

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

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Part A: Selachii. No. 1:

Order: Hexanchiformes - Family: Hexanchidae. Commissural teeth

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Abstract

The commissural teeth of the Hexanchidae are for the first time described and illustrated. Their morphology allows a direct generic assignment.

Key-words: Elasmobranchii - Selachii - Hexanchidae - Odontology.

Résumé

La morphologie des dents commissurales des Hexanchidae est décrite et illustrée pour la première fois; elle permet une identification générique.

Mots-clés: Elasmobranchii - Selachii - Hexanchidae - Odontologie.

Kurzfassung:

Die Zähne der Kieferwinkel von Hexanchidae werden zum ersten Mal beschrieben und illustriert. Ihre Morphologie erlaubt eine direkte generische Zuordnung.

Schlüsselwörter: Elasmobranchii - Selachii - Hexanchidae - Odontologie.

Introduction

Upper and lower, symphyseal, anterior and lateral teeth of the Hexanchidae were many times described and illustrated. But, because of their very small dimensions, the numerous commissural teeth remained ignored.

The authors, as paleontologists, have found several times commissural microteeth of Hexanchidae in different cenozoic levels in Belgium, France, Portugal and U.S.A., of which some have been shortly mentioned (HERMAN, 1975, HOVESTADT, HOVESTADT & SMITH 1983).

* This series is dedicated to the memory of Dr. E. CASIER (1904-1976).

The problem was to find out, whether or not it was possible to elaborate with a relative reliability generic or specific attributions for these small teeth.

Therefore, a careful examination was initiated of the commissural teeth of the four living species belonging to the three genera *Hexanchus*, *Notorhynchus* and *Heptanchias*.

The aim of this series of monographies is to describe and illustrate the tooth characters of supraspecific taxa. The present contribution will only deal with the morphology of the teeth of the three type species *Hexanchus griseus*, *Notorhynchus cepedianus* and *Heptanchias perlo*.

A description of the commissural teeth of *Hexanchus vitulus*, and comments on their possible implications will be the object of a separate publication.

The commissural teeth of the Hexanchidae are very small. The largest one observed in a jaw of a large *Hexanchus griseus* just exceeded 10 mm of length, the smallest one measured less than 0.2 mm and came from a juvenile specimen of *Heptanchias perlo*.

Description of the odontological types

ORDER: HEXANCHIFORMES

Family: Hexanchidae

The sharks of this family show a pronounced dignathic and monognathic heterodonty. The lower jaw presents one symphyseal row with subsymmetrically compressed teeth similar to heraldic crowns. These flanked on both sides by five or six lateral rows of elongated and strongly compressed teeth with many cusplets, resembling combs. Dentition continued towards jaw angles by six to thirteen, or more commissural rows of very small, more or less elongated and flattened, relatively monolithic teeth without a true cusp.

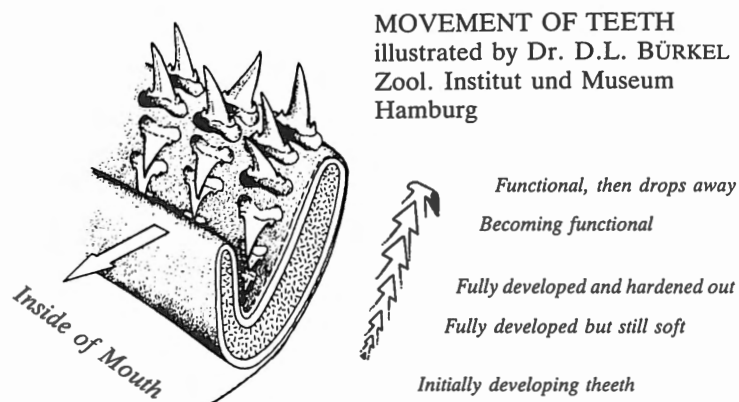
In the upper jaw, we observe on each side of the

symphysis two anterior rows of monocuspid hook-like teeth without additional cusplets. These followed by six to eight lateral rows of elongated and strongly compressed teeth, on which additional cusplets appear on the distal (WARD, 1979) side of the main cusp in variable numbers. Towards jaw angles follow six to thirteen or more (?) commissural rows of very small teeth similar to those of the lower jaw.

Precise distinction between the last lateral row and the first commissural row is sometimes arbitrary.

All these teeth are always strictly anaulacorhizid.

This family includes three living genera, easily distinguishable also by their isolated teeth (see text plate, figs. 1 to 3).



We prefer to use the terms "outer" and "inner" instead of "labial" and "lingual", because the elasmobranch tooth grows firstly with its lingual side turned to the inner side of the jaw cartilage, i.e. with a labial orientation. Being moved then into its functional upright position in the front files, which is a short lasting period only, the inner face would be lingual, the outer labial in orientation. Due to this peculiarity of elasmobranch tooth development in a position and place other than its functional appearance, we prefer the neutral use of "inner" and "outer".

Key to the genera based on odontological characters:

Lower teeth

- 1a – Lower teeth with a distinct main cusp, which at least twice as high as the following cusplets of about equal height, and with strong mesial serrulations resembling small cusplets . . . *Heptranchias*
- 1b – Lower teeth without obvious main cusp, but a variable number of cusplets gradually decreasing in size toward lateral tooth edge . . . — 2
- 2a – Teeth subquadrangle in shape, rather high, with usually five, exceptionally six cusplets and coarse serrulations at mesial edge . . . *Notorhynchus*

- 2b – Teeth subquadrangle in shape, rather low, with seven to twelve cusplets and very fine, sometimes quite indistinct serrulations at mesial edge . . . *Hexanchus*

Upper teeth

- 1a – Anterior teeth, with a single large cusp only
- 2a – Root low and elongated, cusp long and slender curving laterad with a sharp flexure . . . *Heptranchias*
- 2b – Root high and subquadrangle, cusp long and massive, either erect, or slightly oblique only . . . *Notorhynchus*
- 2c – Root high and subtriangular, with somewhat irregular outline, cusp long and massive, weakly oblique . . . *Hexanchus*
- 1b – Lateral teeth, with main cusp plus cusplets
- 3a – Root very low. Crown with very long, sharp and oblique cusp and with mesial serrulations as large and sharp as distal cusplets . . . *Heptranchias*
- 3b – Root very high, shortly subtriangular. Crown with large erect, or slightly oblique cusp and one to three (exceptionally four) cusplets . . . *Notorhynchus*
- 3c – Root relatively high, irregularly subquadrangular to subtriangular and elongated. Crown with few (anterior rows) to several (lateral rows) cusplets, gradually decreasing in size, and fine serrulations at mesial edge, which become indistinct only towards end of jaw . . . *Hexanchus*

Description of the commissural teeth

Genus *Hexanchus* RAFINESQUE, 1810
Hexanchus griseus (BONNATERRE, 1788)
(*Squalus griseus* BONNATERRE, 1788
Tableau encyclopédique et méthodique
des trois règnes de la nature, Paris, p. 9)

The number of the commissural tooth rows is very variable, 6 to 13 or more(?). Usually the size of teeth per row decreases regularly from the first to the last, but in some cases we observed that one was bigger than the preceding one in the file. The number of rows also varies between both halves of the jaw; for example 9 lower right rows, 12 lower left rows, 11 upper left rows and 12 upper right rows. The outermost file or functional row of commissural teeth may have more or fewer teeth than the inner not yet functional files.

