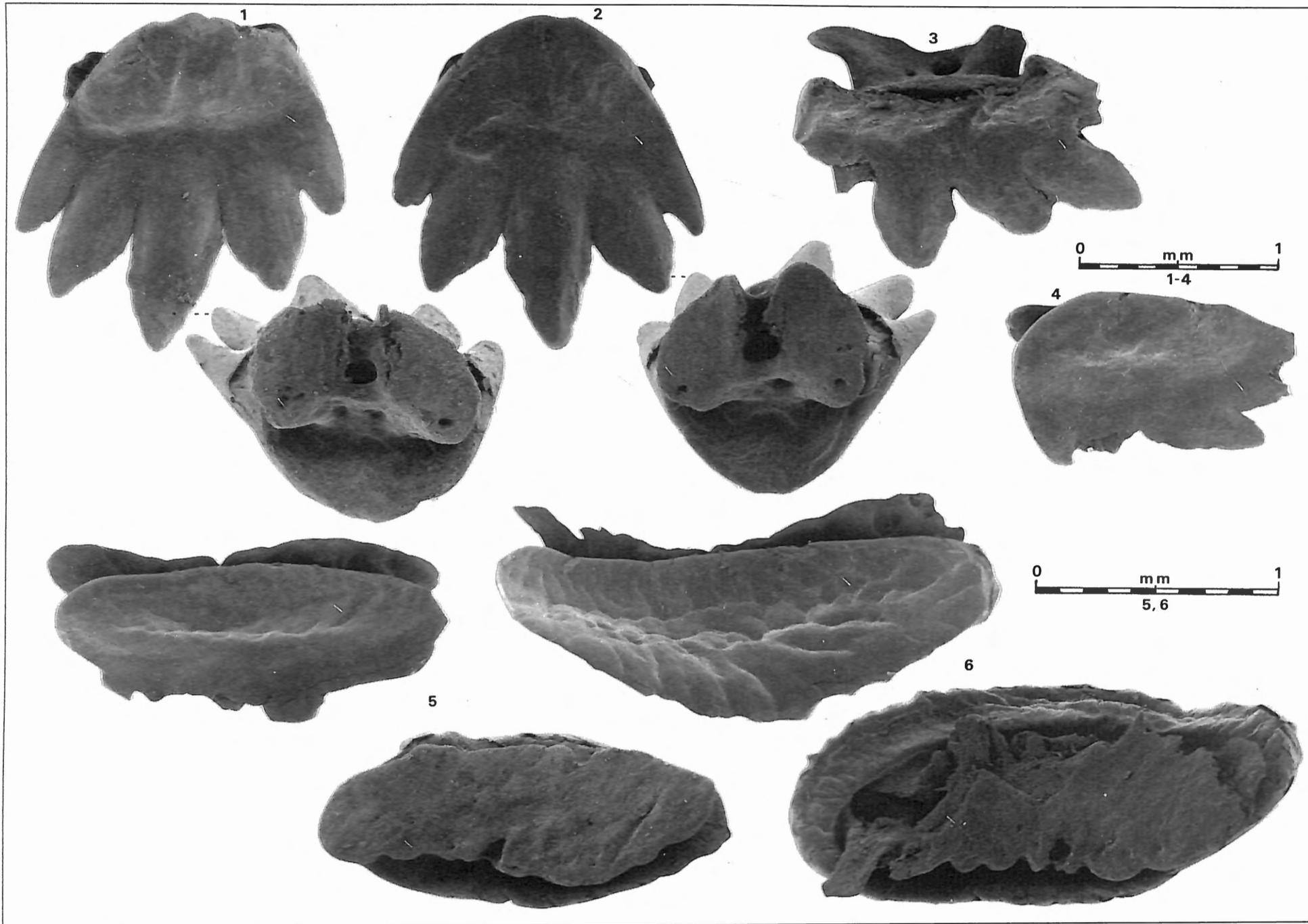


Plate 3. — *Heterodontus portusjacksoni* (MEYER, 1793). Male 335 mm (t.l.), New South Wales, Australia. Upper teeth, outer and basal views.

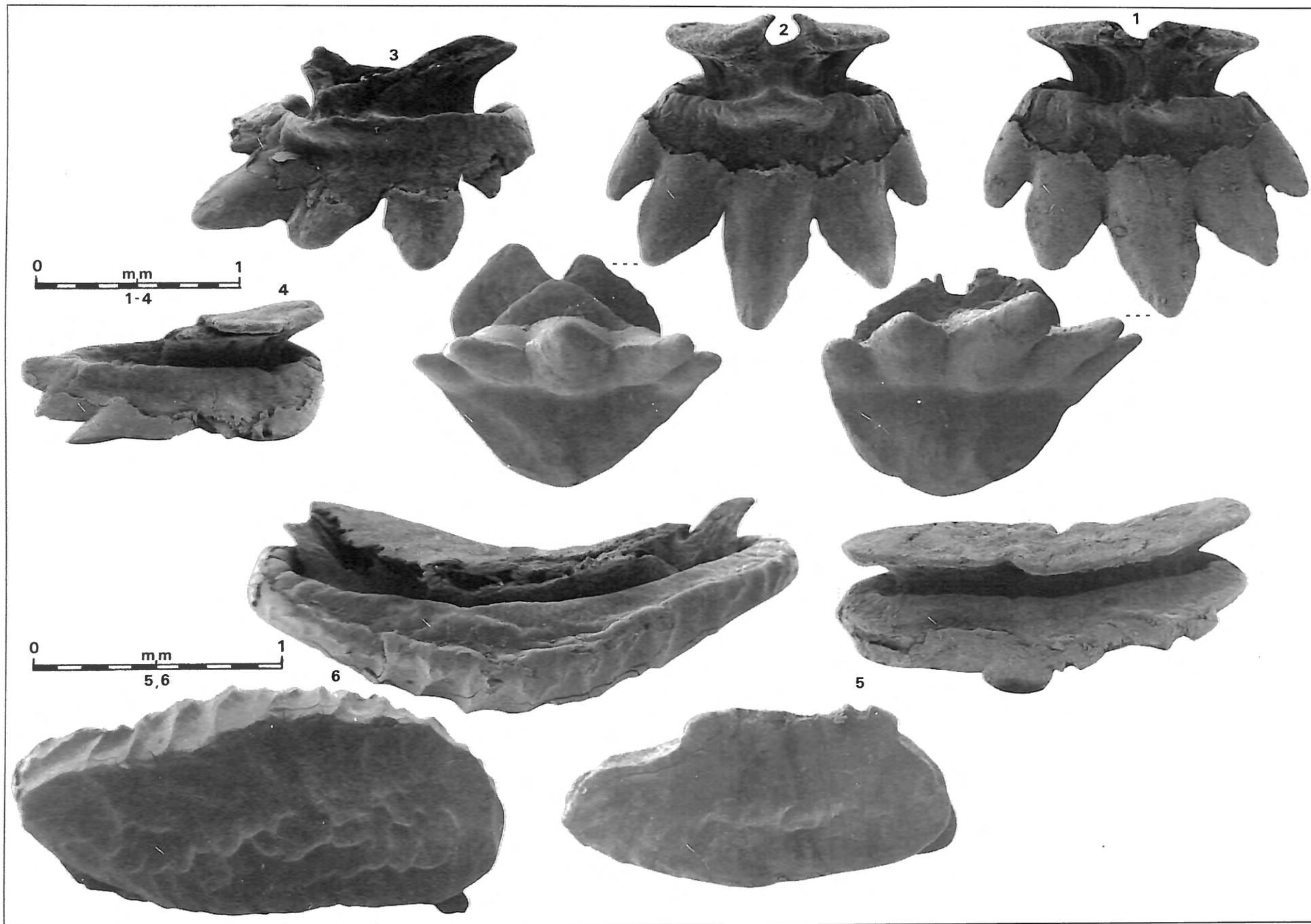


Plate 4. – *Heterodontus portusjacksoni* (MEYER, 1793). Male 335 mm (t.l.), New South Wales, Australia. Upper teeth, inner and occlusal views.

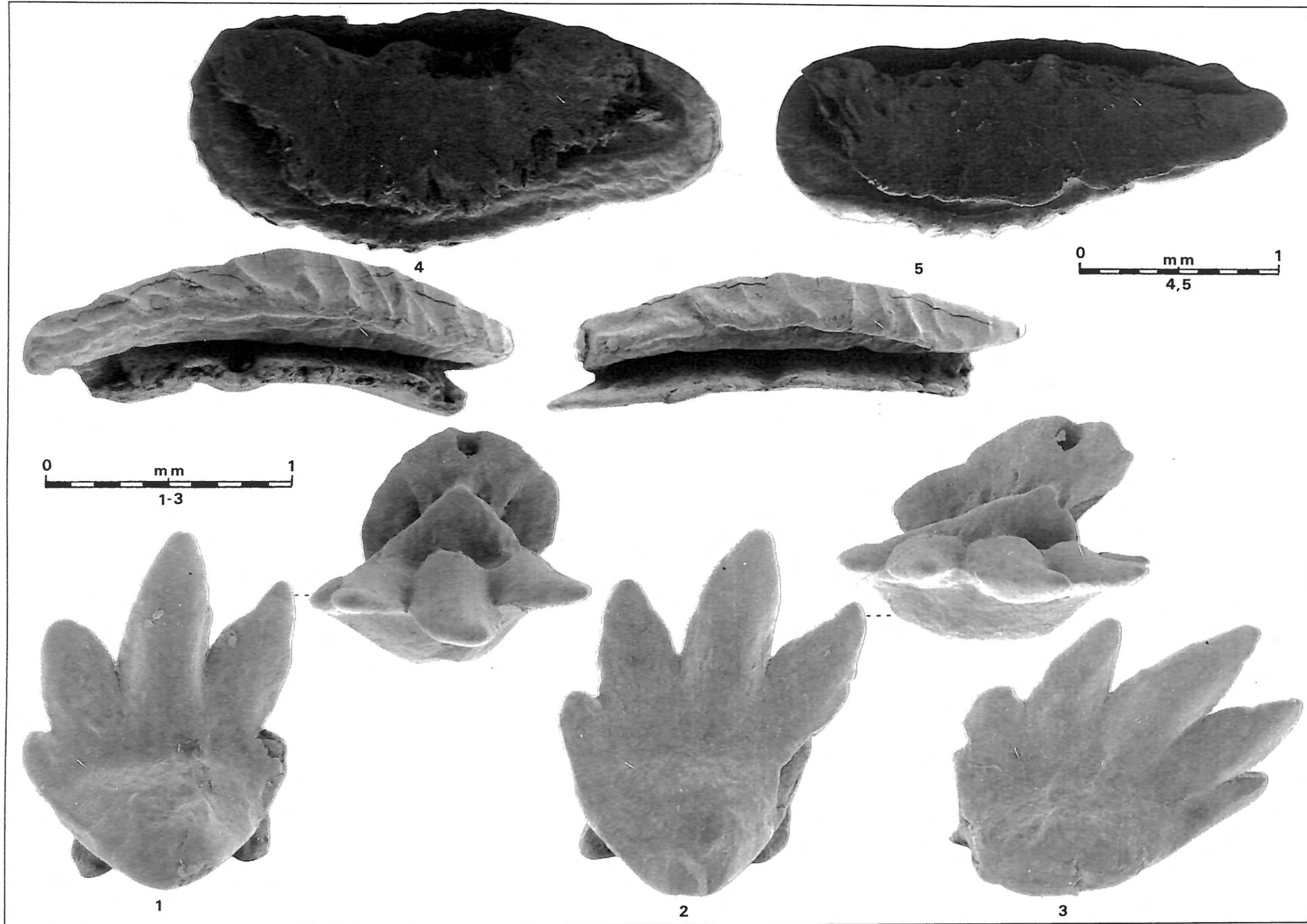


Plate 5. – *Heterodontus portusjacksoni* (MEYER, 1793). Male 335 mm (t.l.), New South Wales, Australia. Lower teeth.

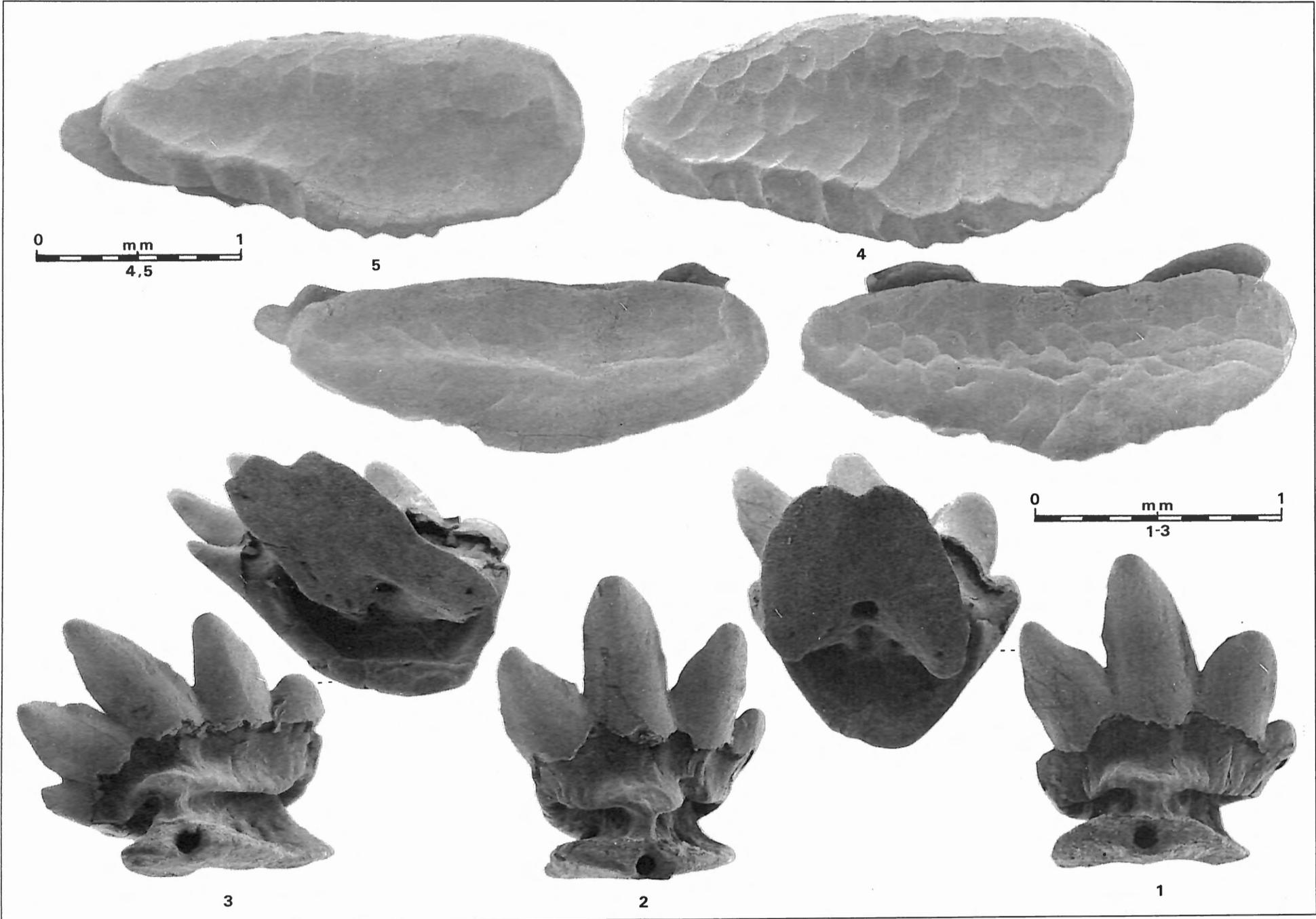


Plate 6. – *Heterodontus portusjacksoni* (MEYER, 1793). Male 335 mm (t.l.), New South Wales, Australia. Lower teeth.

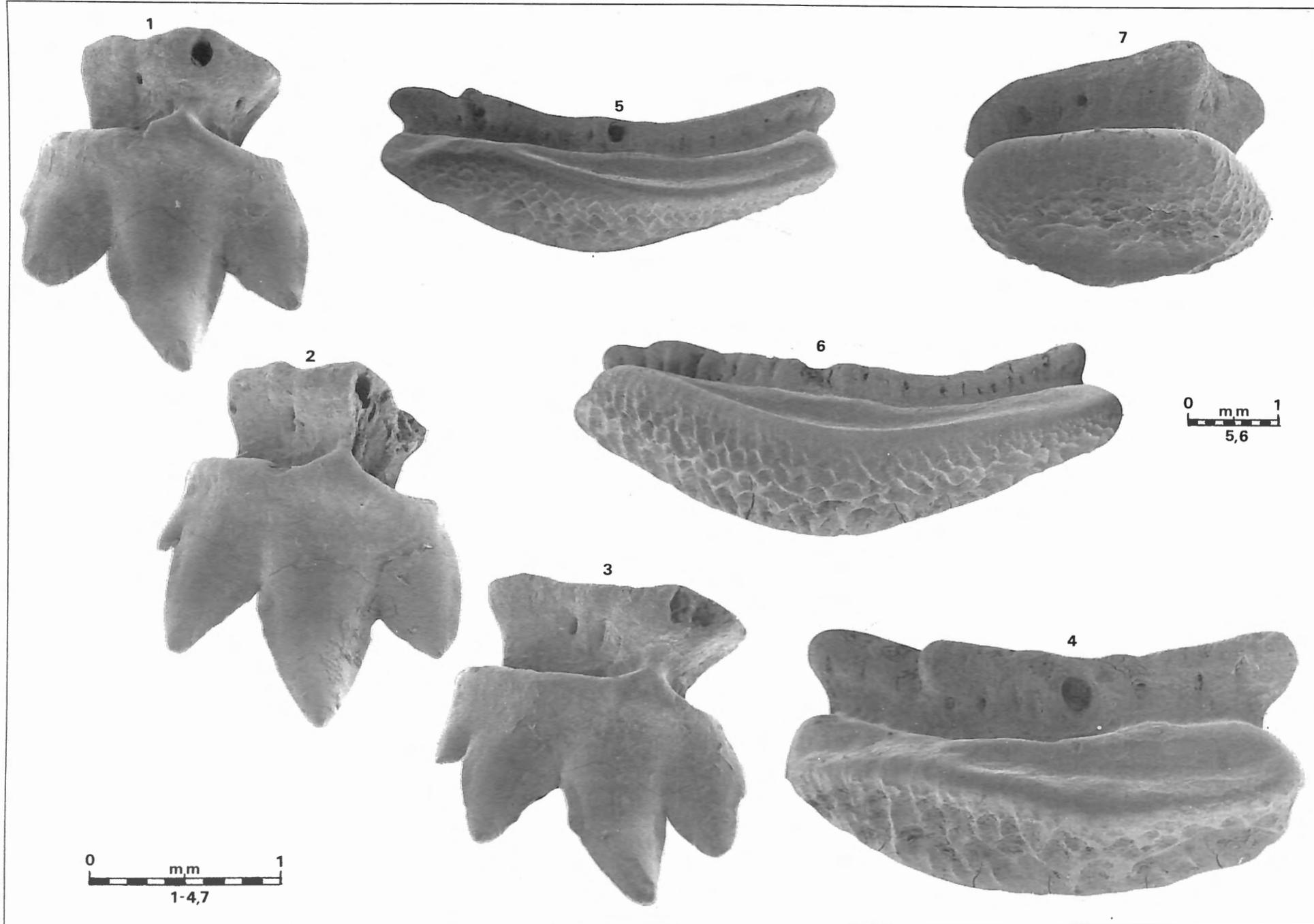


Plate 7. – *Heterodontus portusjacksoni* (MEYER, 1793). Female 430 mm (t.l.), Australia. Upper teeth, inner views.

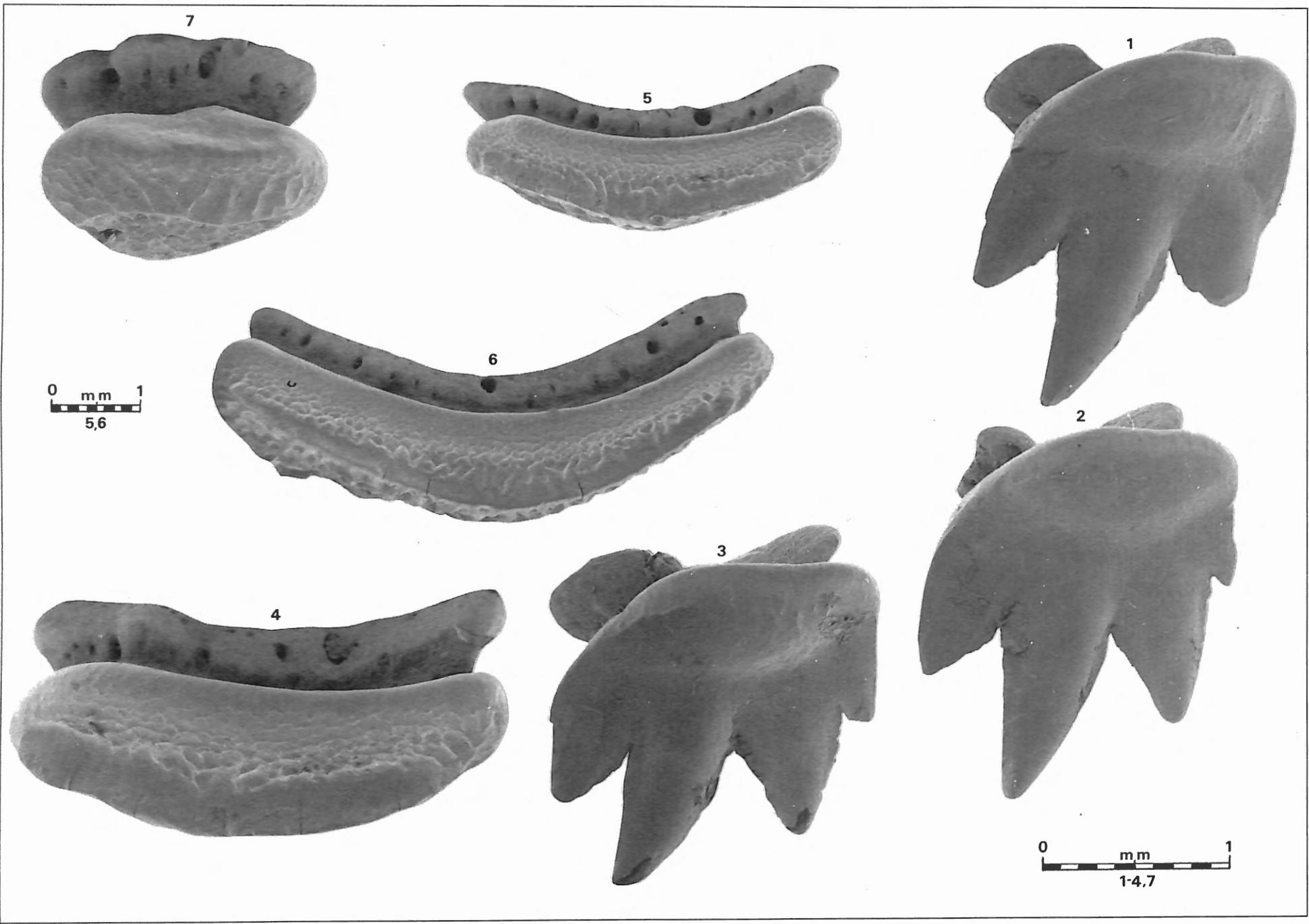


Plate 8. – *Heterodontus portusjacksoni* (MEYER, 1793). Female 430 mm (t.l.), Australia. Upper teeth, outer views.