However, all of them have a common general shape:

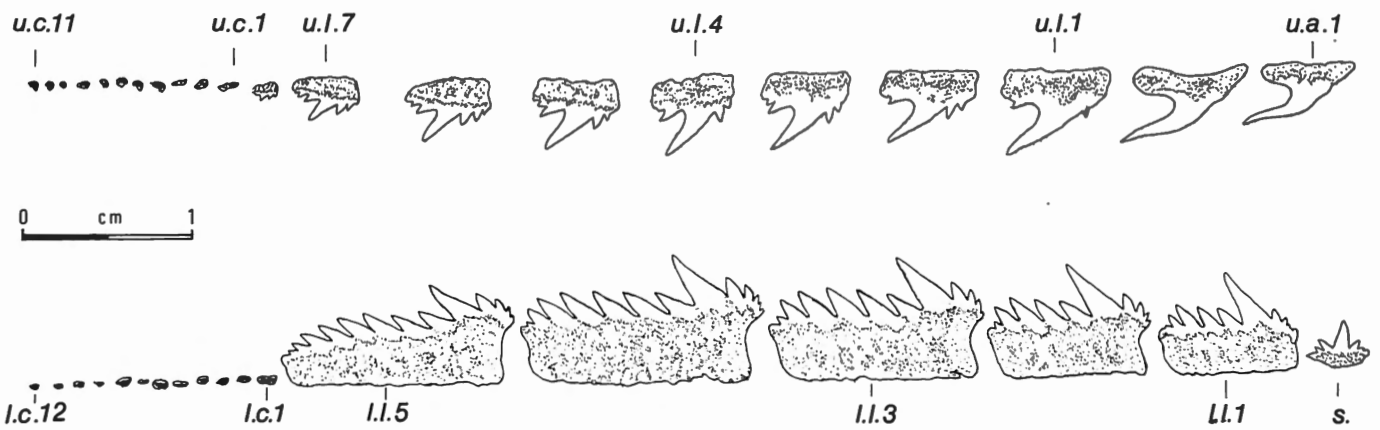


Fig. 1. *Heptanchias perlo* (BONNATERRE, 1788) mature male, 94 cm (t.l.), from Southern Mozambique.

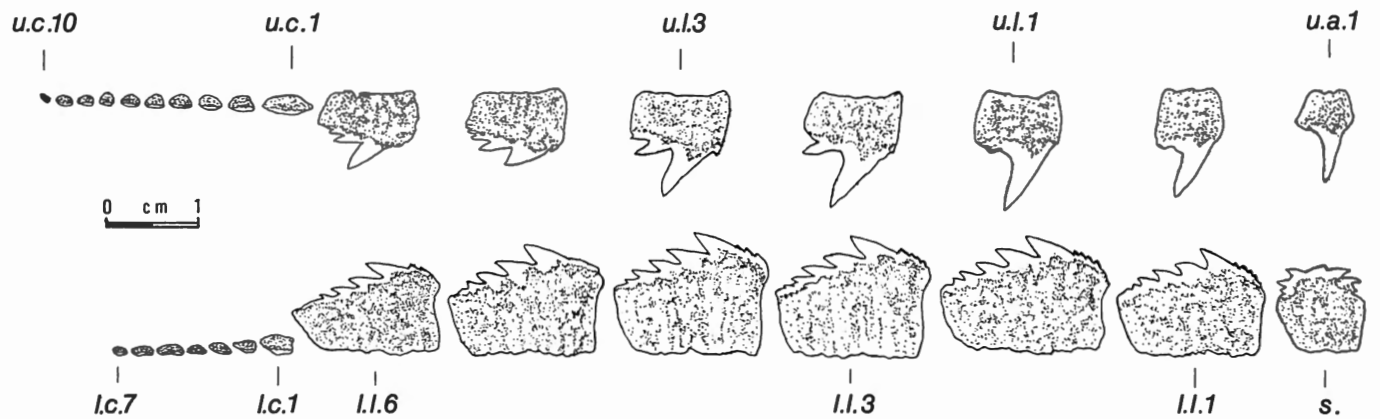


Fig. 2. *Notorynchus cepedianus* (PERON, 1807) mature female, 192 cm (t.l.), from Eastern Cape.

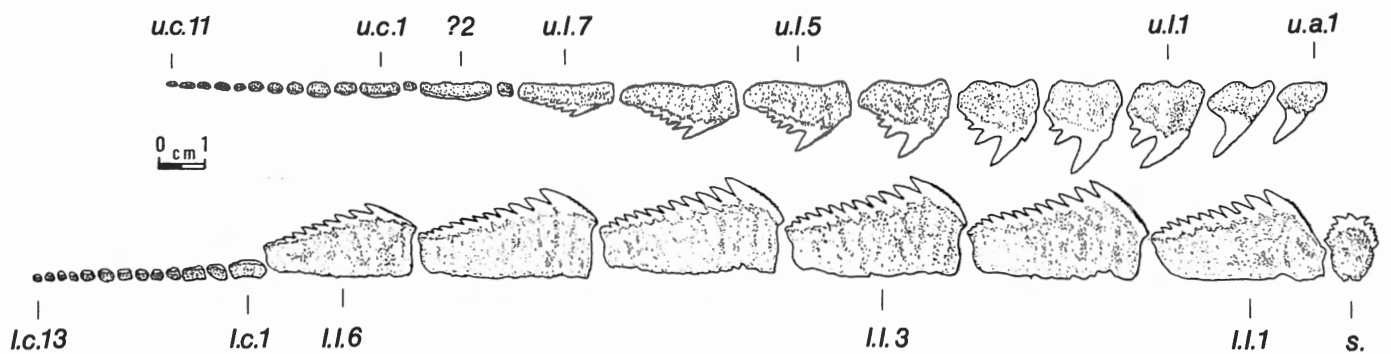


Fig. 3. *Hexanchus griseus* (BONNATERRE, 1788) female, about 4 m (t.l.), from Natal.

Text plate: Comparison between tooth sets of *Heptanchias*, *Notorynchus* and *Hexanchus* type species, all redrawn (D. Hovestadt) after plates 1, 4, 5 of Bass, d'Aubrey and Kistnasamy 1975. Characteristic aspect of serrulation is slightly enhanced.

u.c. : upper commissural
 l.c. : lower commissural
 t.l. : total length

u.l. : upper lateral
 l.l. : lower lateral
 ? : traumatic origin?

u.a. : upper anterior
 s. : symphyisial



Plate 1. *Hexanchus griseus* (BONNATERRE, 1788), adult female, 2m70 (t.l.), Sète, France.
 Second, third and fourth upper commissural teeth; outer, occlusal and inner views.

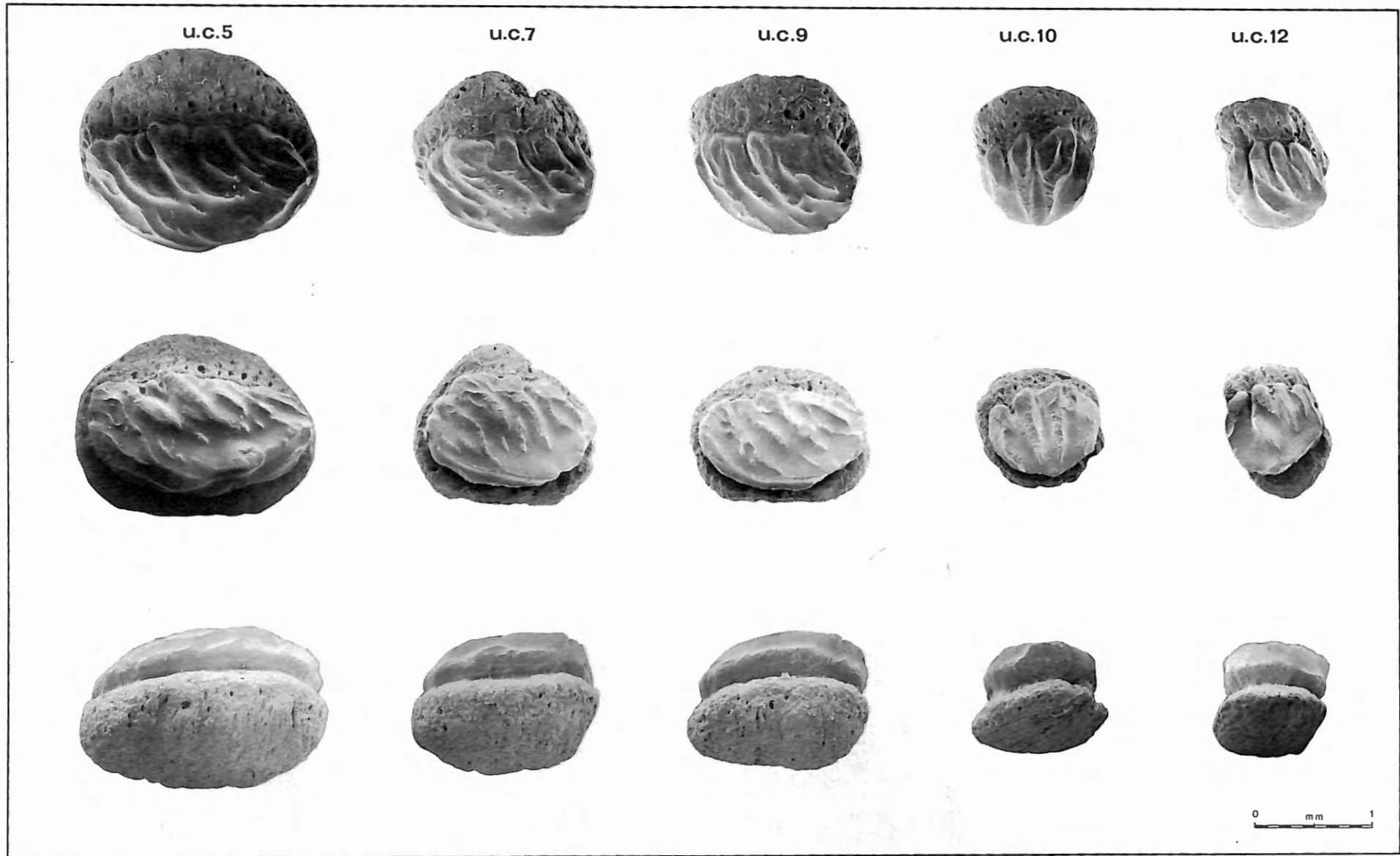


Plate 2. *Hexanchus griseus* (BONNATERRE, 1788), adult female, 2m70 (t.l.), Sète, France.
Fifth, seventh, ninth, tenth and twelfth upper commissural teeth; outer, occlusal and inner views.