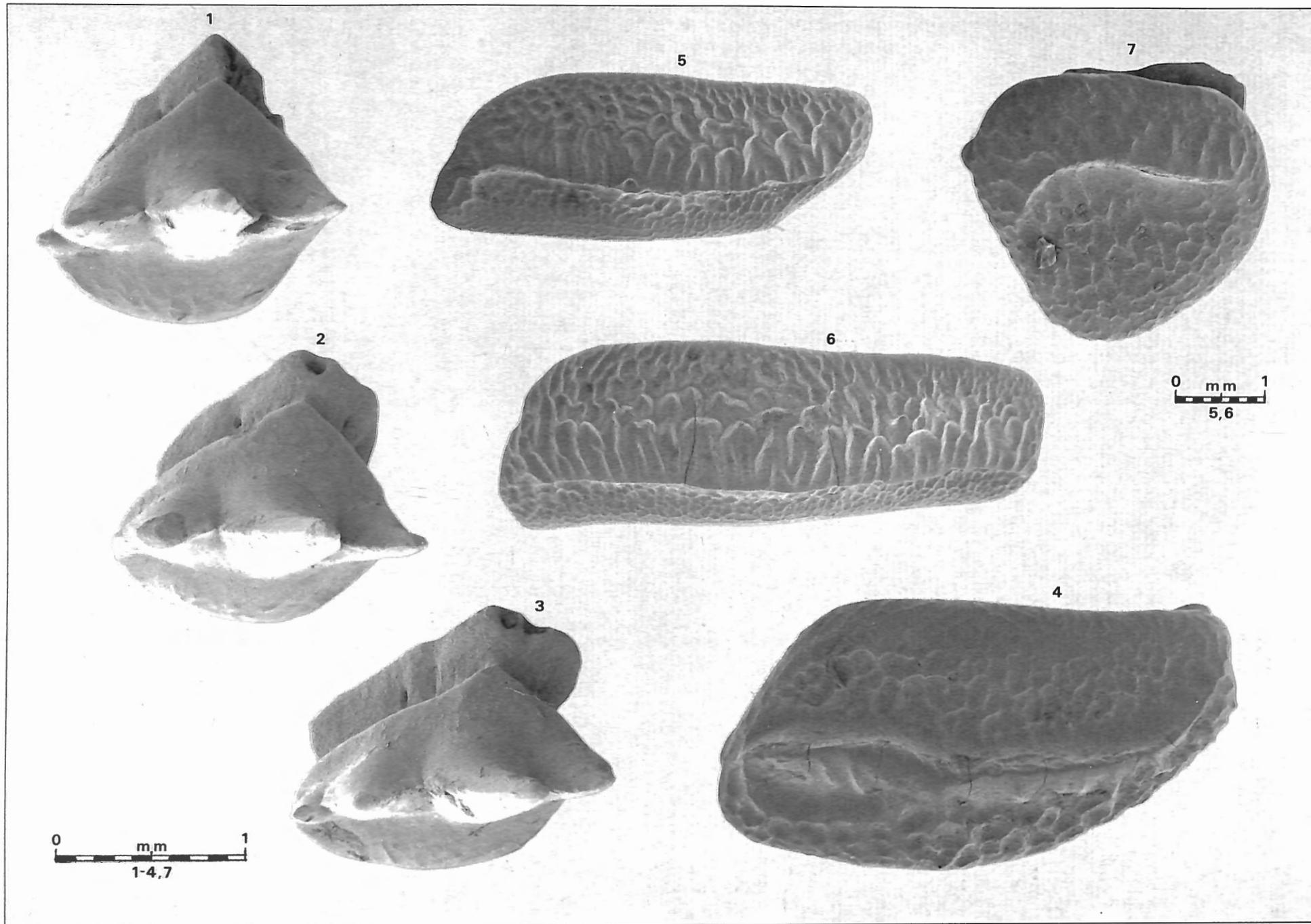


Plate 9. — *Heterodontus portusjacksoni* (MEYER, 1793). Female 430 mm (t.l.), Australia. Upper teeth, occlusal views.

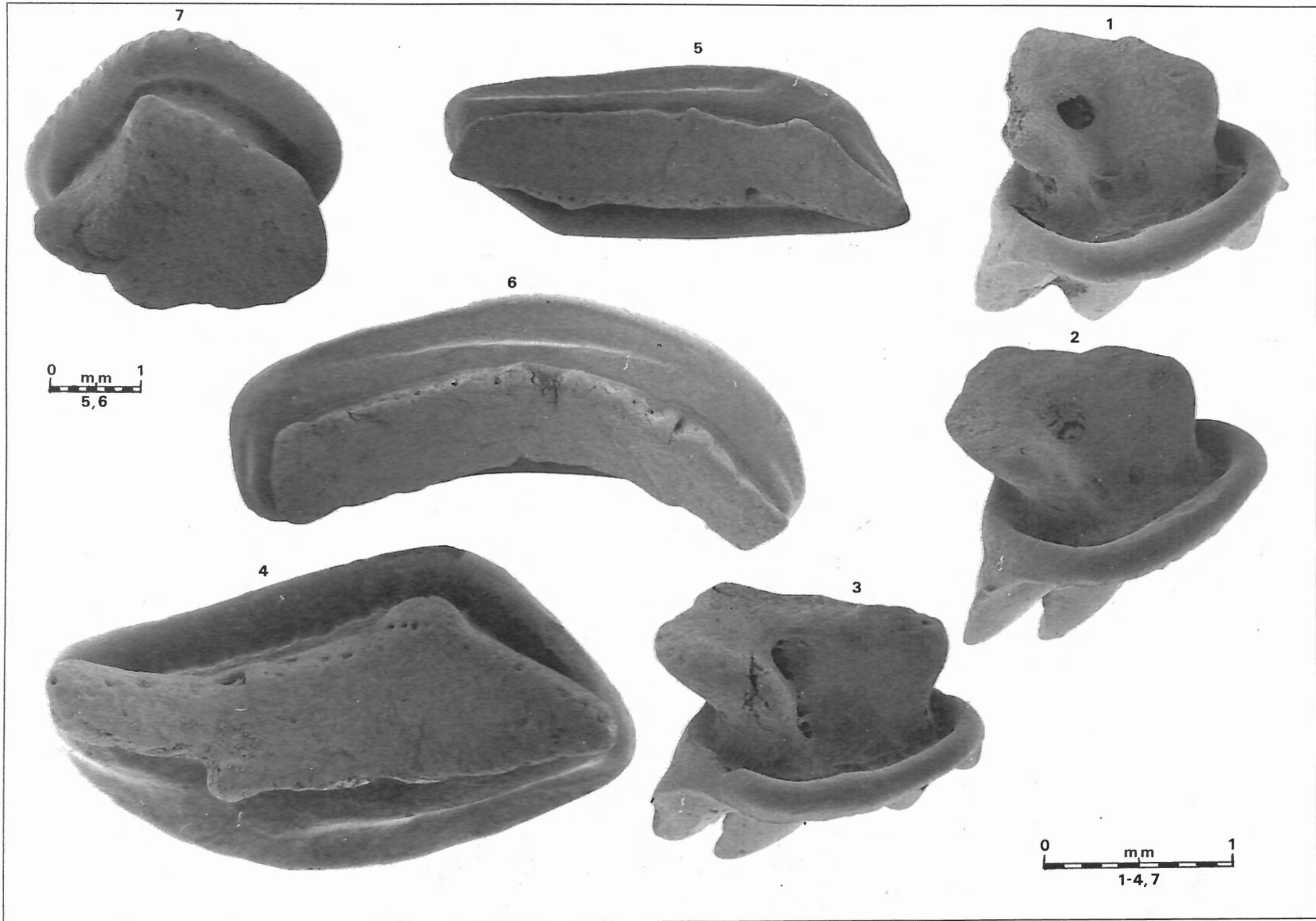


Plate 10. – *Heterodontus portusjacksoni* (MEYER, 1793). Female 430 mm (t.l.), Australia. Upper teeth, basal views.

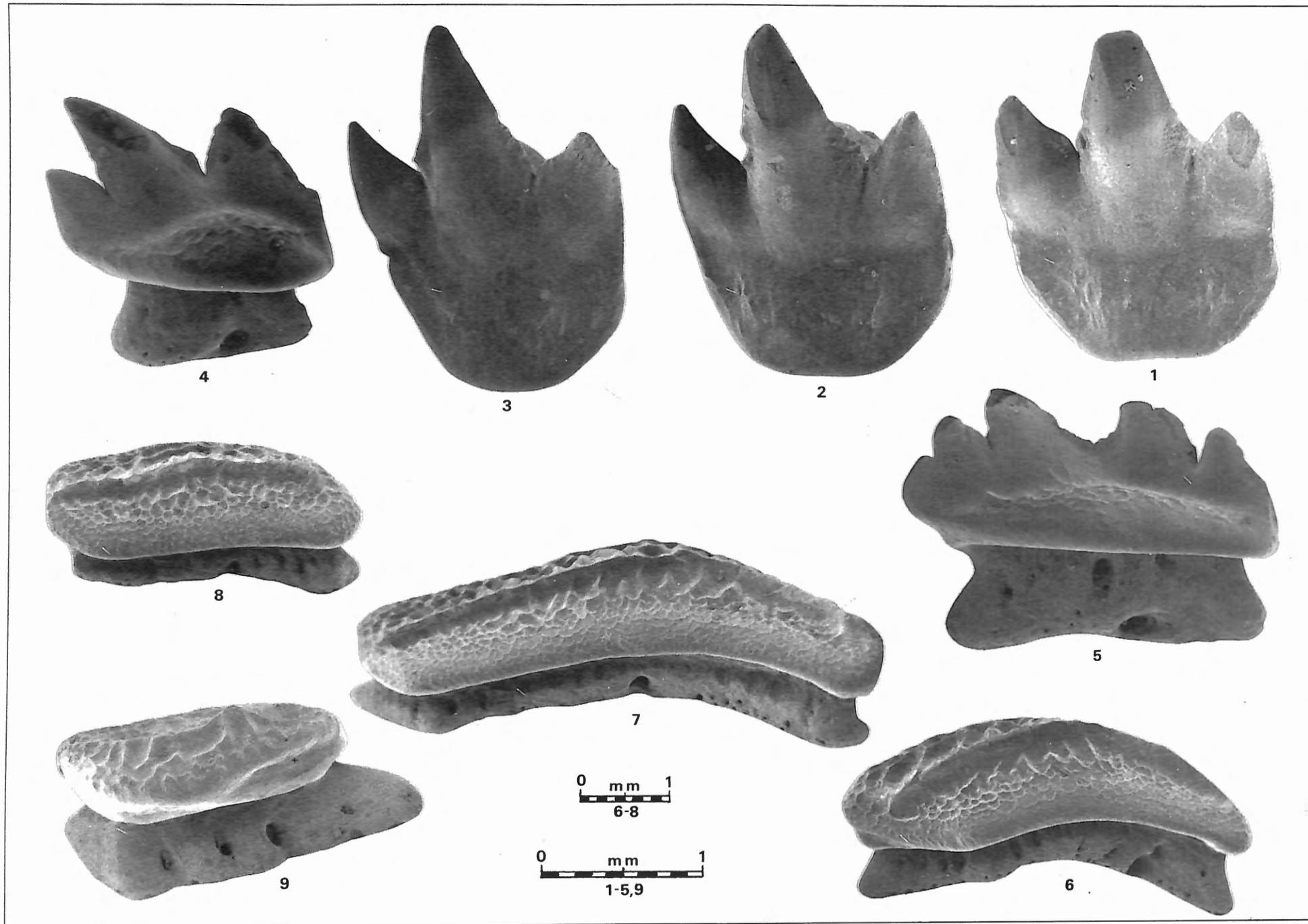


Plate 11. – *Heterodontus portusjacksoni* (MEYER, 1793). Female 430 mm (t.l.), Australia. Lower teeth, outer views.

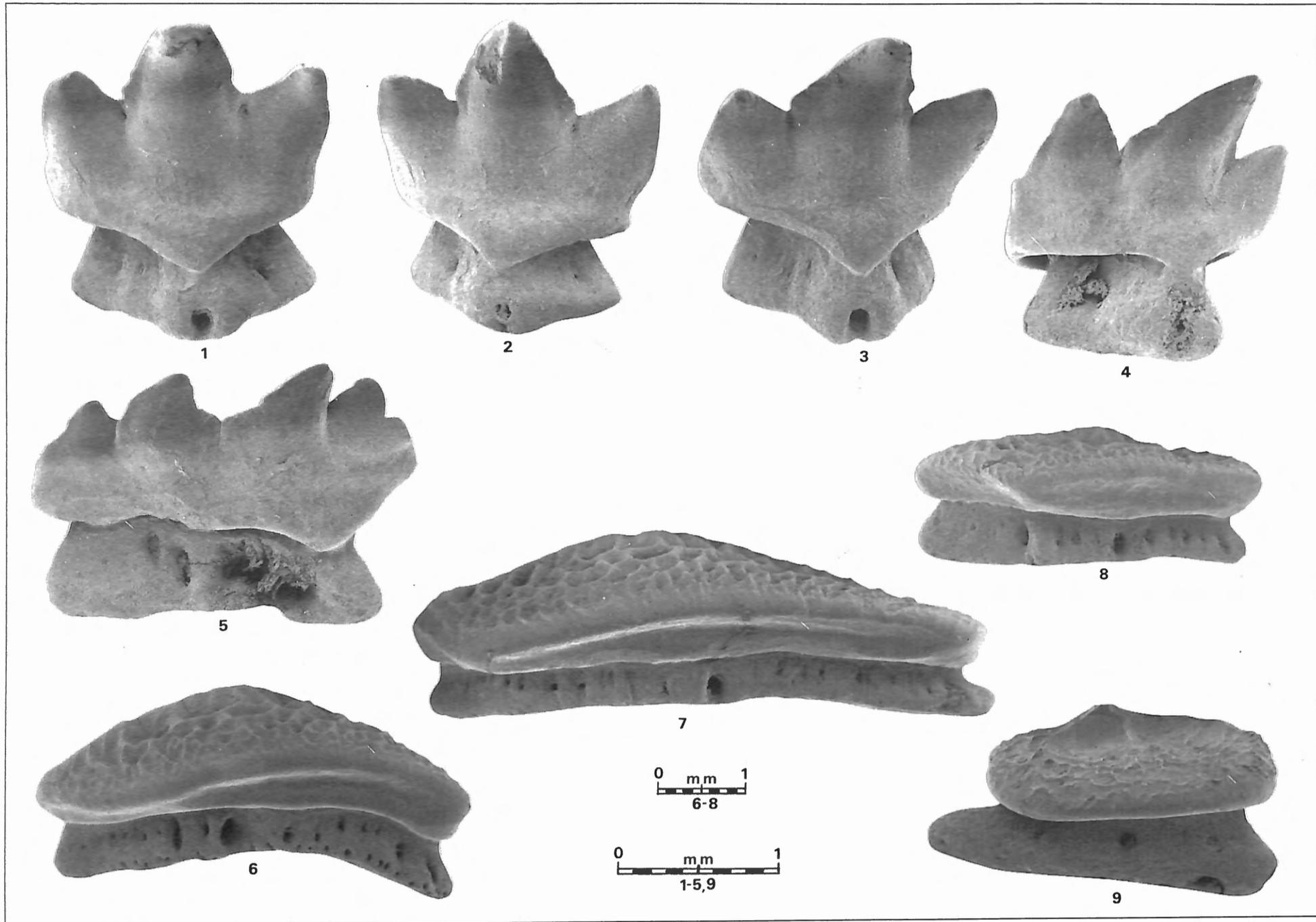


Plate 12. – *Heterodontus portusjacksoni* (MEYER, 1793). Female 430 mm (t.l.), Australia. Lower teeth, inner views.

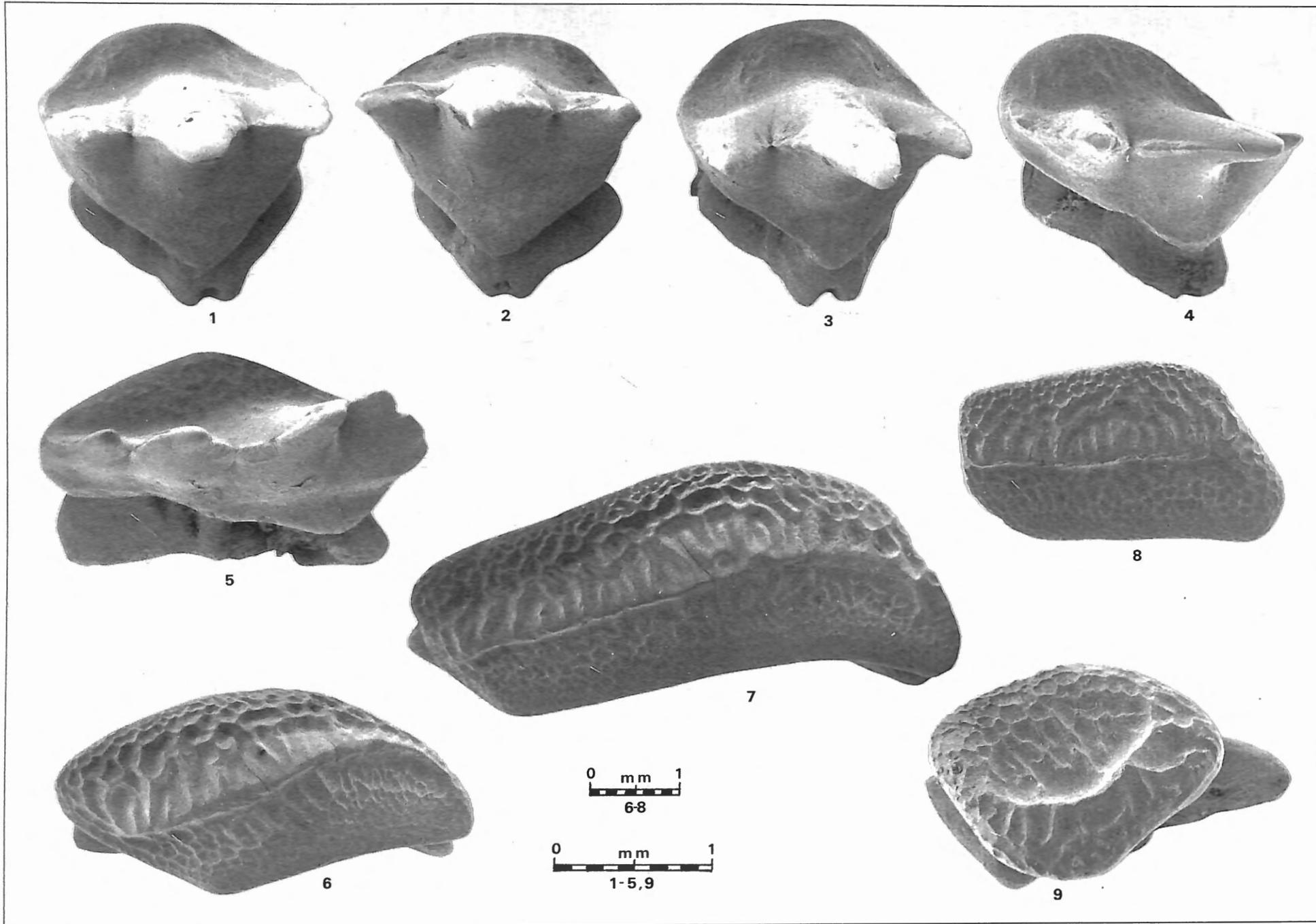


Plate 13. – *Heterodontus portusjacksoni* (MEYER, 1793). Female 430 mm (t.l.), Australia. Lower teeth, occlusal views.

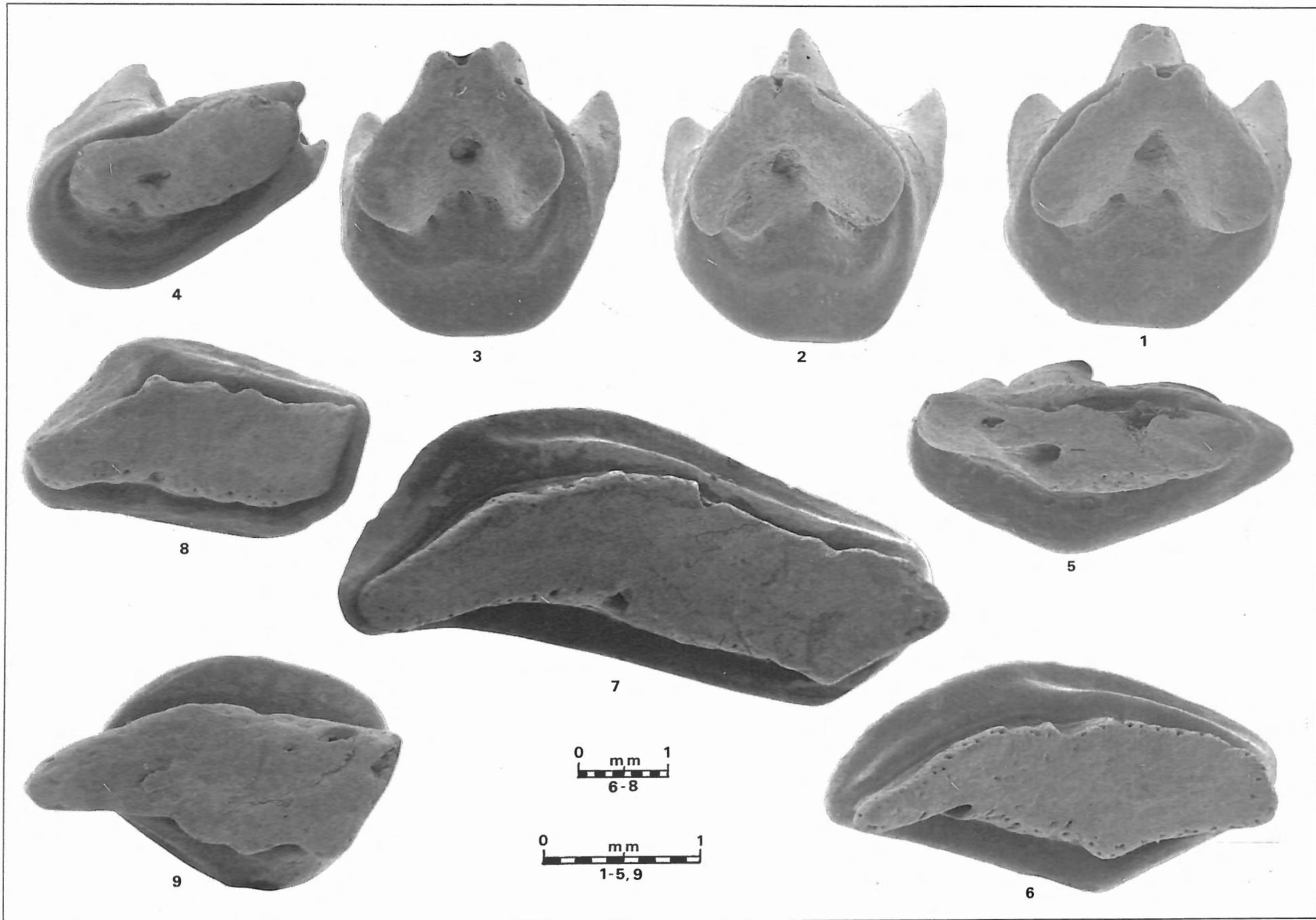


Plate 14. – *Heterodontus portusjacksoni* (MEYER, 1793). Female 430 mm (t.l.), Australia. Lower teeth, basal views.