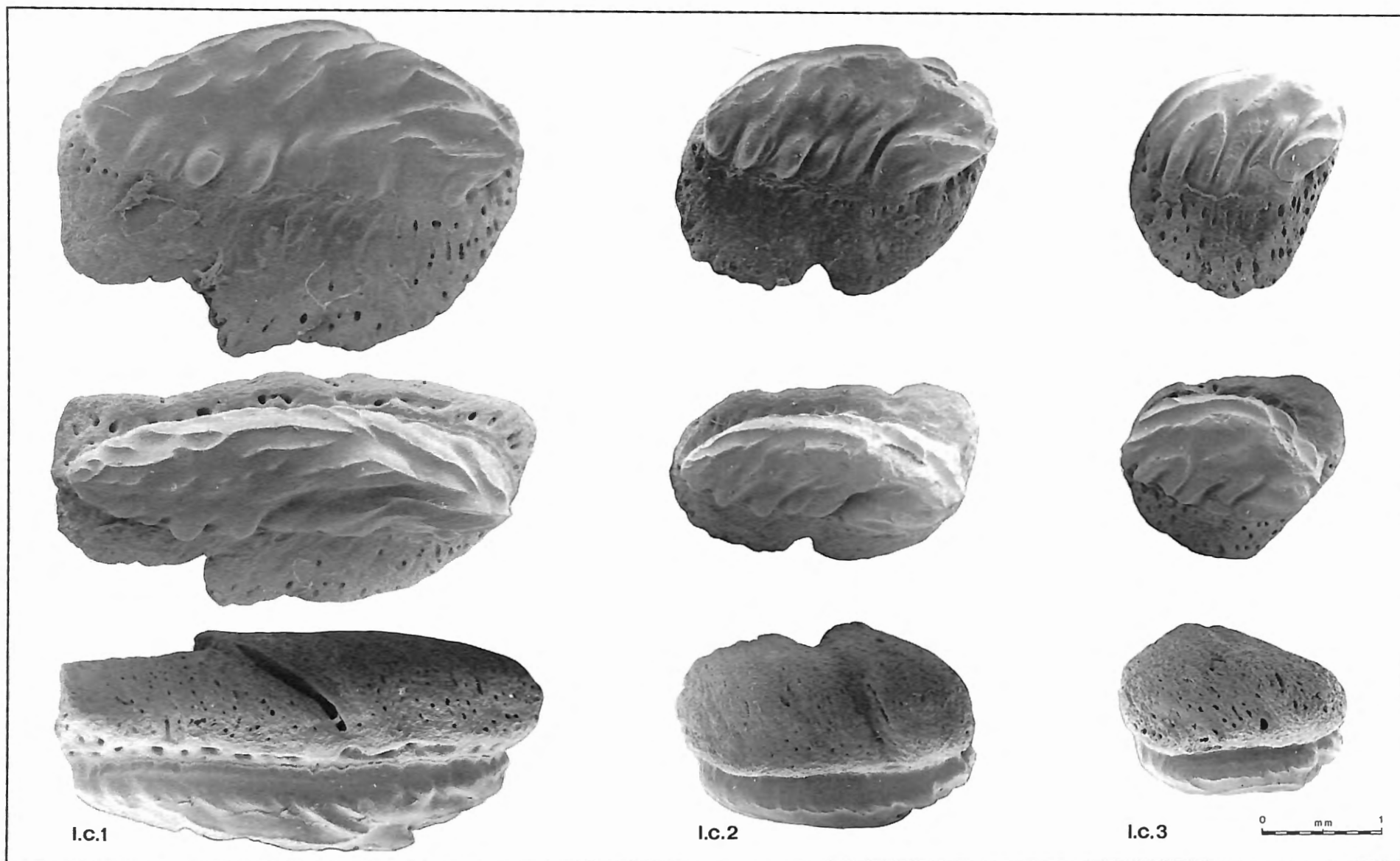


Plate 3. *Hexanchus griseus* (BONNATERRE, 1788), adult female, 2m70 (t.l.), Sète, France.
First, second and third lower commissural teeth; outer, occlusal and inner views.

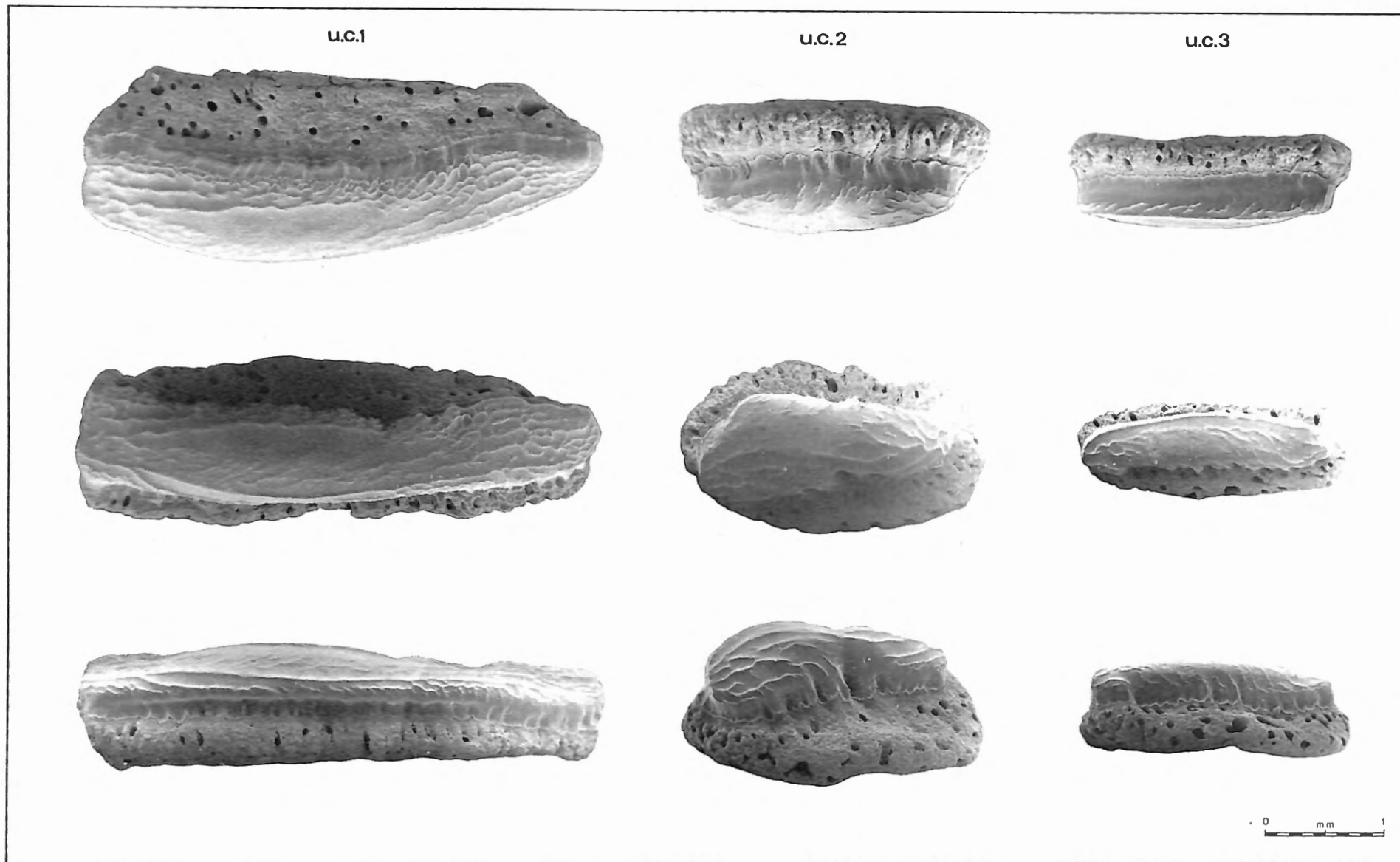


Plate 4. *Notorynchus cepedianus* (PERON, 1807), adult male, 2m40 (t.l.), San Francisco, U.S.A.
First, second and third upper commissural teeth; outer, occlusal and inner views.