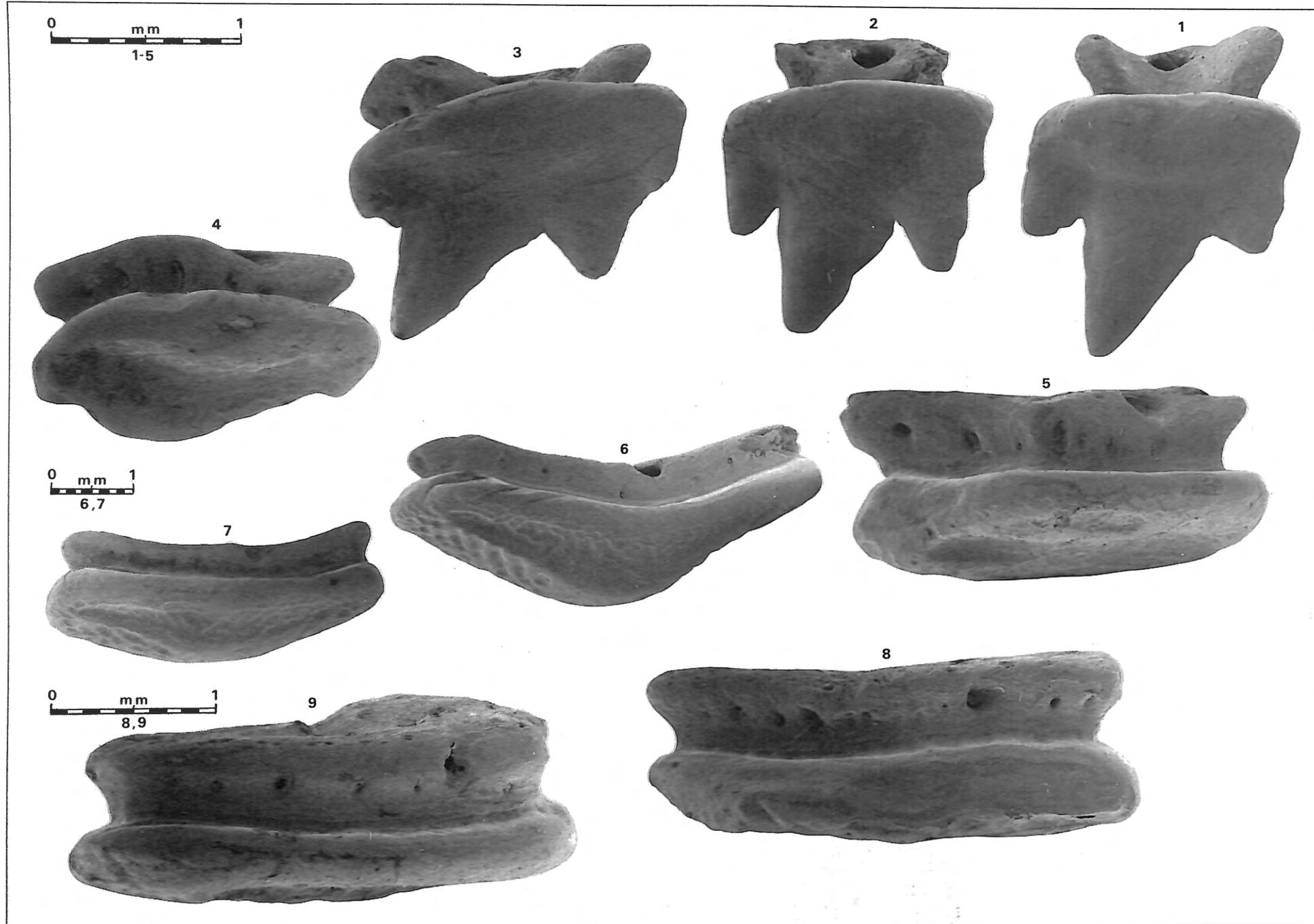


Plate 15. — *Heterodontus portusjacksoni* (MEYER, 1793). Male 450 mm (t.l.), Australia. Upper teeth, outer views.

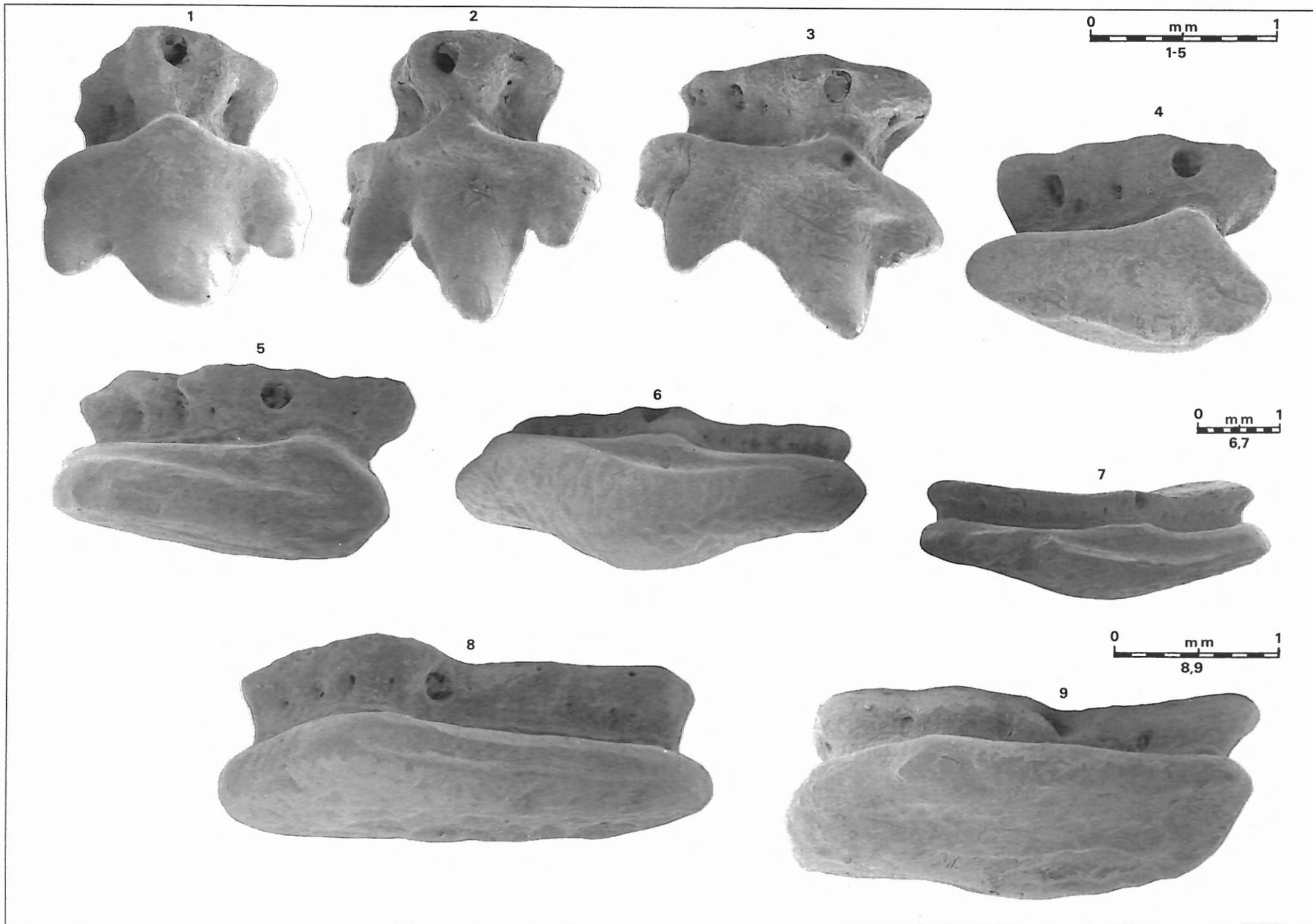


Plate 16. – *Heterodontus portusjacksoni* (MEYER, 1793). Male 450 mm (t.l.), Australia. Upper teeth, inner views.

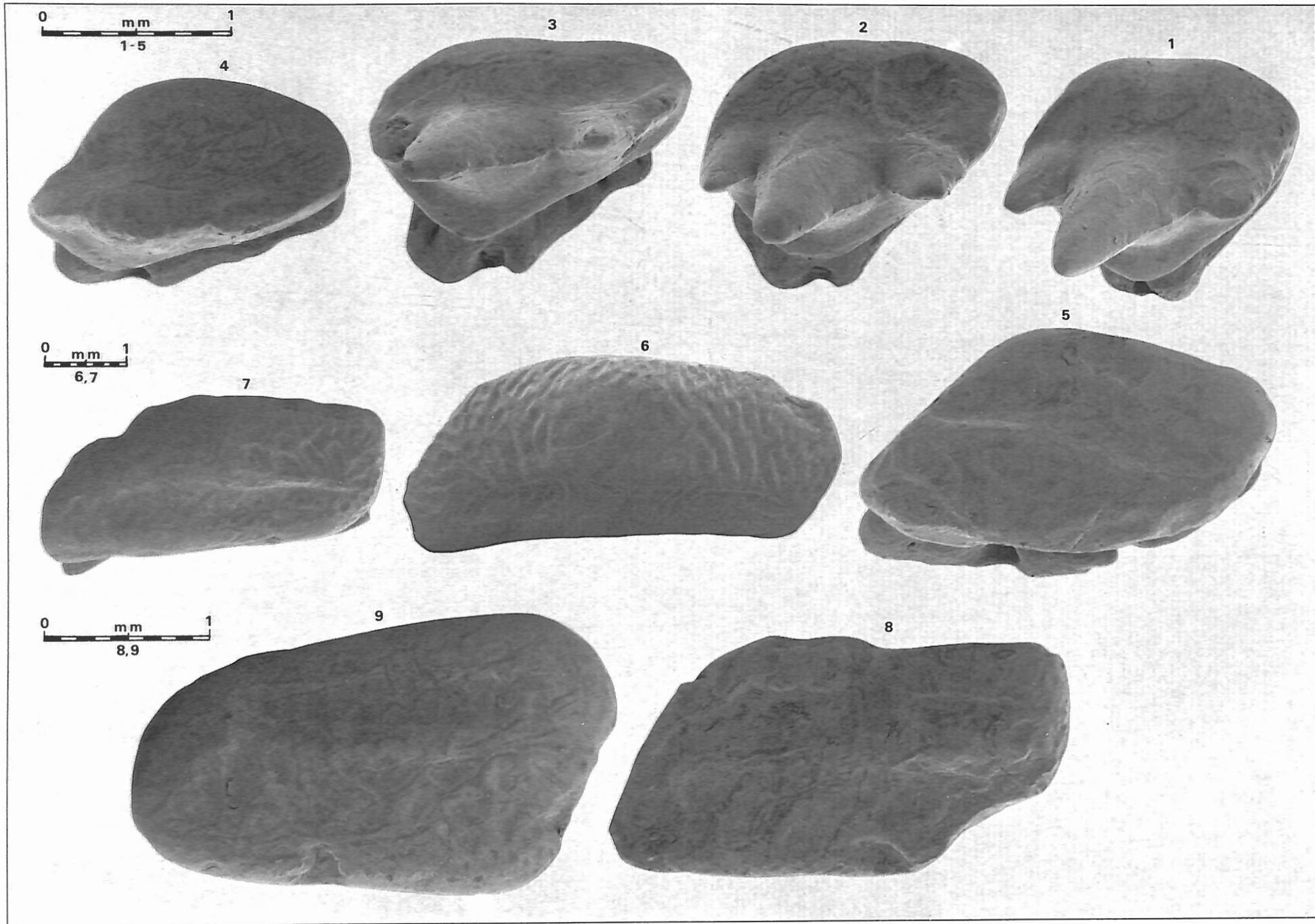


Plate 17. – *Heterodontus portusjacksoni* (MEYER, 1793). Male 450 mm (t.l.), Australia. Upper teeth, occlusal views.

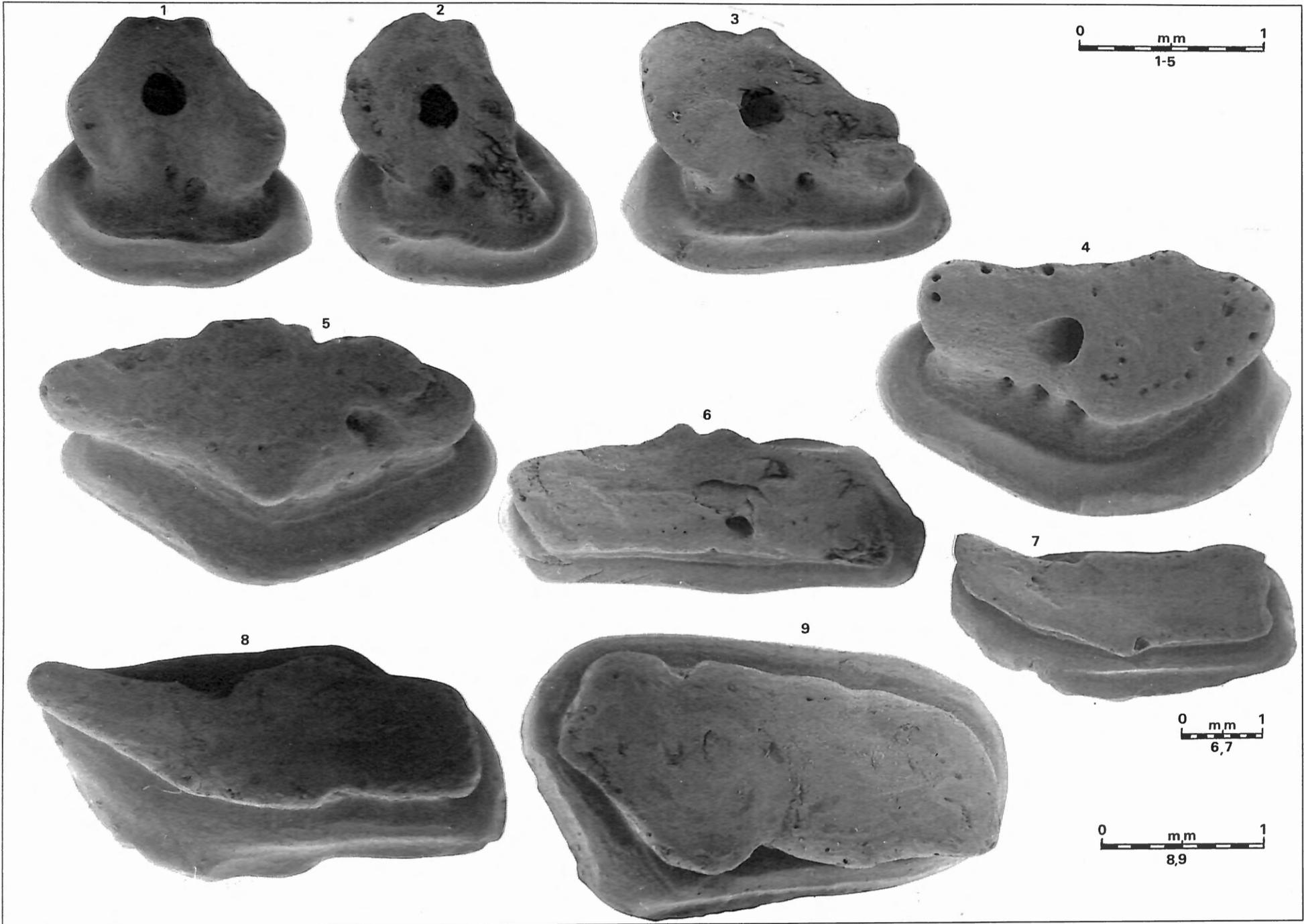


Plate 18. – *Heterodontus portusjacksoni* (MEYER, 1793). Male 450 mm (t.l.), Australia. Upper teeth, basal views.

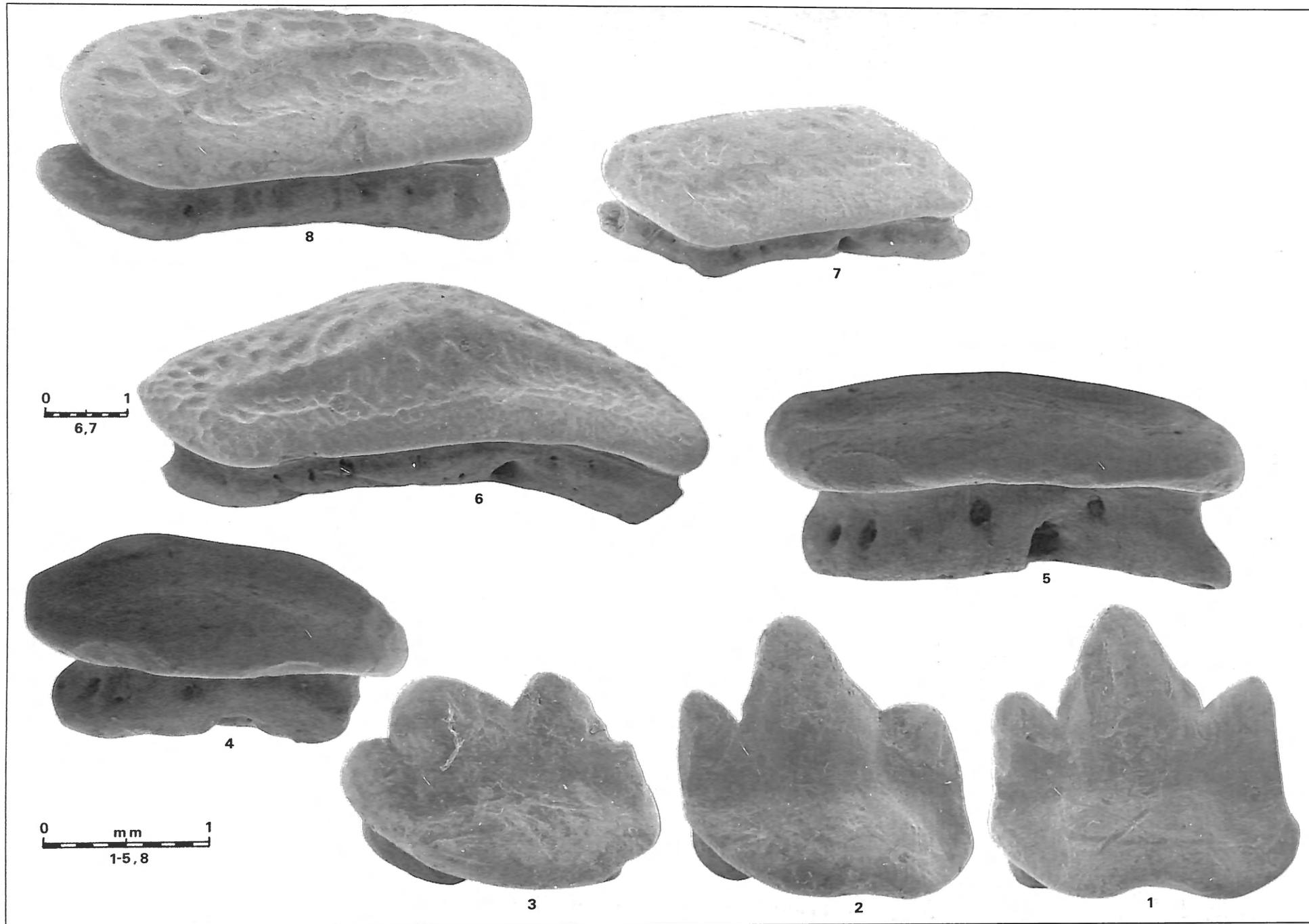


Plate 19. – *Heterodontus portusjacksoni* (MEYER, 1793). Male 450 mm (t.l.), Australia. Lower teeth, outer views.

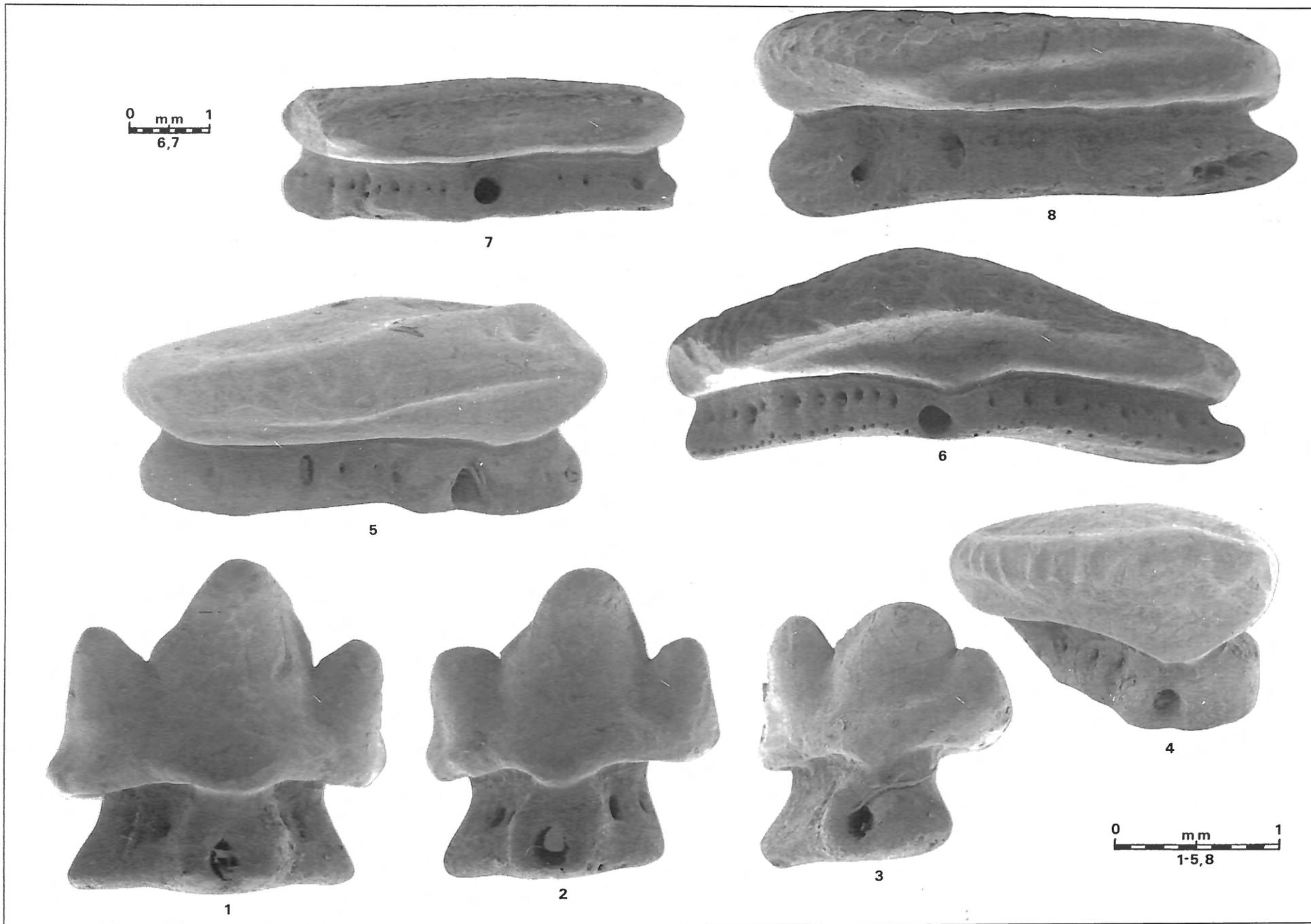


Plate 20. – *Heterodontus portusjacksoni* (MEYER, 1793). Male 450 mm (t.l.), Australia. Lower teeth, inner views.