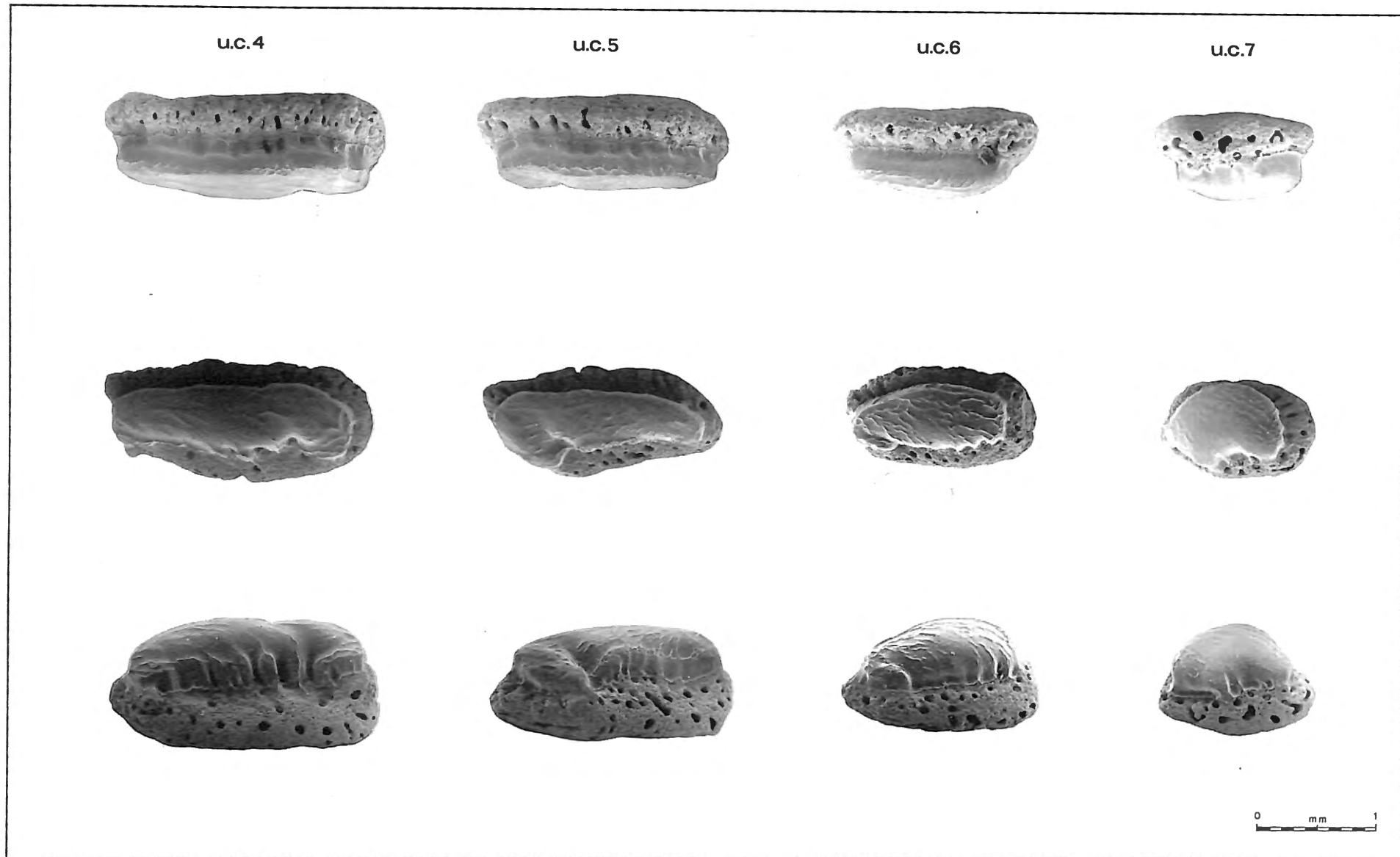


Plate 5. *Notorynchus cepedianus* (PERON, 1807), adult male, 2m40 (t.l.), San Francisco, U.S.A.
 Fourth, fifth, sixth and seventh upper commissural teeth; outer, occlusal and inner views.

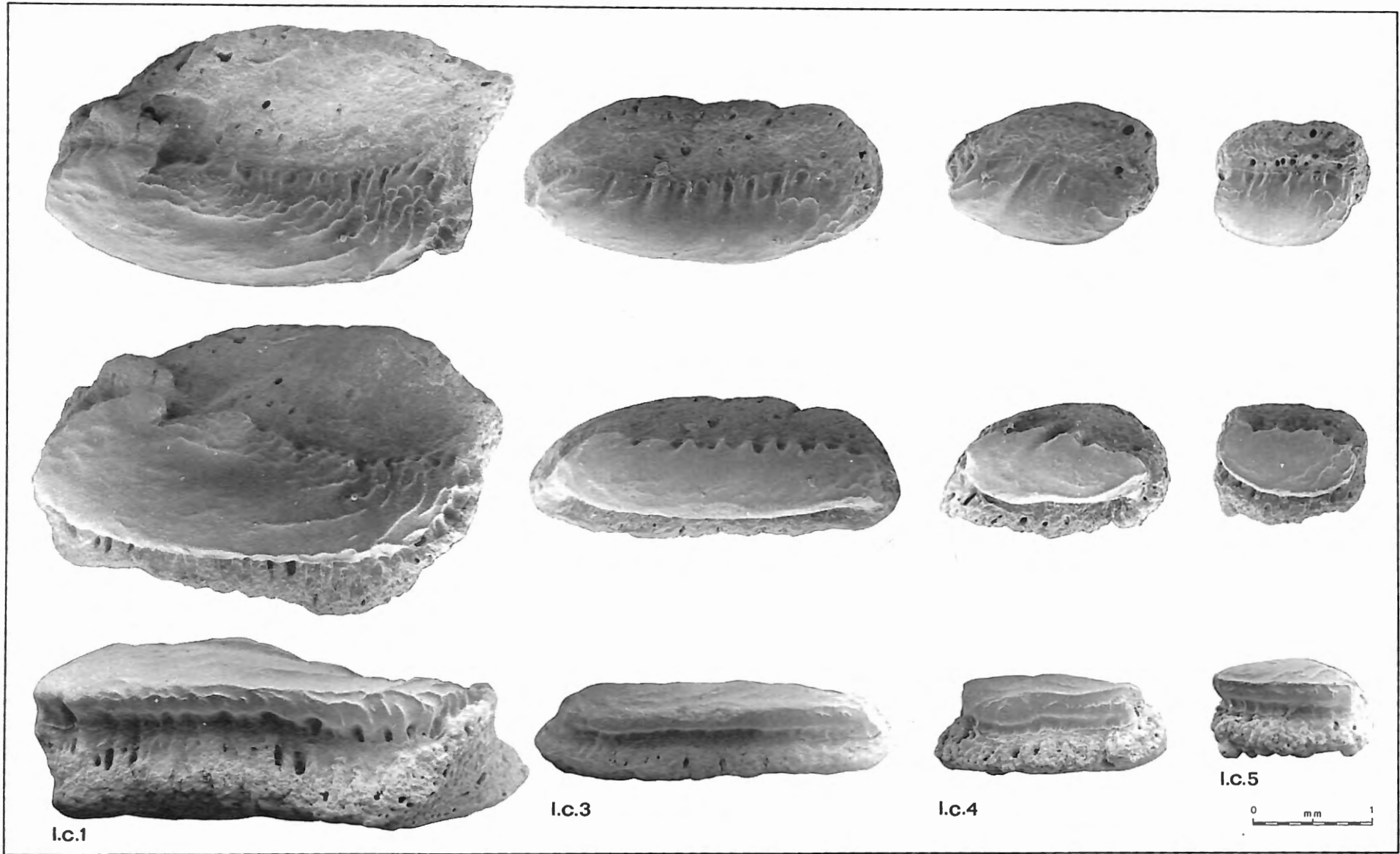


Plate 6. *Notorynchus cepedianus* (PERON, 1807), adult male, 2m40 (t.l.), San Francisco, U.S.A.
 First, third, fourth and fifth lower commissural teeth; outer, occlusal and inner views.

- a – A root that is always higher at the outer than at the inner face and basally large, contracted at the inner face.
- b – No plan of symmetry or no particular organisation of the vascularization of the root, which shows a variable number of discrete foramina irregularly scattered and sporadic attempts of superficial subvertical grooves.
- c – A crown showing a very discrete pseudocusp elevating distally, a very strong ornamentation at the outer face consisting of distinct distally sloping longitudinal ridges, discrete ripples at the inner face of the enamel being more obvious on the lower than on the upper teeth.

Genus *Notorhynchus* AYRES, 1855

Notorhynchus cepedianus (PERON, 1807)

(*Squalus cepedianus* PERON, 1807.

Voyages de découvertes aux Terres Australes

Tome 1, p. 377)

Number of rows, dispositions and proportions of the commissural teeth show the same irregularities as in *Hexanchus*. But they also have a lot of distinctive characteristic features:

- a – The commissural teeth of *Notorhynchus* look relatively rounded, or even slightly flattened; they are never as high as those of *Hexanchus*.
- b – Their root has basally a large and flat surface. The root of the upper teeth at both inner and outer face are virtually of the same size. The roots of the lower teeth are slightly, but obviously higher on outer than on the inner face.
- c – Inner and outer faces of the roots show strong vascularization. Numerous randomly scattered foramina in particular on roots of upper commissural teeth and extraordinarily large on outer face.
- d – Crown lacking a cusp, and with a less obvious ornamentation than in *Hexanchus* teeth. Ornamentation consisting of a basal constriction, edged by costules and more or less numerous short, fine, undulating longitudinal ridges of the same nature forming occasionally a pseudo-median keel. Such ridges more obvious in first rows than in those towards end of jaw. In addition, still finer transverse ridges between the obvious longitudinal ones forming a fine reticulation, which is very obvious on crowns of the first upper, less obvious in first lower row and becoming more and more vague towards outermost rows.

Genus *Heptranchias* RAFINESQUE, 1810

Heptranchias perlo (BONNATERRE, 1788)

(*Squalus perlo* BONNATERRE, 1788.

Tableau encyclopédique et méthodique
des trois règnes de la nature, Paris, p. 10)

The extremes observed vary from 4 to 12 rows, for individuals reaching a total length of 93 cm to 121 cm.

The so-called first commissural row shows often teeth with an evident single cusp making it difficult to ascertain whether we must consider this as a true commissural, or as an additional lateral one.

The commissural teeth are very elongated and very low, with a slightly rounded, a flattened, or even a flattened crown with a central depression.

The latter case occurs frequently in the first rows. Except for the first commissural row, we never observed a keel or a cusp.

The root is basally large, plane to subconcave, strongly elongated. Both outer and inner faces of the root are very low and of similar size.

The vascularization is poor and consists of very small foramina, that are more numerous on inner than on outer face.

Basally some large and irregular foramina appear on the root.

The rounded crowns (last rows), with flattened to flat and depressed crowns (first rows) present an obvious but very fine reticulate ornamentation with a relatively large mesh size.

The top of the crown often elevates towards the commissure.

We never observed the strong protuberances, constrictions or costules, typical for commissural teeth of *Hexanchus* or *Notorhynchus*.

Key to the genera of living Hexanchidae, based on the characters of the commissural teeth:

- 1a – Teeth greatly depressed, elongated.
Roots very low and with poorly developed small foramina only. Crowns lacking cusps or median keels but showing fine reticulation with large mesh size *Heptranchias*
- 1b – Teeth high to very high 2
- 2a – Root very high, with few small foramina only. Crown with strongly ribbed ornamentation and vestigial cusp *Hexanchus*
- 2b – Root medium height, with numerous distinct, large foramina. Crown with finely ribbed ornamentation, occasionally forming a low median keel, and sometimes intermediate very fine reticulation *Notorhynchus*

Irregularity in the number of rows seems maximal.