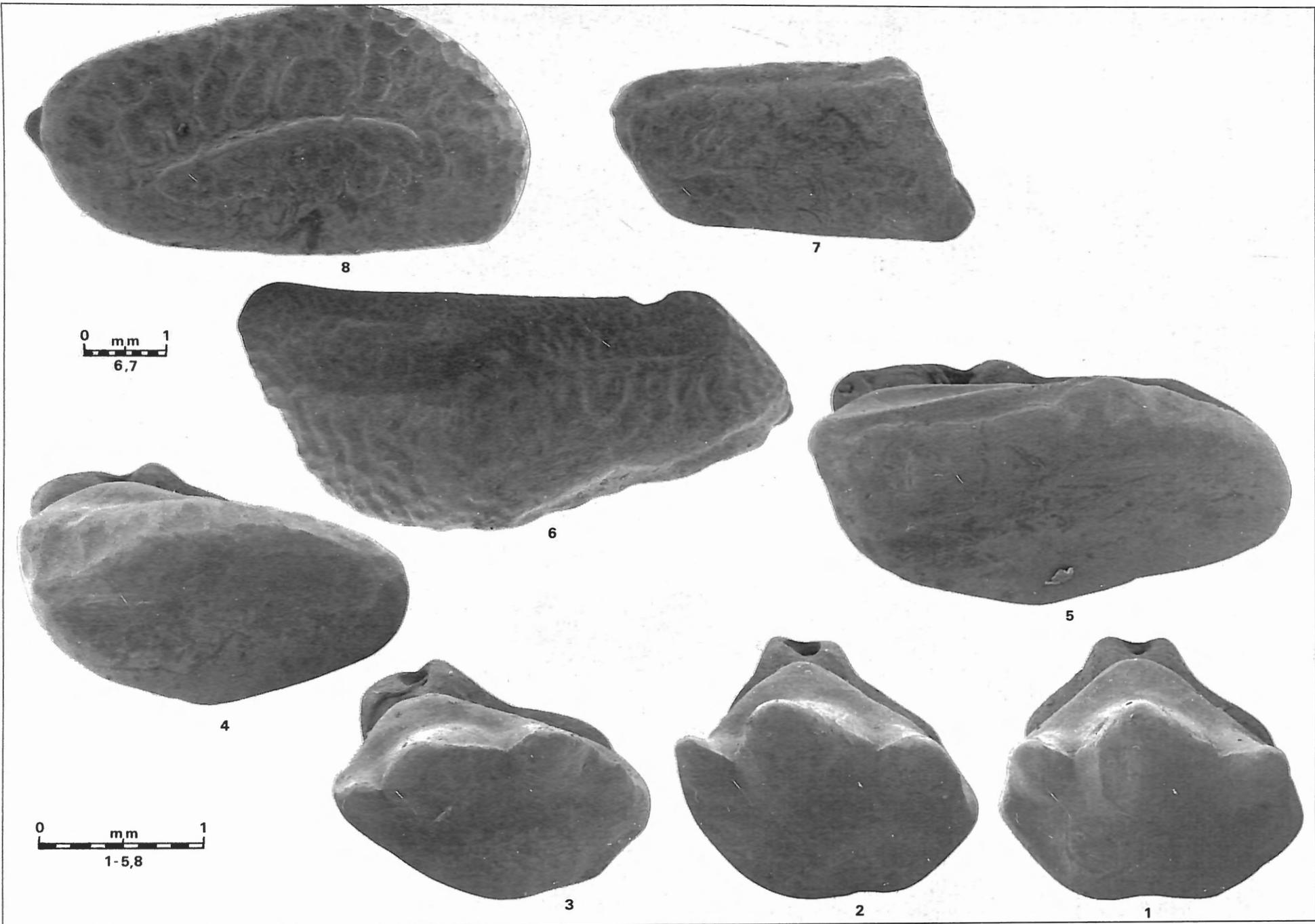


Plate 21. — *Heterodontus portusjacksoni* (MEYER, 1793). Male 450 mm (t.l.), Australia. Lower teeth, occlusal views.

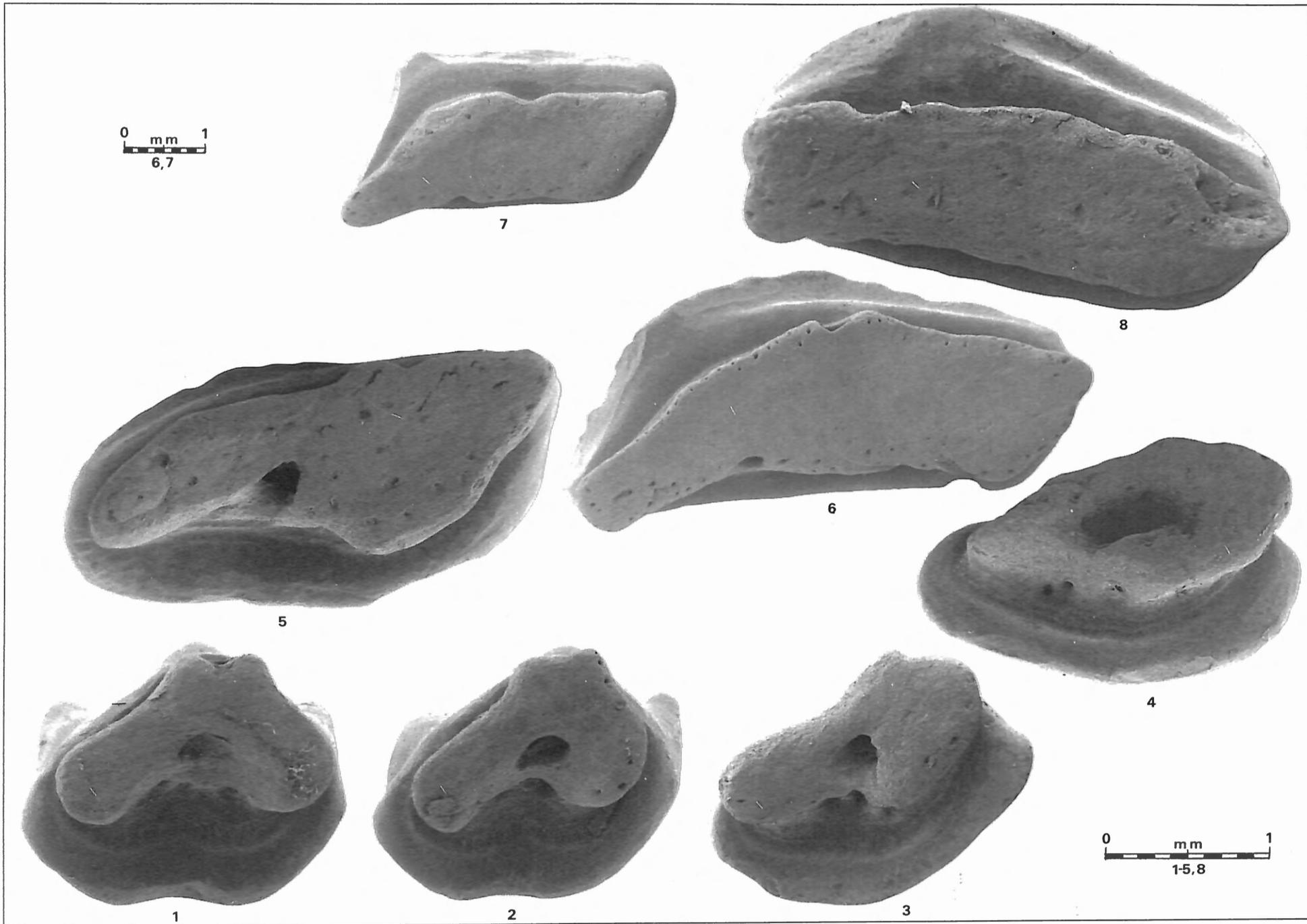


Plate 22. – *Heterodontus portusjacksoni* (MEYER, 1793). Male 450 mm (t.l.), Australia. Lower teeth, basal views.



Plate 23. — *Heterodontus francisci* (GIRARD, 1854). Male 630 mm (t.l.), Baja California, Mexico. Upper teeth, outer views.

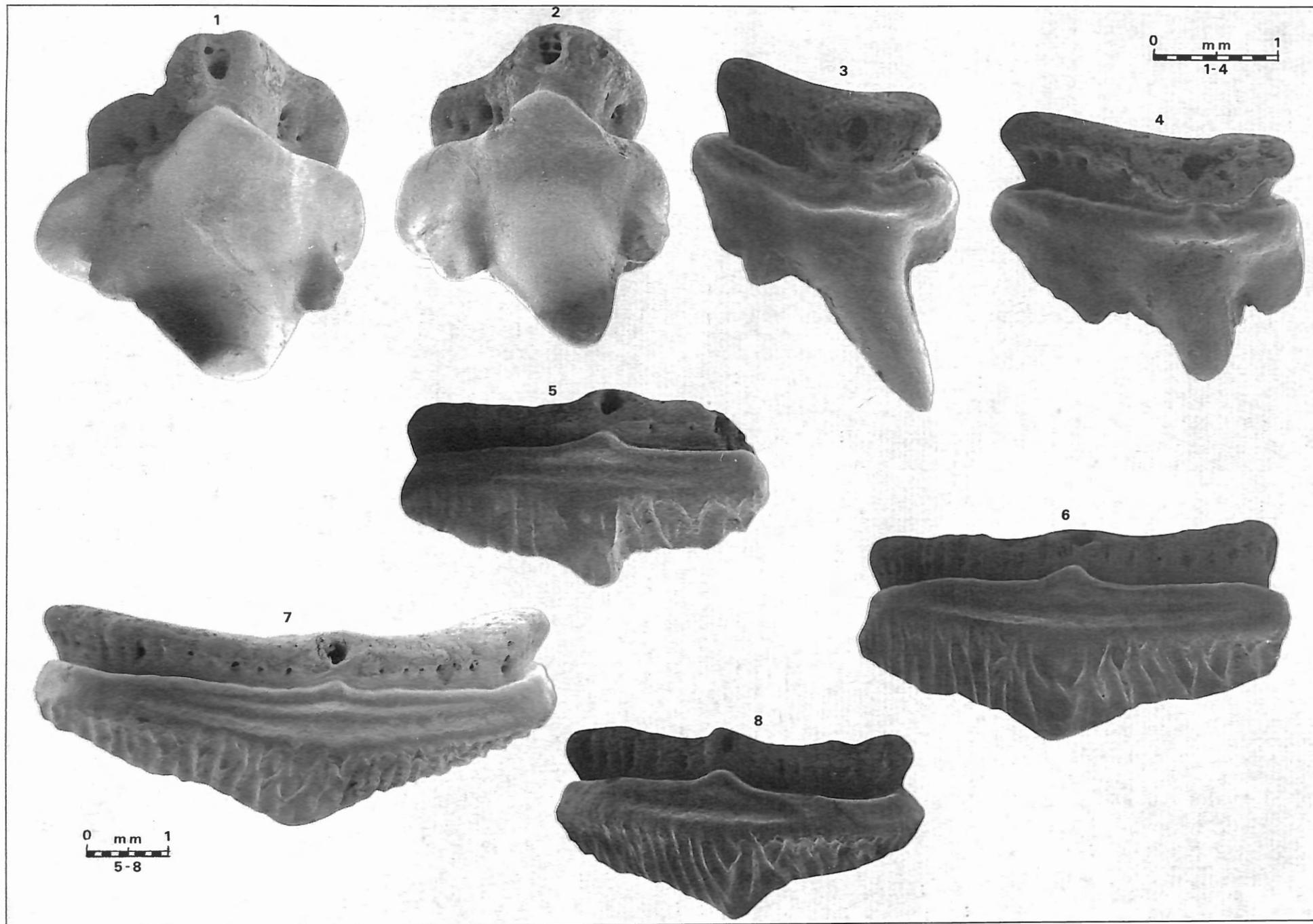


Plate 24. — *Heterodontus francisci* (GIRARD, 1854). Male 630 mm (t.l.), Baja California, Mexico. Upper teeth, inner views.

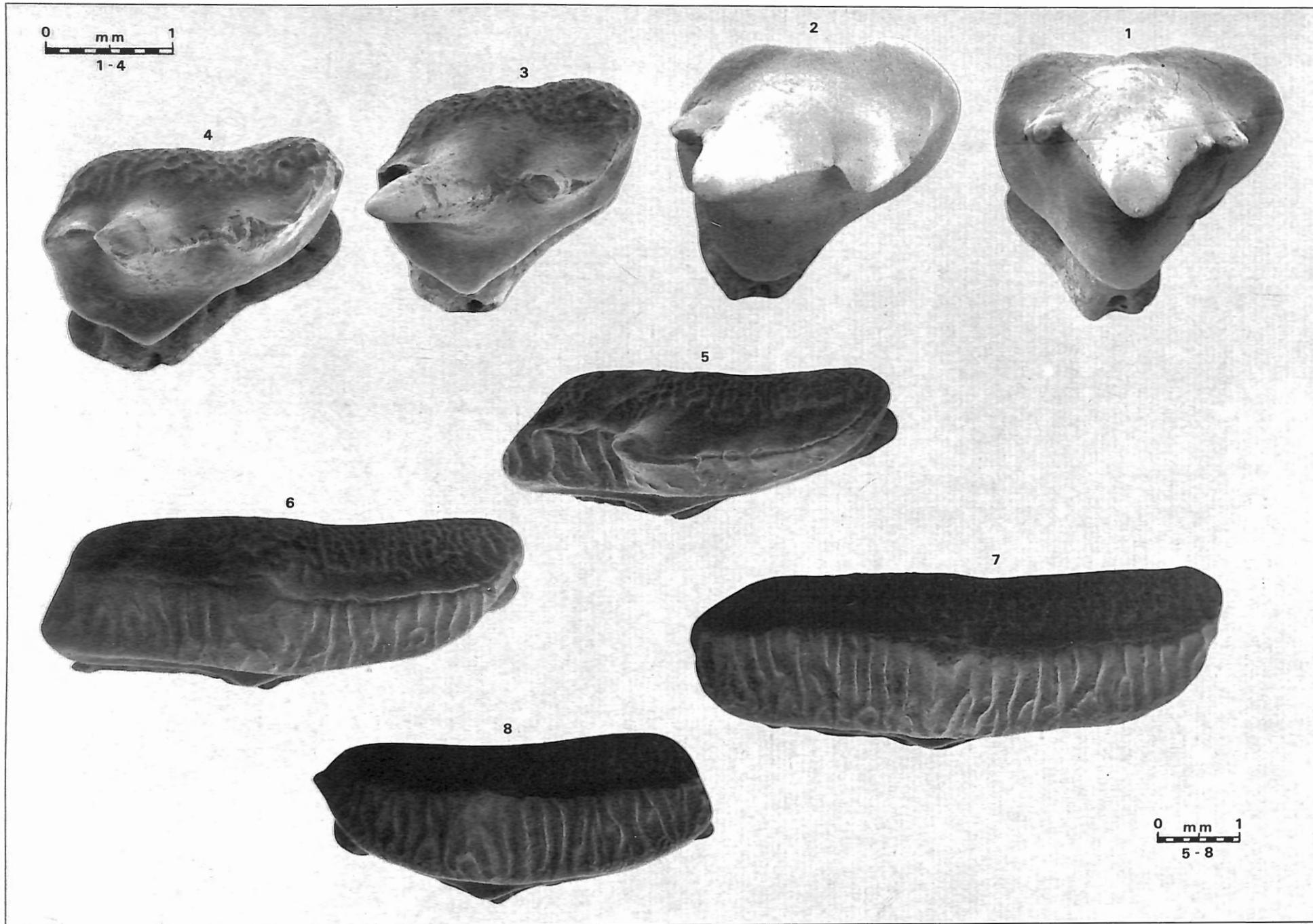


Plate 25. — *Heterodontus francisci* (GIRARD, 1854). Male 630 mm (t.l.), Baja California, Mexico. Upper teeth, occlusal views.

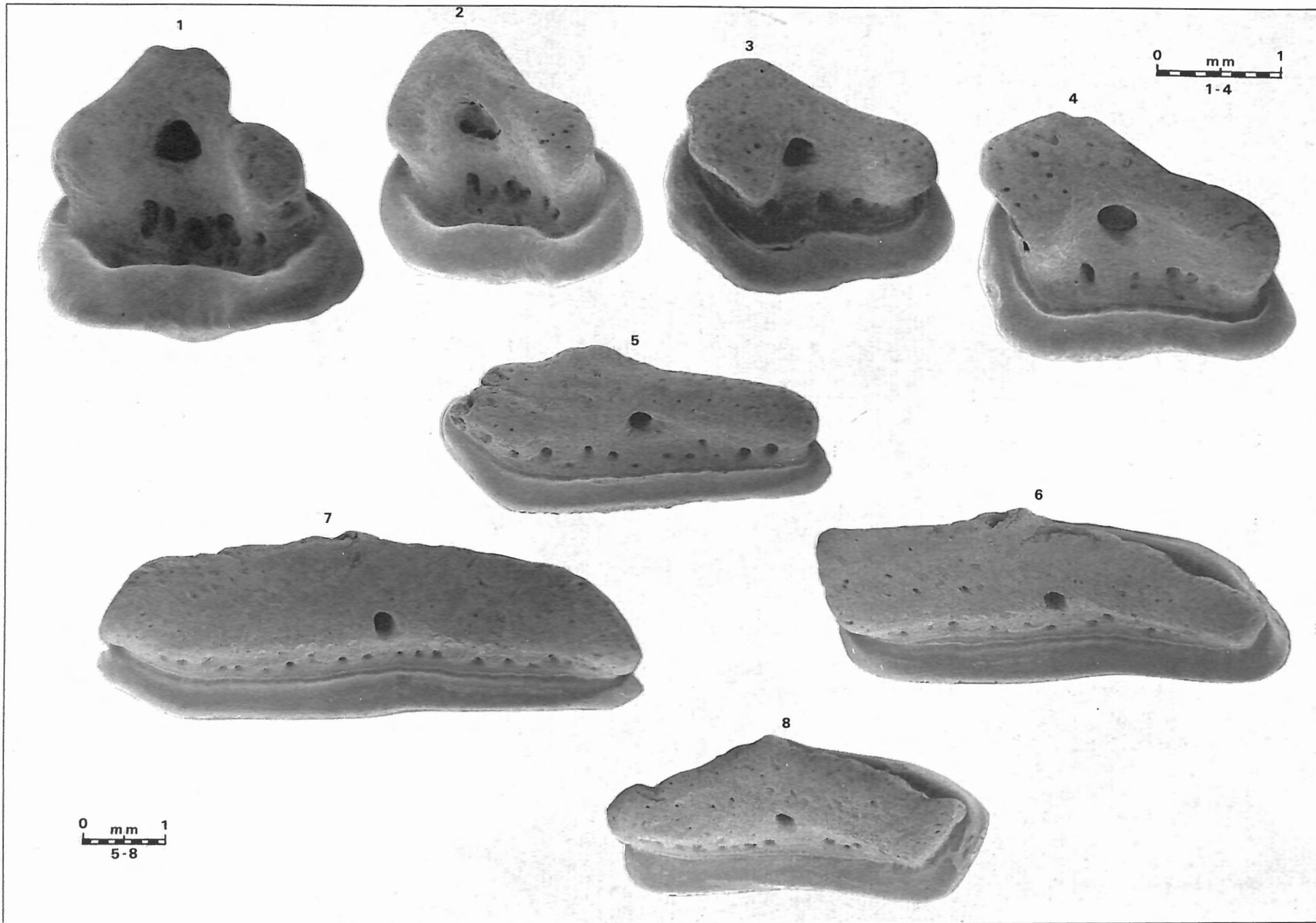


Plate 26. — *Heterodontus francisci* (GIRARD, 1854). Male 630 mm (t.l.), Baja California, Mexico. Upper teeth, basal views.

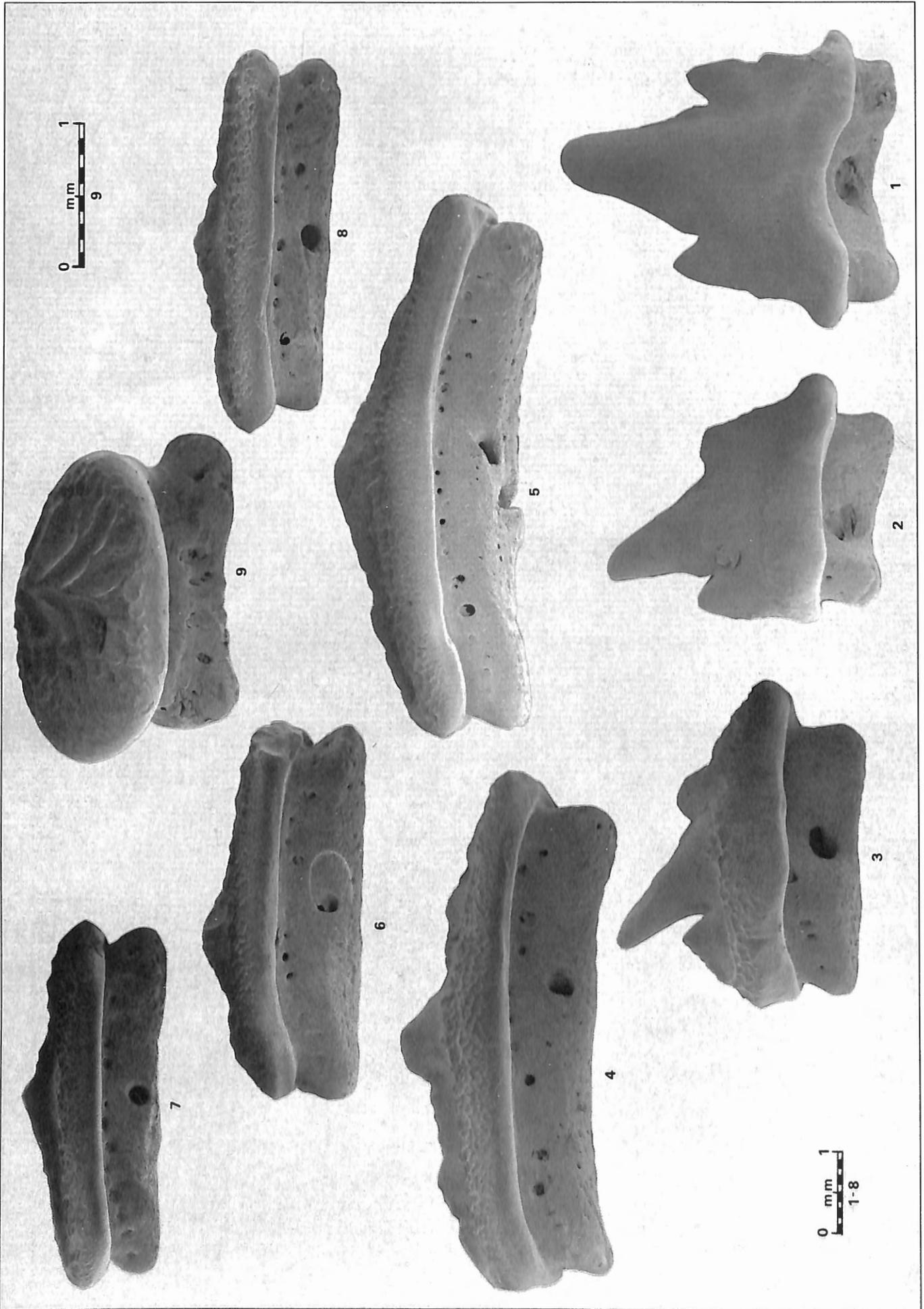


Plate 27. -- *Heterodontus francisci* (GIRARD, 1854). Male 630 mm (t.l.), Baja California, Mexico. Lower teeth, outer views.