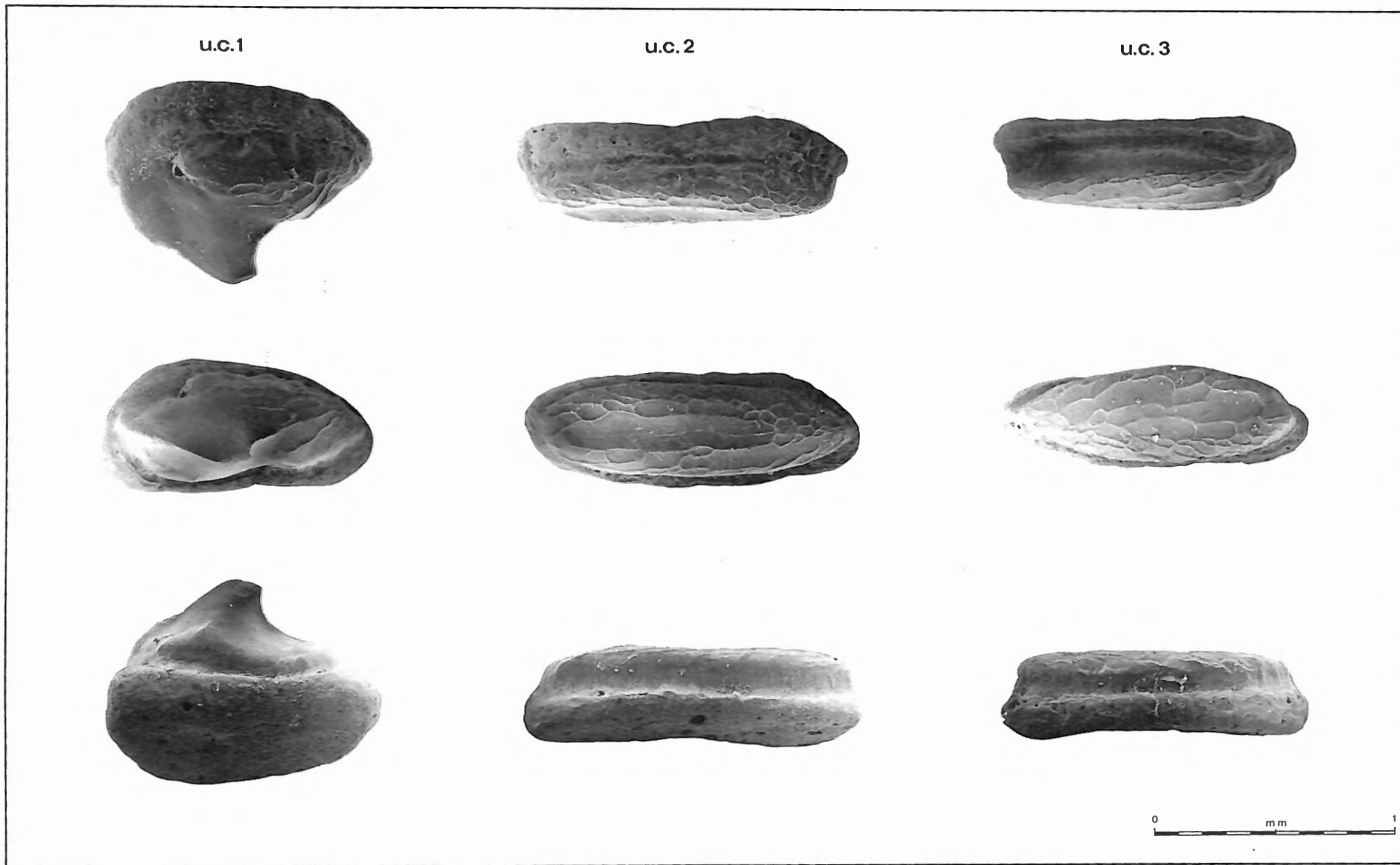


Plate 7. *Heptranchias perlo* (BONNATERRE, 1788), adult male, 1m15 (t.l.), Dakar, Sénégal.
First, second and third upper commissural teeth; outer, occlusal and inner views.