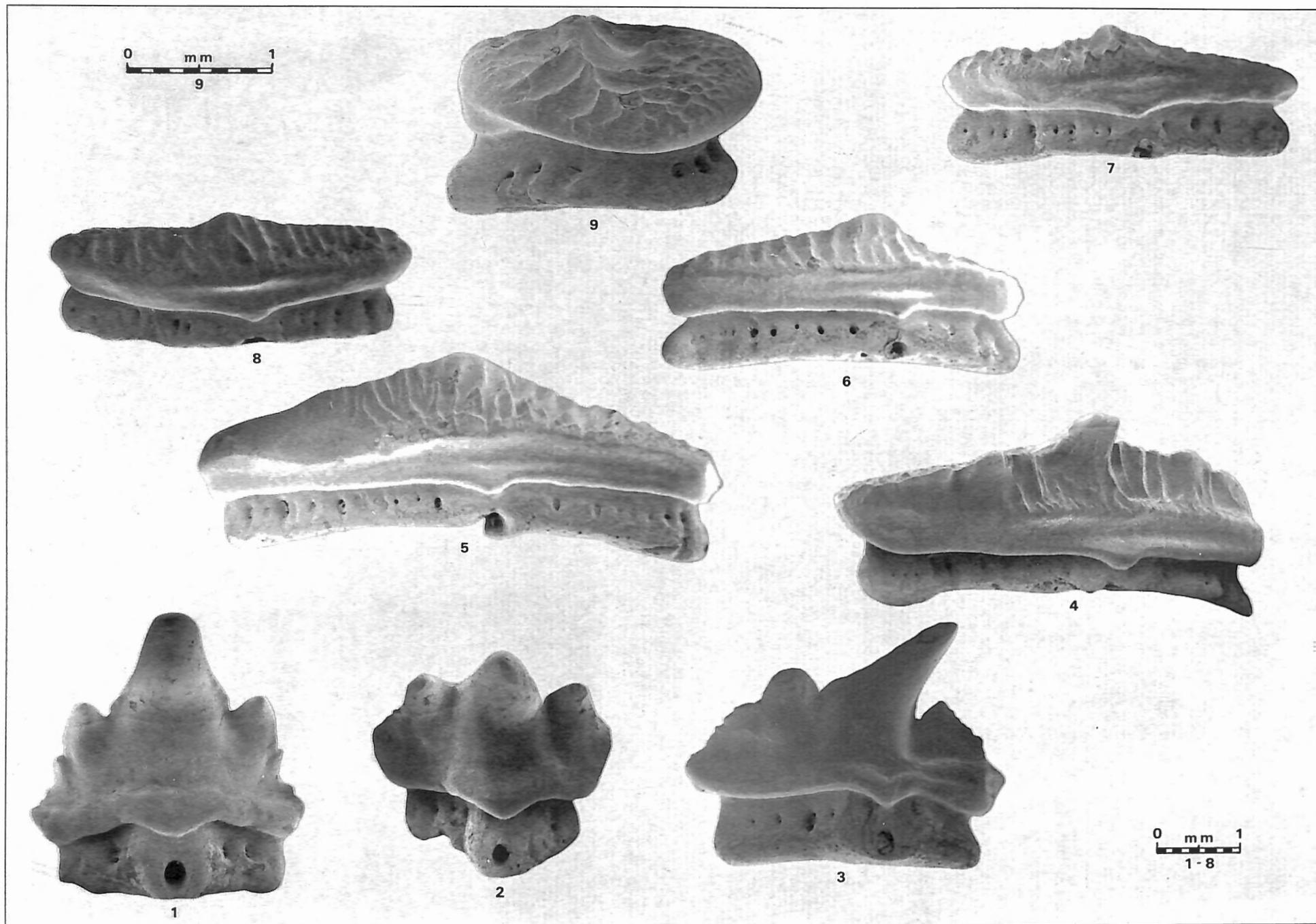


Plate 28. — *Heterodontus francisci* (GIRARD, 1854). Male 630 mm (t.l.), Baja California, Mexico. Lower teeth, inner views.

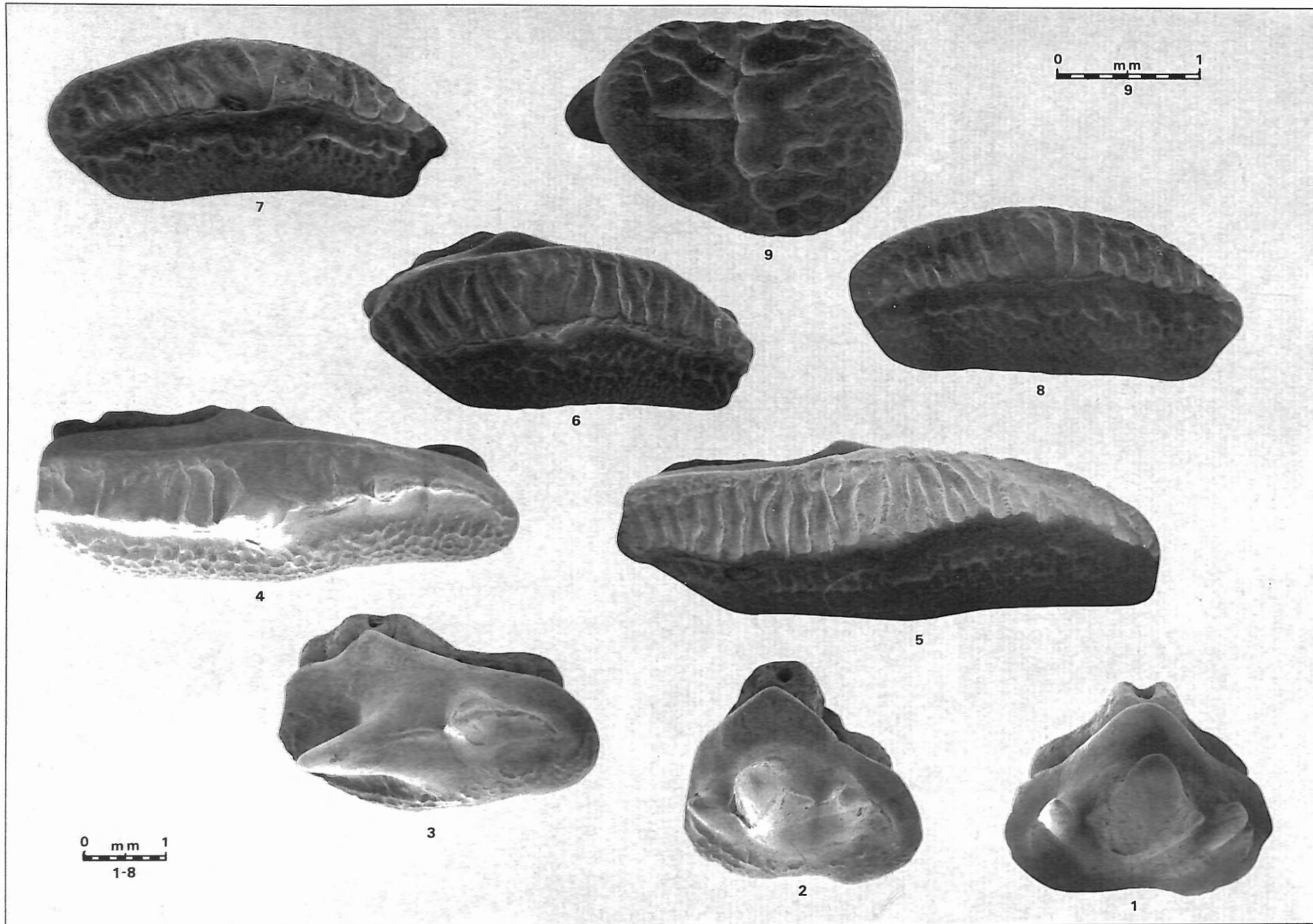


Plate 29. – *Heterodontus francisci* (GIRARD, 1854). Male 630 mm (t.l.), Baja California, Mexico. Lower teeth, occlusal views.

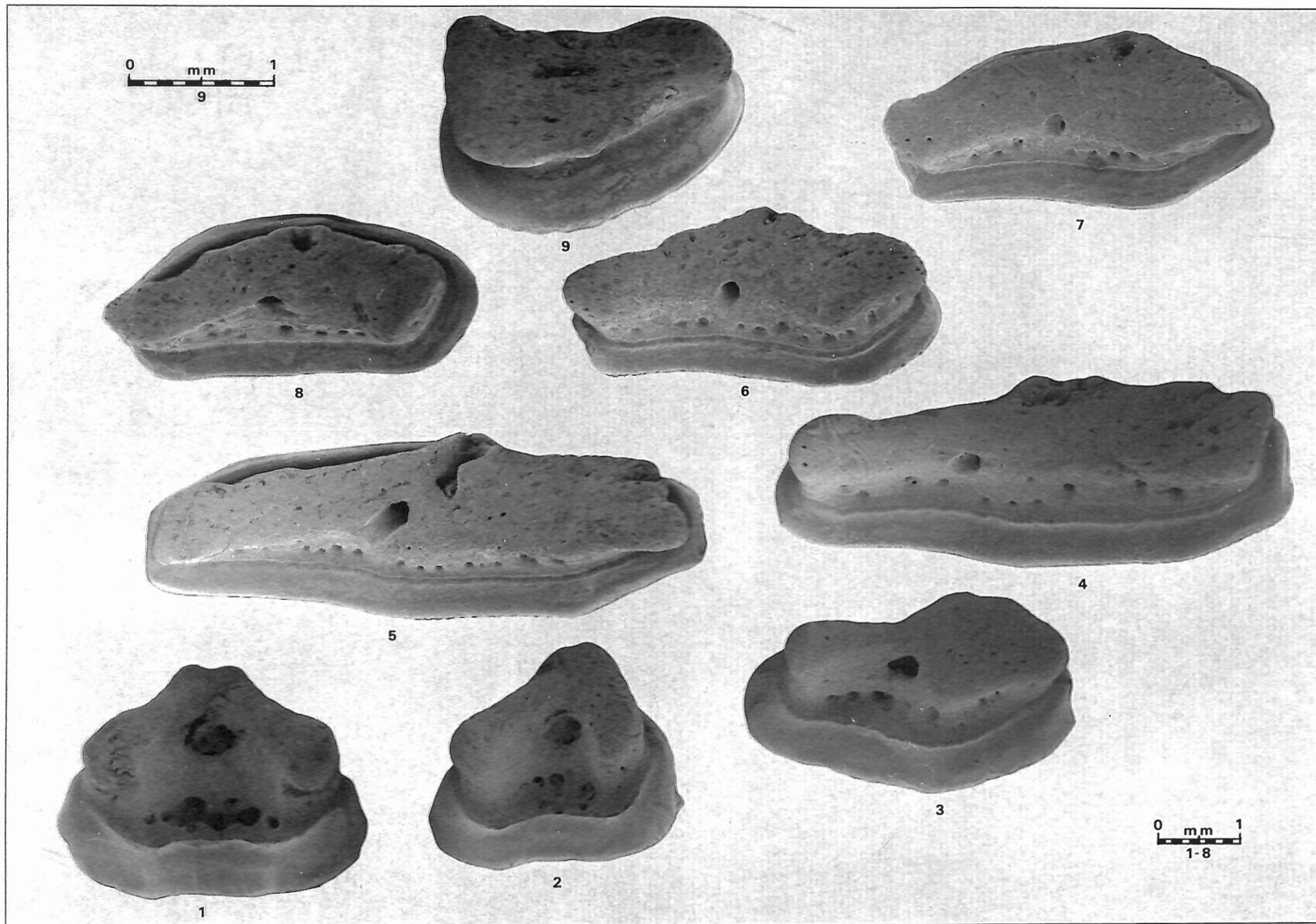


Plate 30. — *Heterodontus francisci* (GIRARD, 1854). Male 630 mm (t.l.), Baja California, Mexico. Lower teeth, basal views.

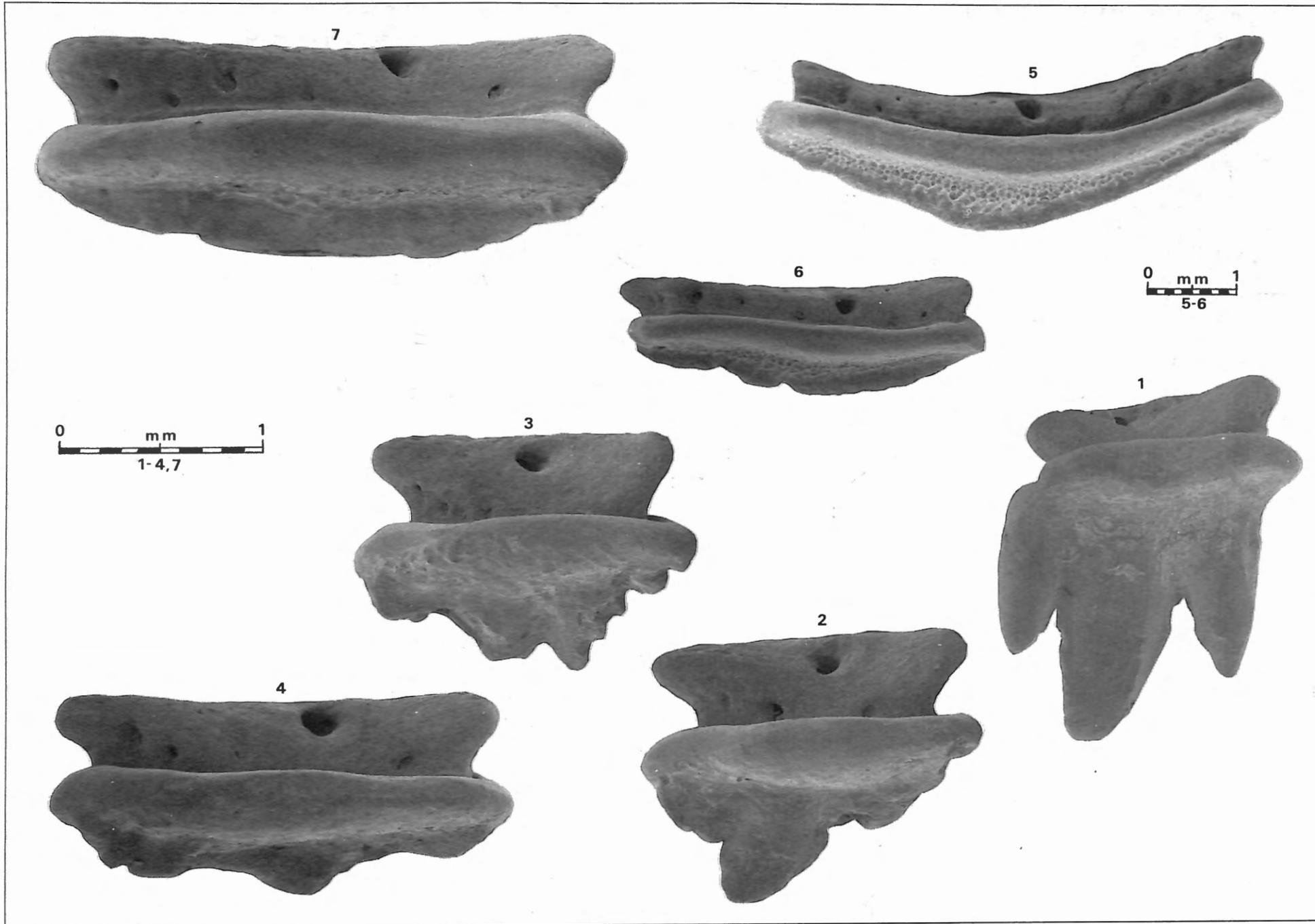


Plate 31. – *Heterodontus quoyi* (FREMENVILLE, 1840). Male 475 mm (t.l.), Galapagos Islands. Upper teeth, outer views.

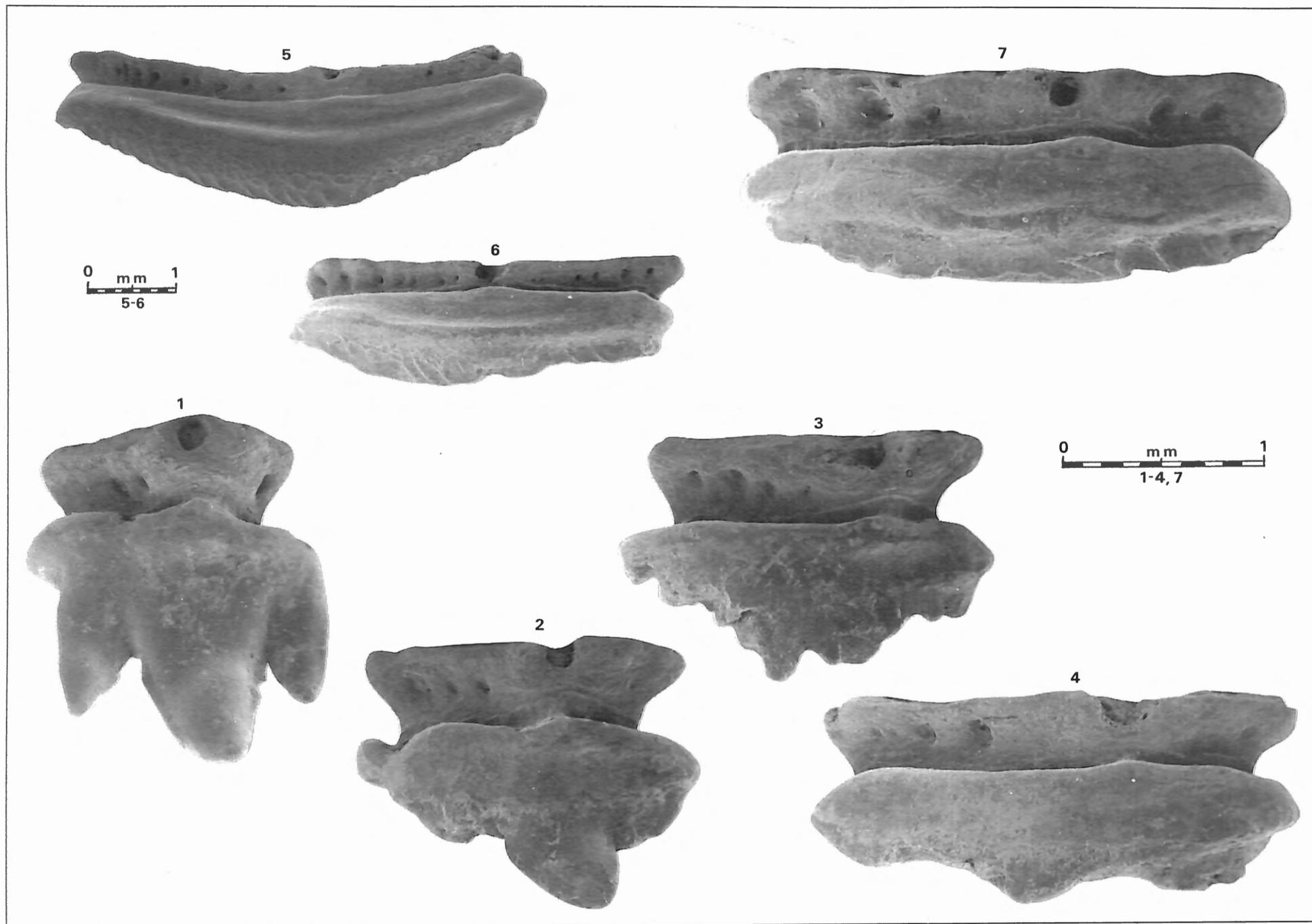


Plate 32. – *Heterodontus quoyi* (FREMENVILLE, 1840). Male 475 mm (t.l.), Galapagos Islands. Upper teeth, inner views.

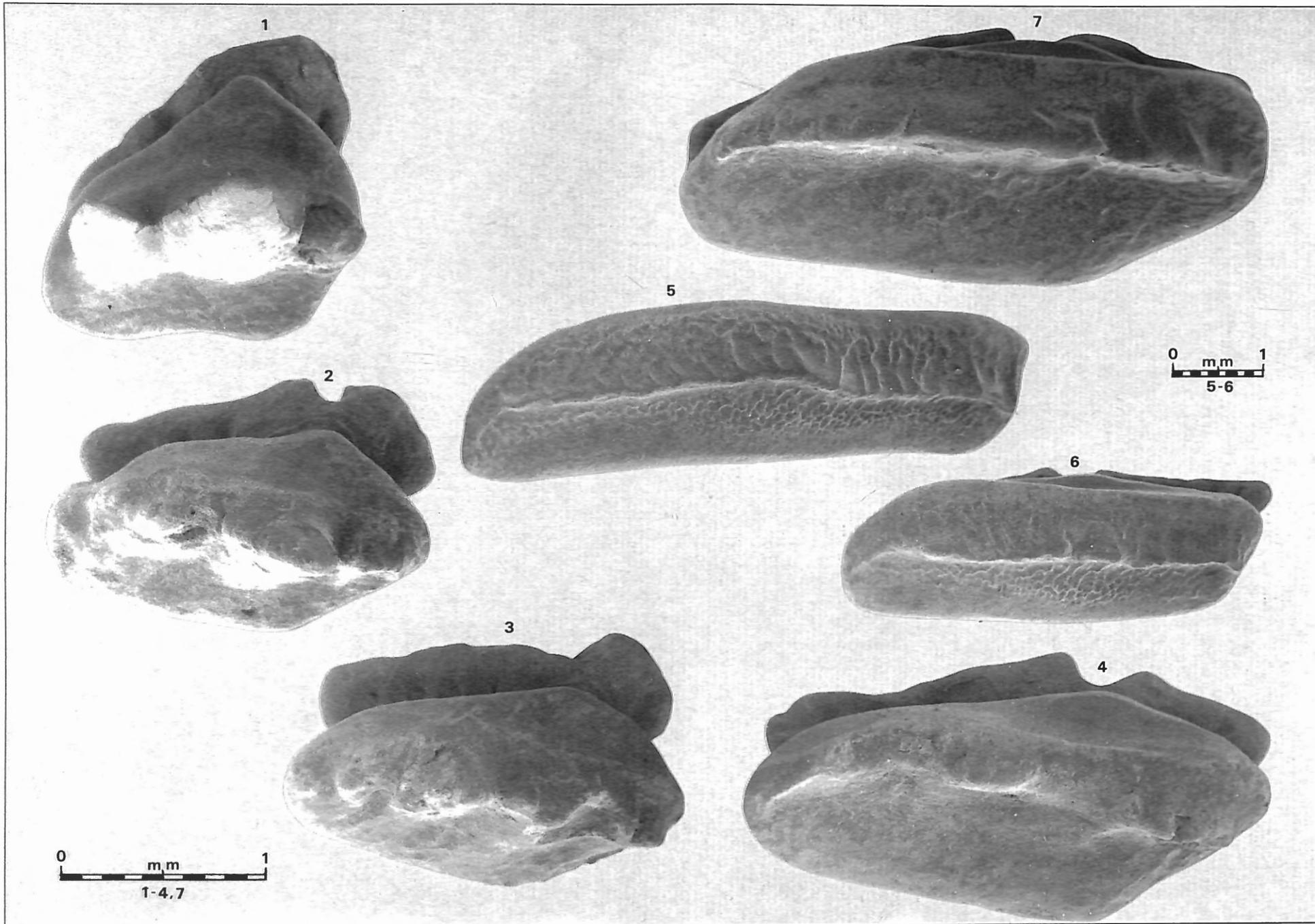


Plate 33. — *Heterodontus quoyi* (FREMIVILLE, 1840). Male 475 mm (t.l.), Galapagos Islands. Upper teeth, occlusal views.

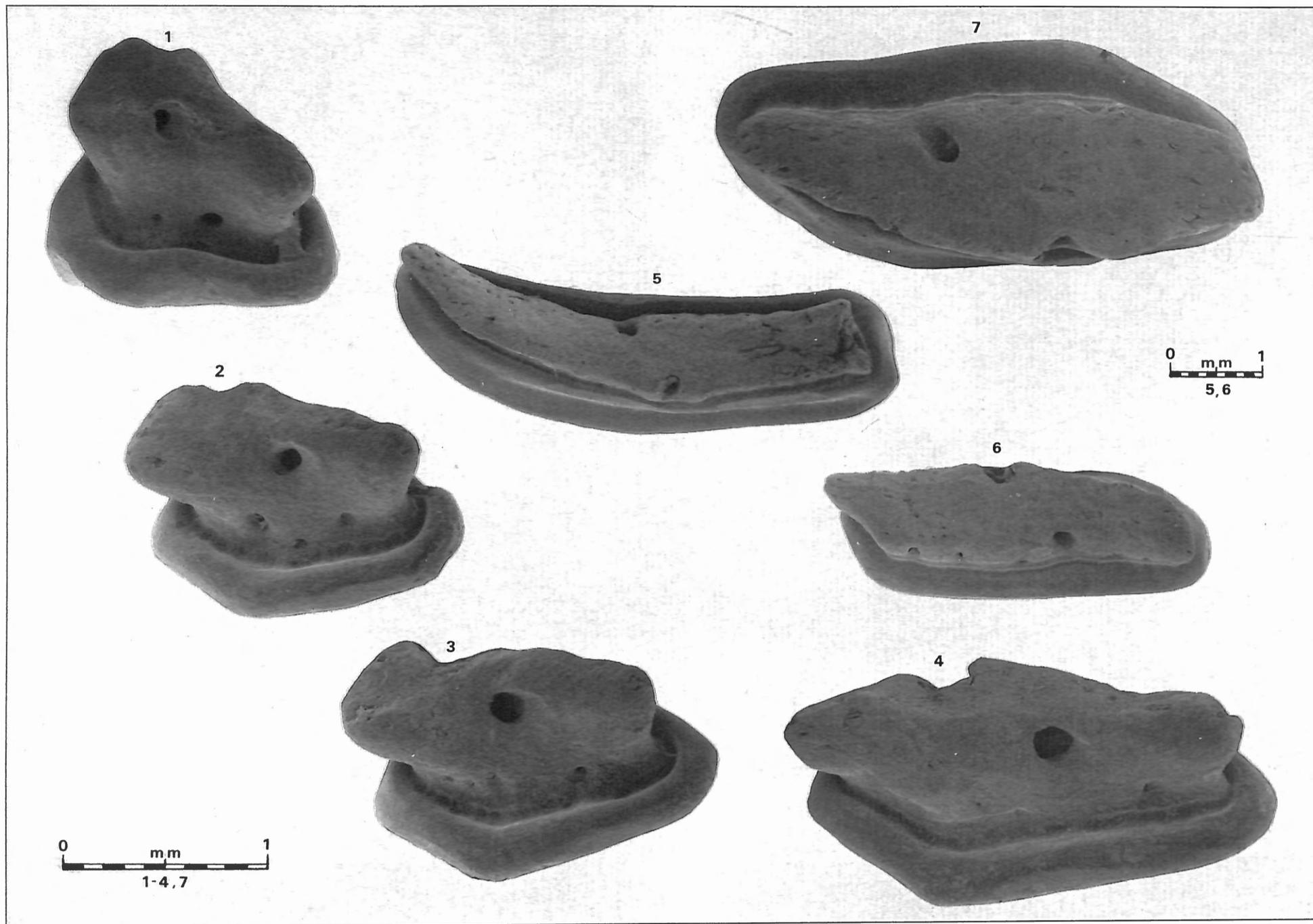


Plate 34. – *Heterodontus quoyi* (FREMENVILLE, 1840). Male 475 mm (t.l.), Galapagos Islands. Upper teeth, basal views.

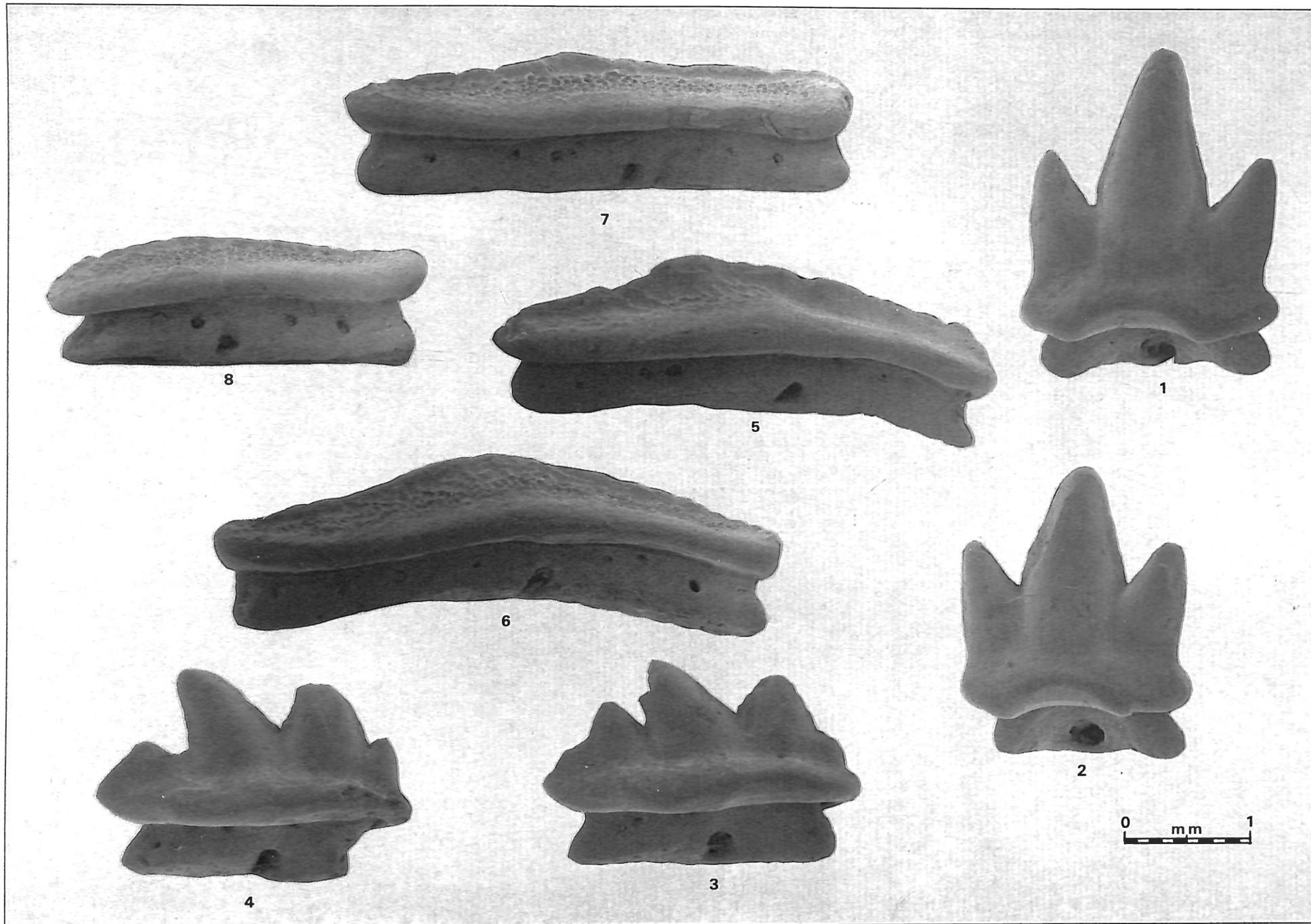


Plate 35. — *Heterodontus quoyi* (FREMENVILLE, 1840). Male 475 mm (t.l.), Galapagos Islands. Lower teeth, outer views.

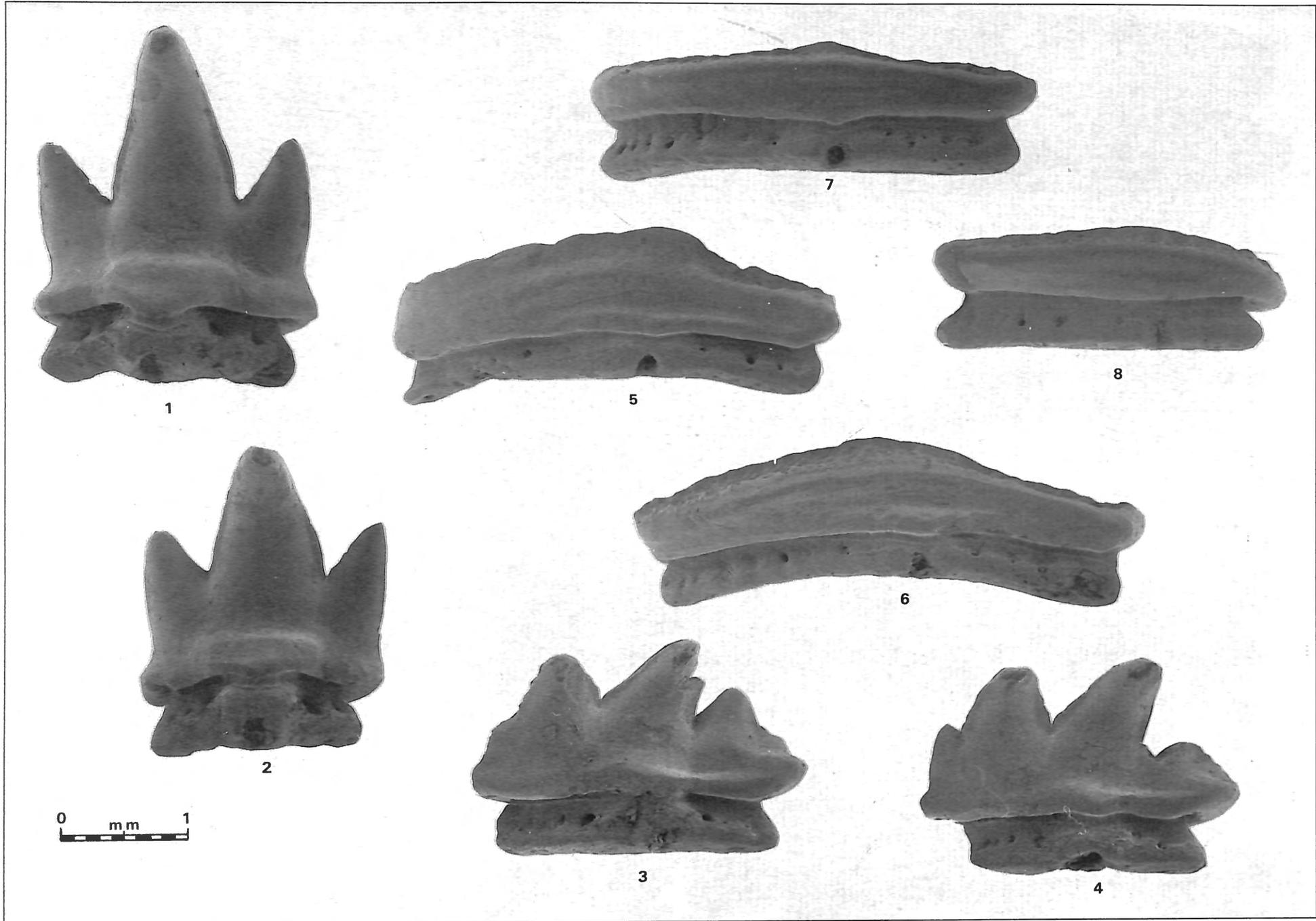


Plate 36. – *Heterodontus quoyi* (FREMENVILLE, 1840). Male 475 mm (t.l.), Galapagos Islands. Lower teeth, inner views.

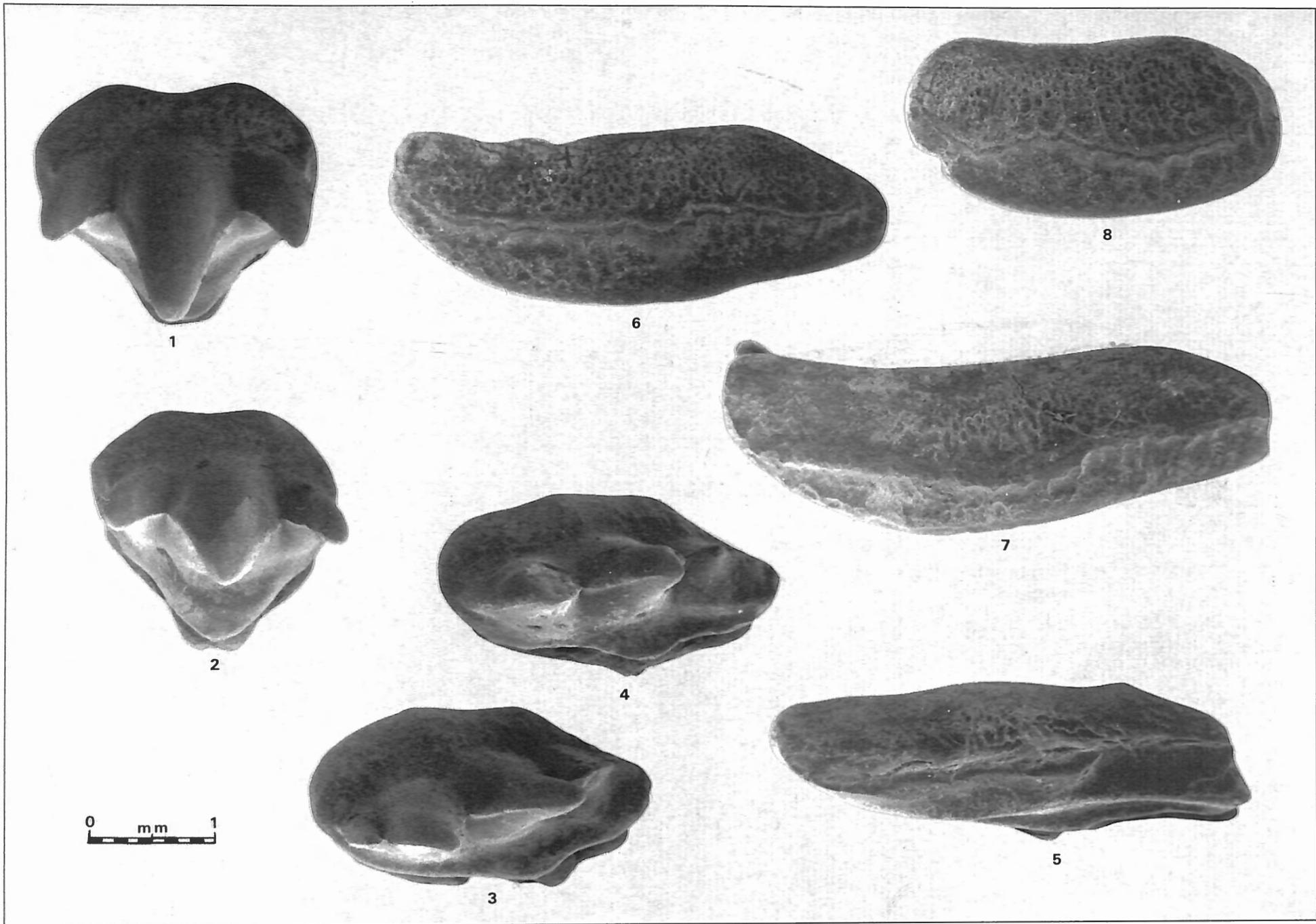


Plate 37. – *Heterodontus quoyi* (FREMENVILLE, 1840). Male 475 mm (t.l.), Galapagos Islands. Lower teeth, occlusal views.

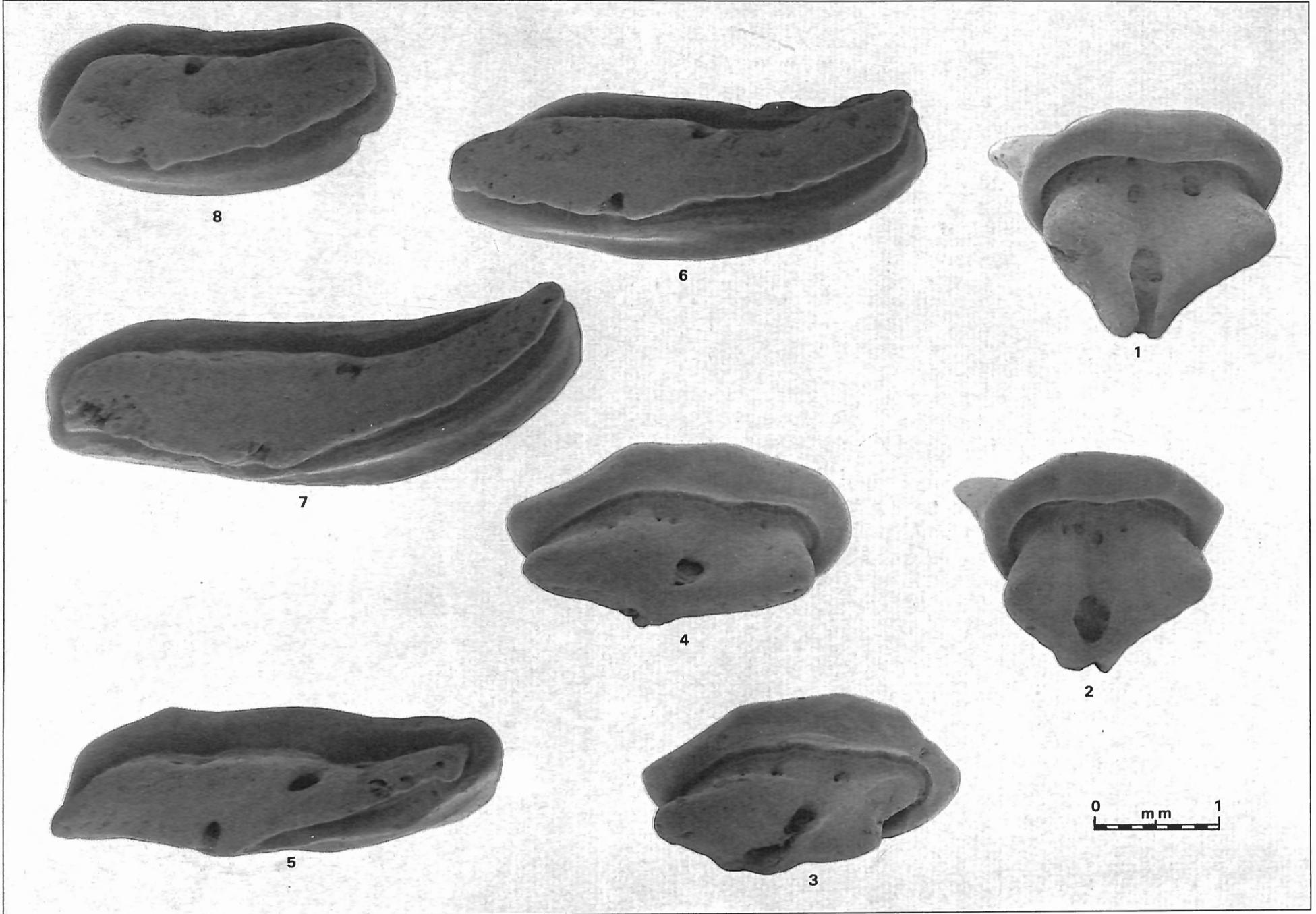


Plate 38. – *Heterodontus quoyi* (FREMENVILLE, 1840). Male 475 mm (t.l.), Galapagos Islands. Lower teeth, basal views.