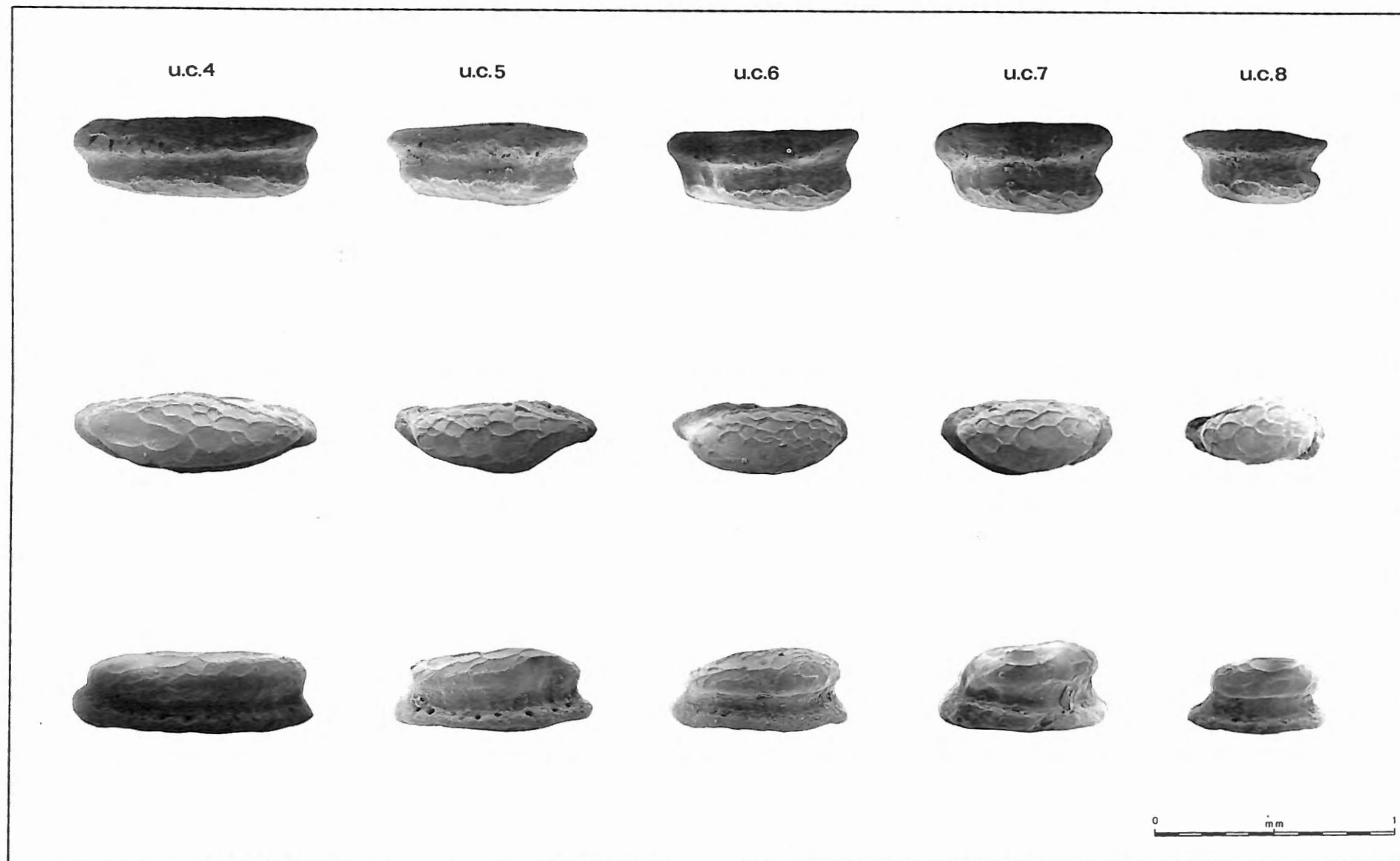


Plate 8. *Heptranchias perlo* (BONNATERRE, 1788), adult male, 1m15 (t.l.), Dakar, Sénégal.
Fourth, fifth, sixth, seventh and eighth upper commissural teeth; outer, occlusal and inner views.

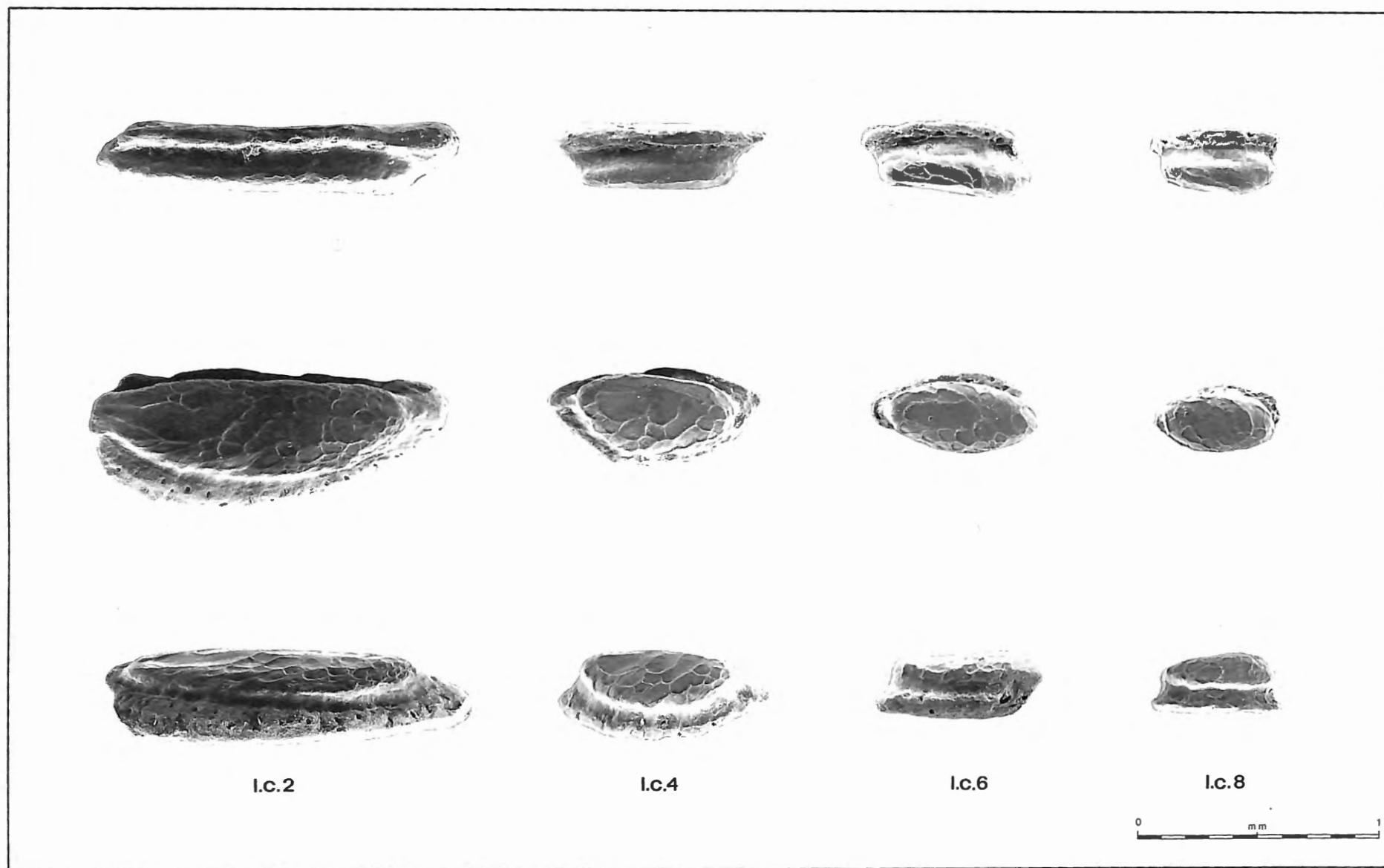


Plate 9. *Heptanchias perlo* (BONNATERRE, 1788), adult male, 1m15 (t.l.), Dakar, Sénégal.
Second, fourth, sixth and eighth lower commissural teeth; outer, occlusal and inner views.

Conclusions

Though the commissural teeth of Hexanchidae may be minute they are nevertheless generically diagnostic. Their roots are always strictly anaulacorhizid (CASIER, 1947) with foramina, being variable in size and number but always randomly scattered. This type of root is also typical for the most primitive Elasmobranchs, such as the extinct Hybodonts (*Hybodus*, *Acrodus* and related genera).

The commissural teeth of *Hexanchus* present the most primitive type of crown in having an original strong longitudinally ribbed ornamentation and a vestigial cusp. Their roots are greatly vertically expanded as a result of a long evolution. The commissural teeth of *Heptranchias* preserve the most primitive type of roots, which are elongated and very low; but they show a very specialized reticulated ornamentation of the entire crowns.

The commissural teeth of *Notorhynchus* show a particular adaptative evolution. Their roots have a distinct vascularization through numerous large foramina. Their crowns show the original longitudinally ribbed

ornamentation reduced, as well as a reticulation being reduced in size and to parts of the lower surface only.

It has been demonstrated, that commissural teeth present intergeneric differences as important as symphyseal, anterior and lateral teeth in living Hexanchidae. The individual results indicate furthermore, that the three genera concerned had a long evolutionary development independent of each other, despite their origin from a common ancestor.

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