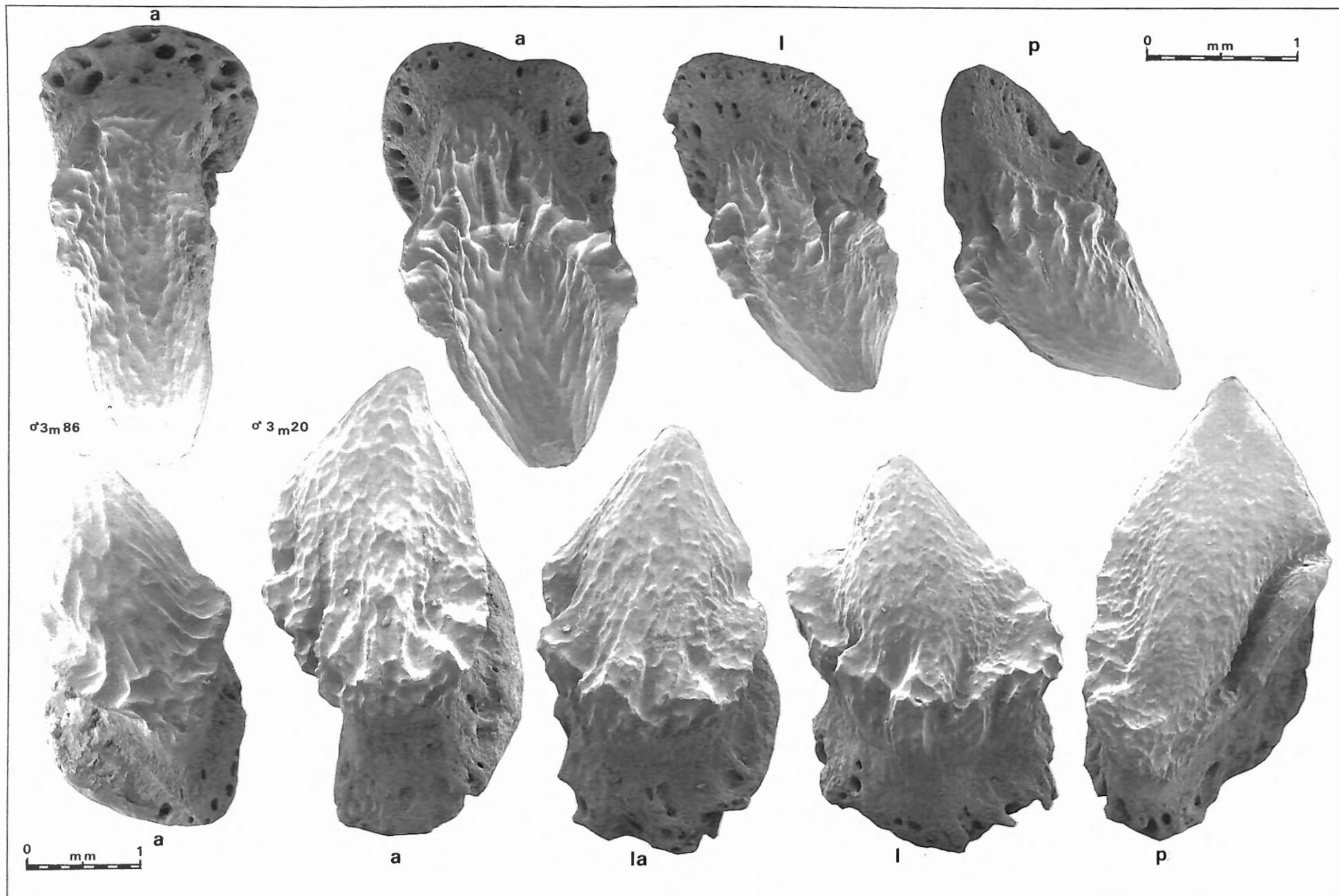


Plate 39. - *Cetorhinus maximus* (GUNNERUS, 1765). Male 386 cm (t.l.), North Sea, one upper and one lower anterior tooth. - Male 320 cm (t.l.), Gulf of Gascogne, France. Upper and lower teeth. All outer views.

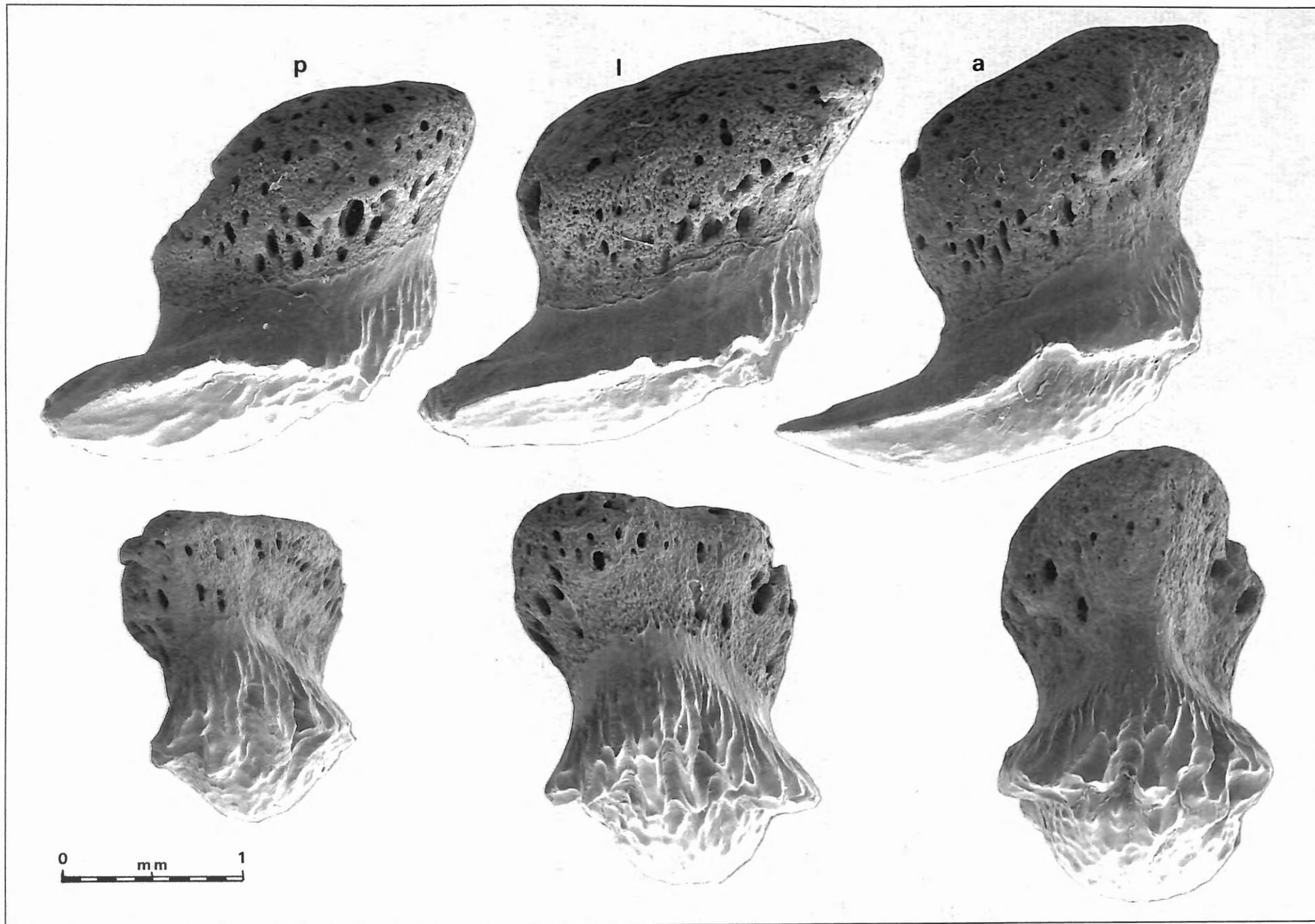


Plate 40. – *Cetorhinus maximus* (GUNNERUS, 1765). Male 320 cm (t.l.), Gulf of Gascogne, France. Upper teeth, profile and outer views.

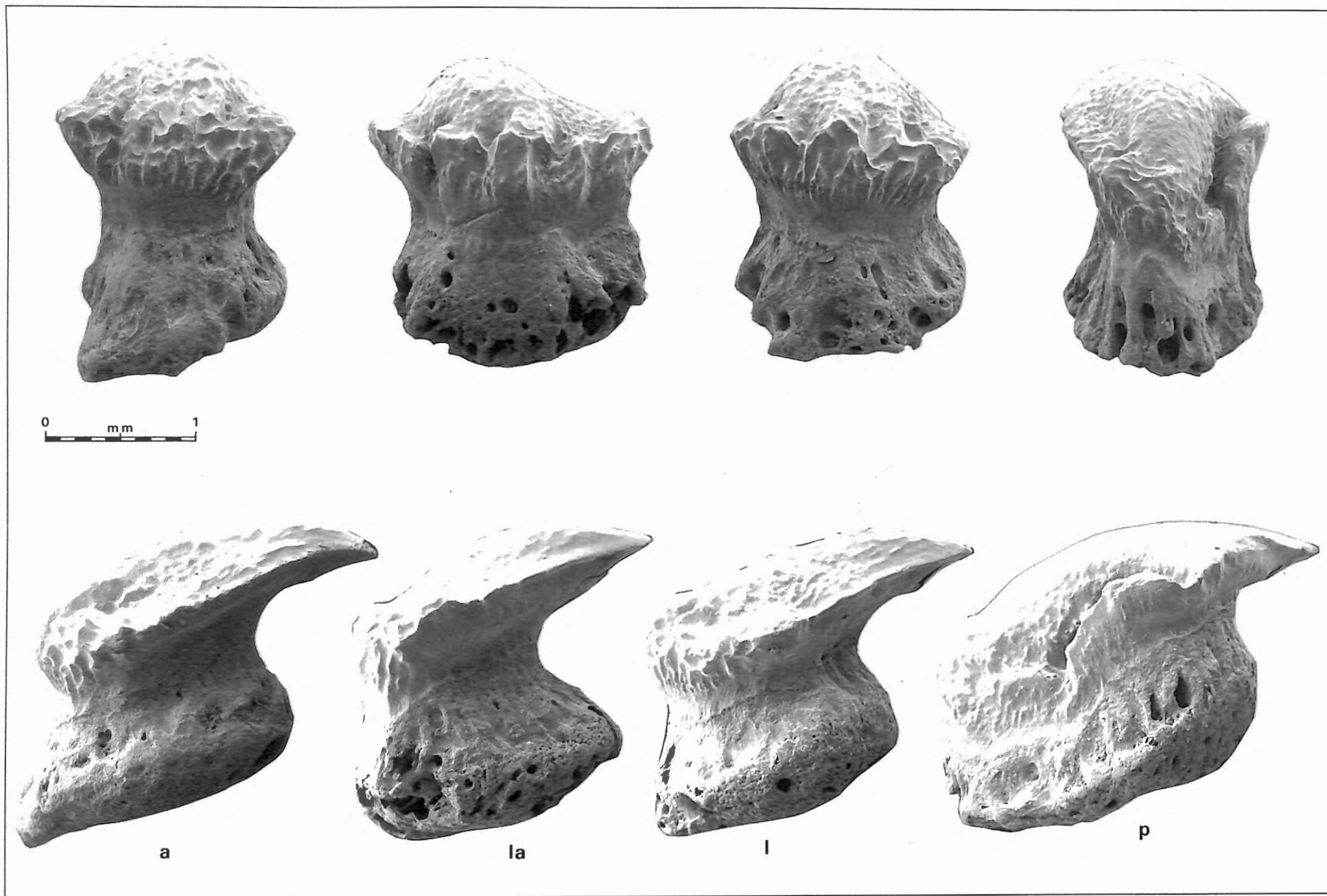


Plate 41. – *Cetorhinus maximus* (GUNNERUS, 1765). Male 320 cm (t.l.), Gulf of Gascogne, France. Lower teeth, profile and outer views.



Plate 42. — *Cetorhinus maximus* (GUNNERUS, 1765). Female circa 800 cm (t.l.), South of Britany, France. Upper (outer and occlusal views) and lower teeth (outer and profile views).

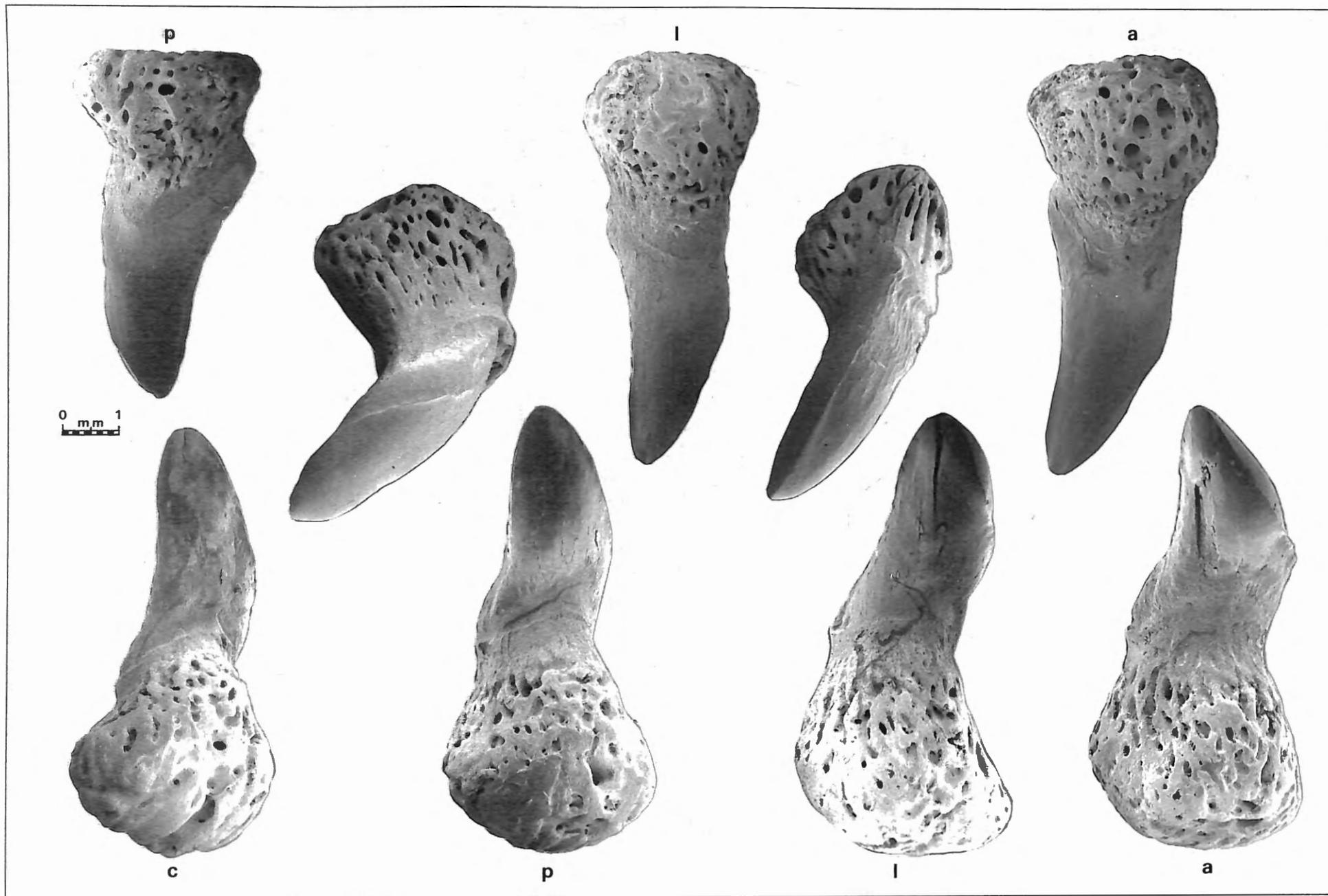


Plate 43. – *Cetorhinus maximus* (GUNNERUS, 1765). Female circa 800 cm (t.l.), South of Britany, France. Upper (inner and profile views) and lower teeth (inner views).

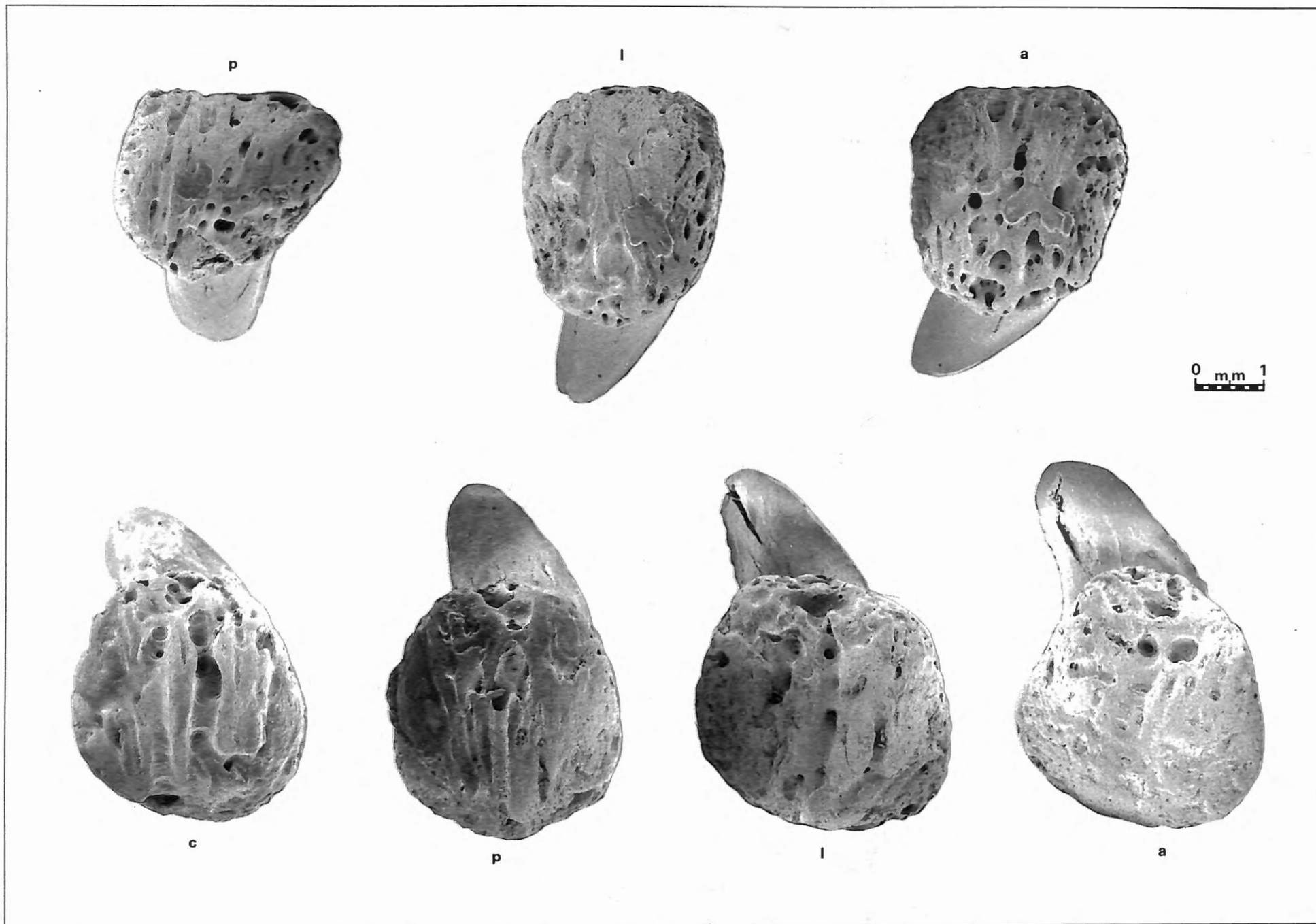


Plate 44. – *Cetorhinus maximus* (GUNNERUS, 1765). Female circa 800 cm (t.l.), South of Britany, France. Upper and lower teeth, basal views.



Plate 45. - *Megachasma pelagios* TAYLOR, COMPAGNO & STRUHSKER, - 1983. Male 449 cm (t.l.), Santa Catalina Island, Mexico. - Upper and lower teeth, outer views.

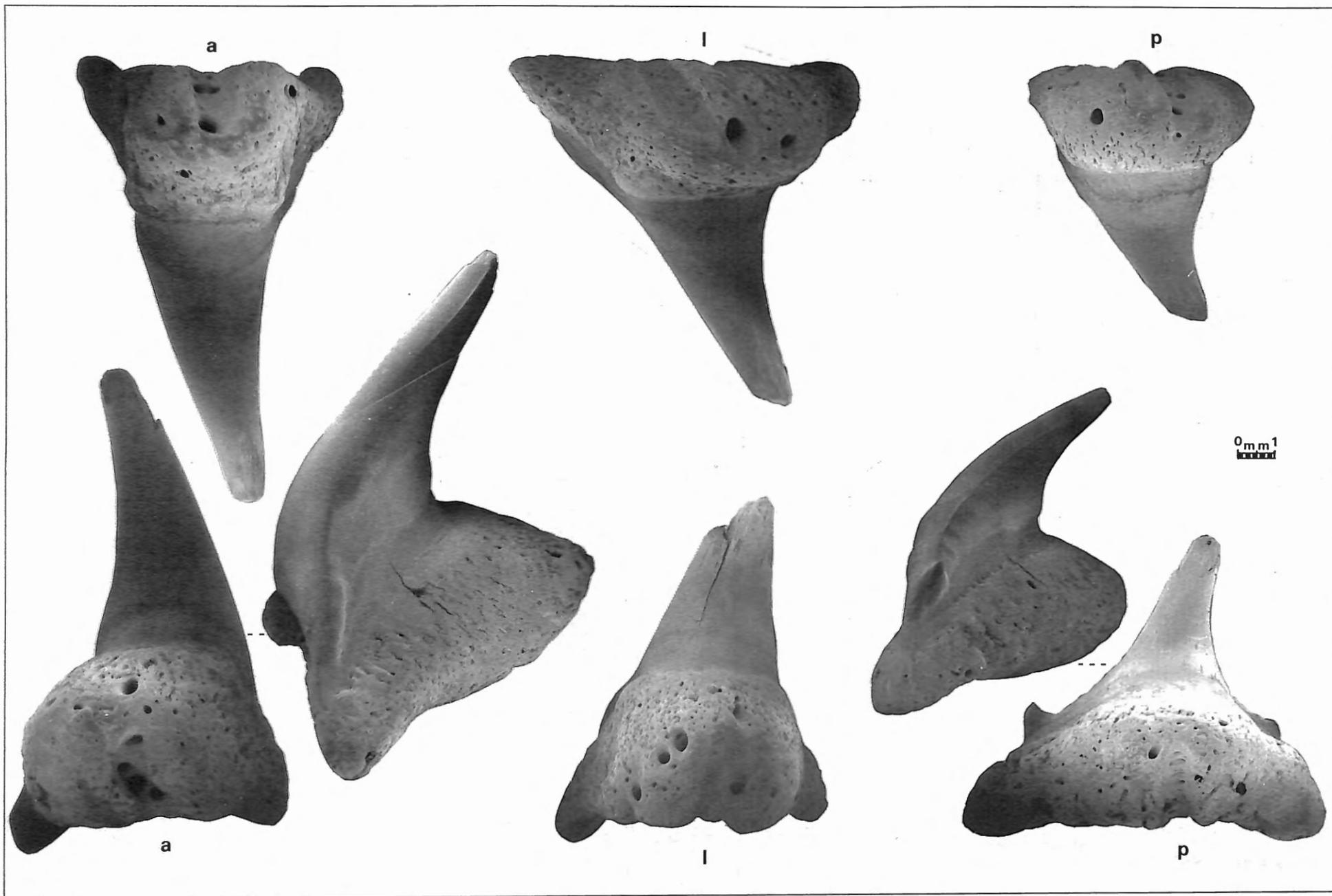


Plate 46. — *Megachasma pelagios* TAYLOR, COMPAGNO & STRUHSKER, - 1983. Male 449 cm (t.l.), Santa Catalina Island, Mexico. - Upper (outer views) and lower teeth ( outer and profile views).



Plate 47. - *Megachasma pelagios* TAYLOR, COMPAGNO & STRUHSAKER, - 1983. Male 449 cm (t.l.), Santa Catalina Island, Mexico. - Upper (occlusal and profile views) and lower teeth (occlusal views).

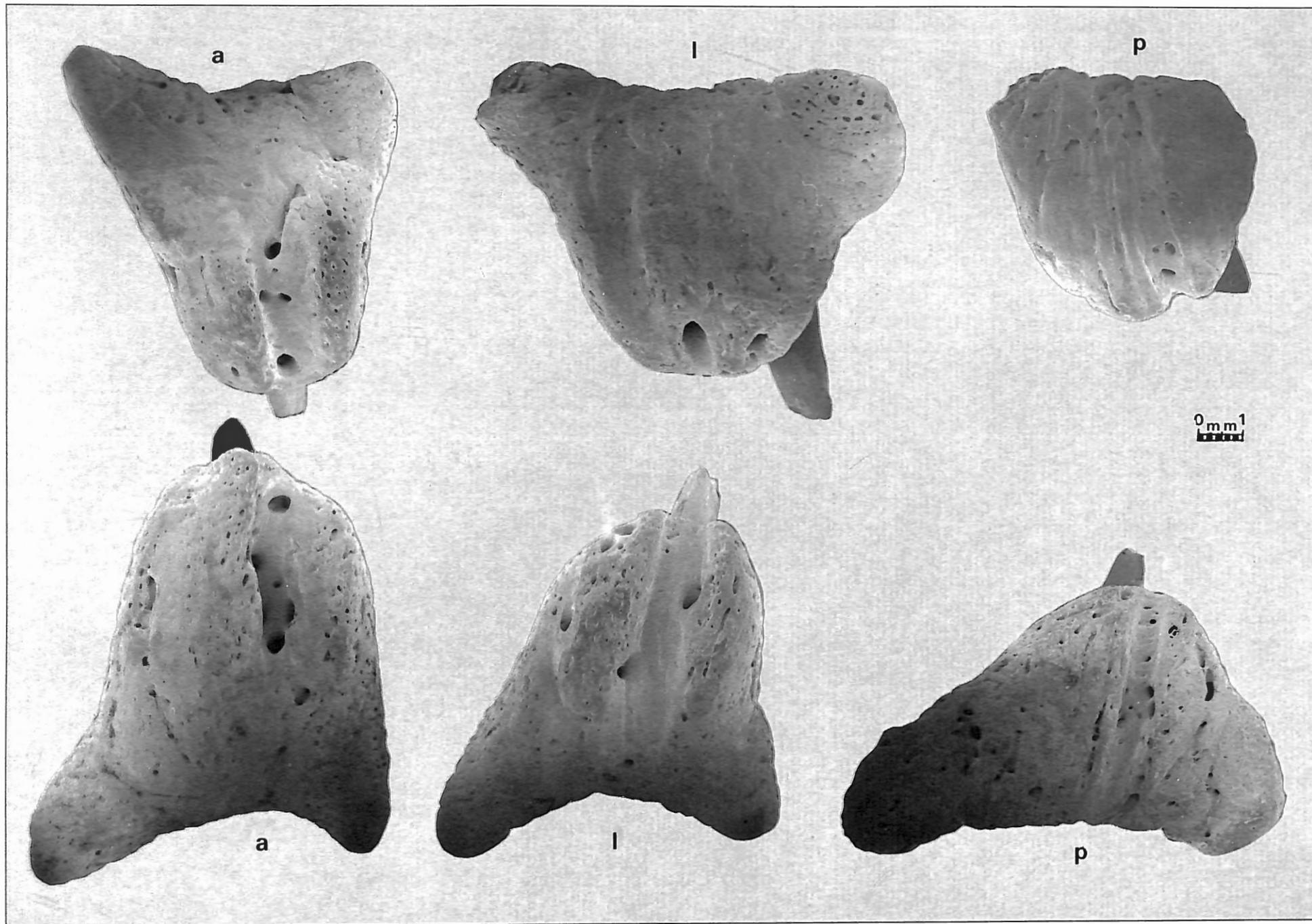


Plate 48. – *Megachasma pelagios* TAYLOR, COMPAGNO & STRUHSAKER, - 1983. Male 449 cm (t.l.), Santa Catalina Island, Mexico. Upper and lower teeth, basal views.

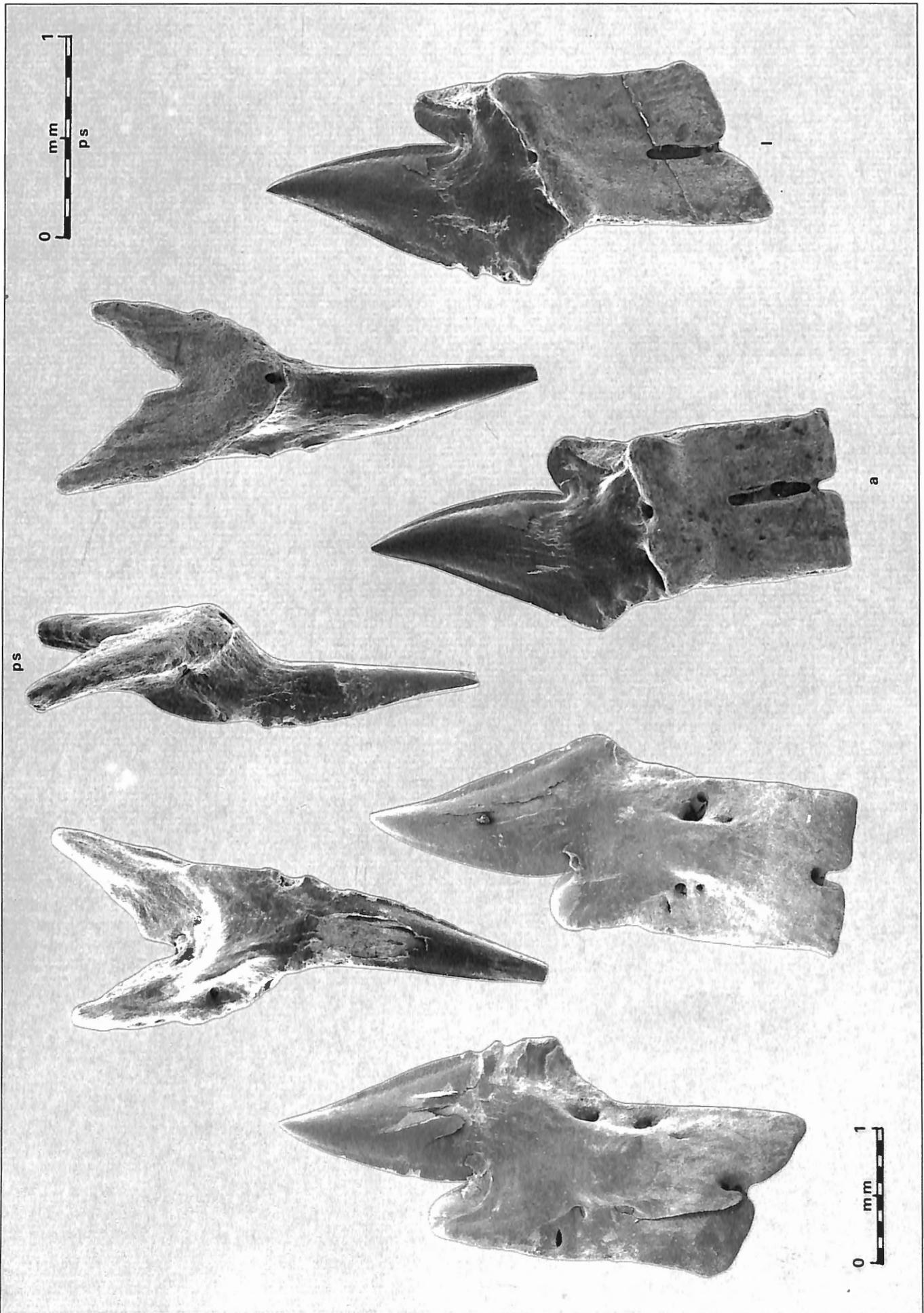


Plate 49. - *Scymnodon squamulosus* (GÜNTHER, 1877). Male 49 cm (t.l.), Japan. Upper and lower teeth (formerly *Zameus*).



Plate 50. - *Scymnodon obscurus* (VAILLANT, 1888). Male 41 cm (t.l.), Senegal. Upper and lower teeth.

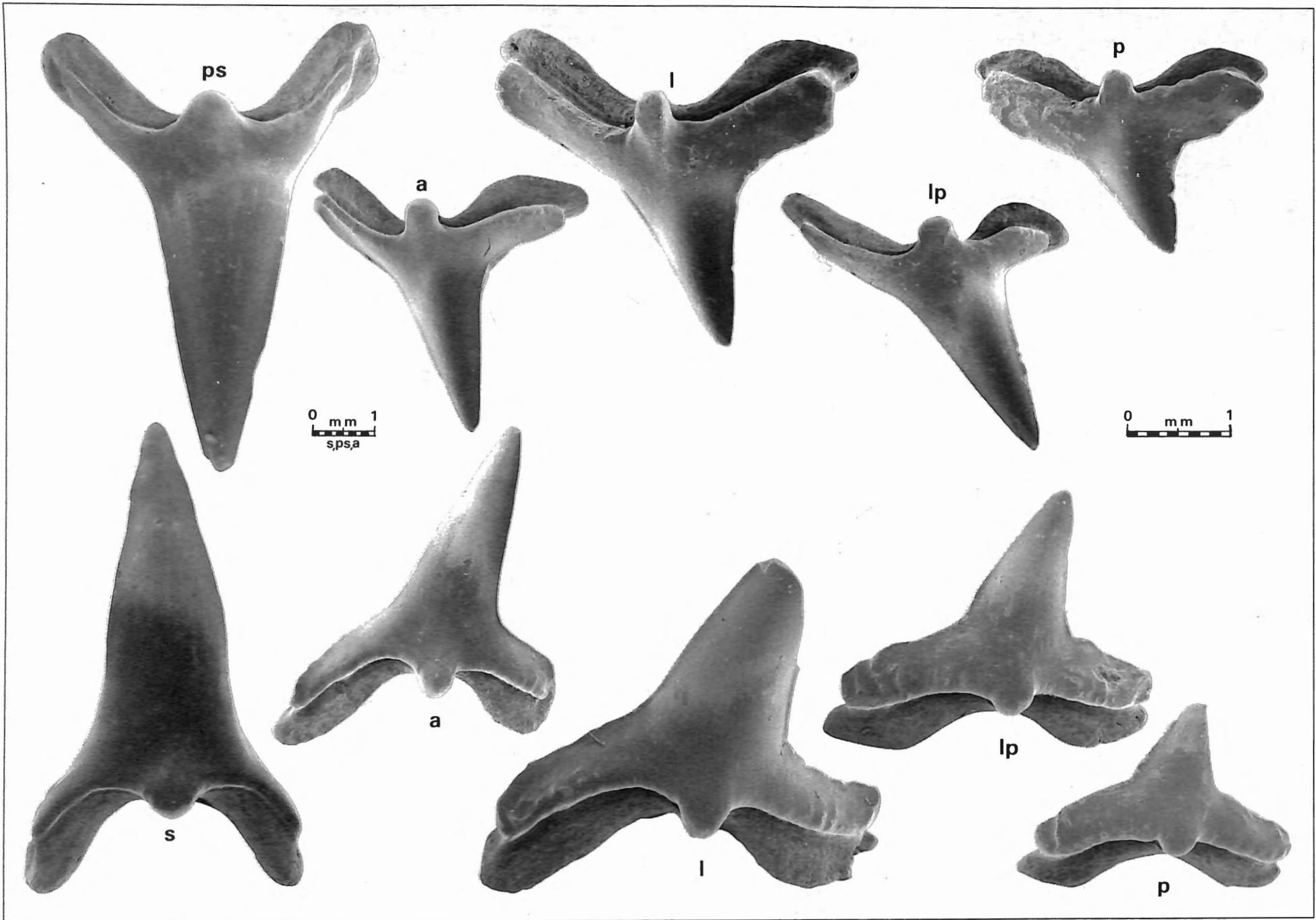


Plate 51. – *Sutorectus tentaculatus* (PETERS, 1864). Male 73 cm (t.l.), Australia. Upper and lower teeth, outer views.

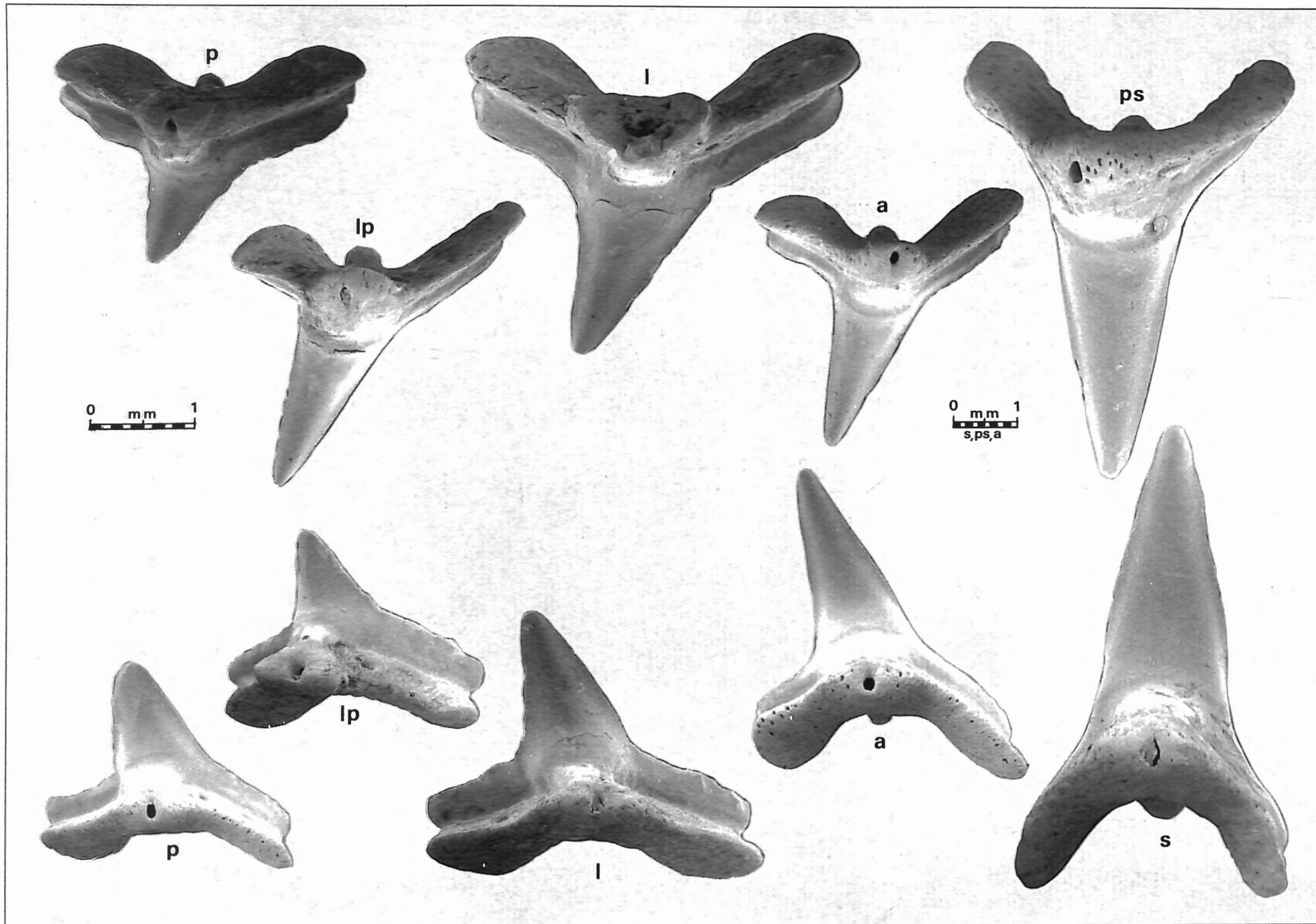


Plate 52. – *Sutorectus tentaculatus* (PETERS, 1864). Male 73 cm (t.l.), Australia. Upper and lower teeth, inner views.

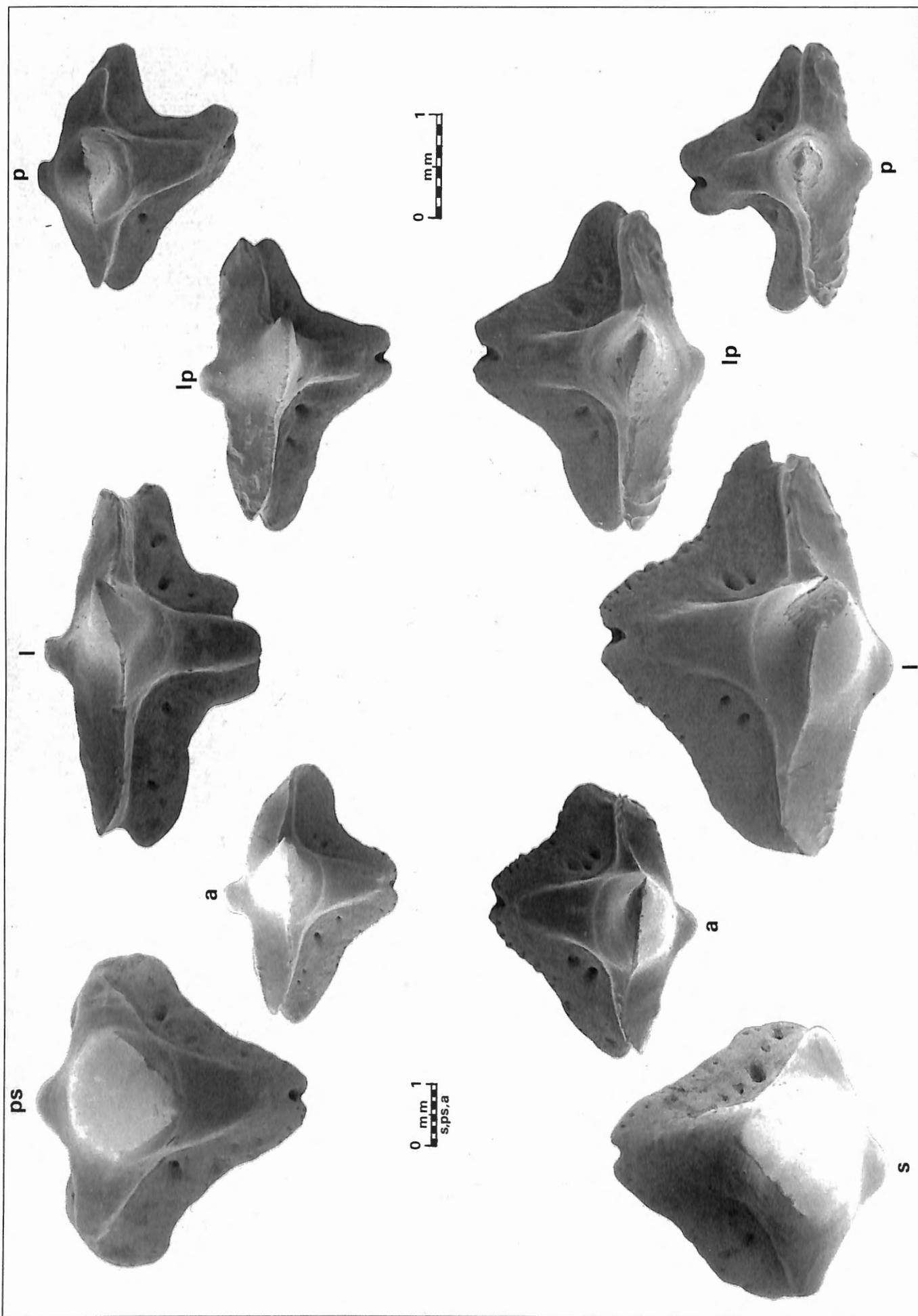


Plate 53. - *Sutorectus tentaculatus* (PETERS, 1864). Male 73 cm (t.l.), Australia. Upper and lower teeth, occlusal views.

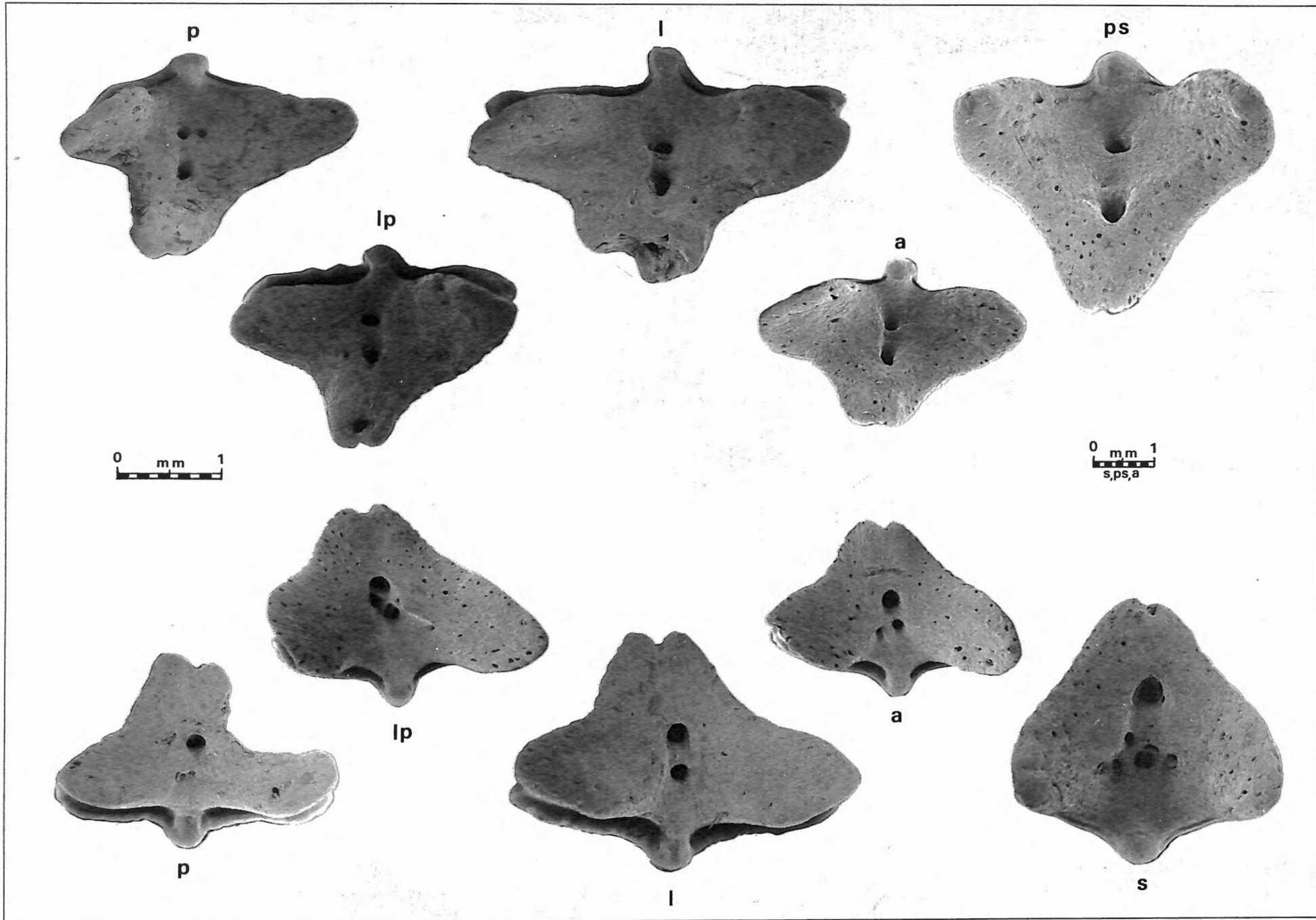


Plate 54. – *Sutorectus tentaculatus* (PETERS, 1864). Male 73 cm (t.l.), Australia. Upper and lower teeth, basal views.