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Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supra-specific taxa of Chondrichthyan fishes

Editor : M. STEHMANN

Addendum to Part A, No. 1 :
Order : Hexanchiformes - Family : Hexanchidae.
Odontological results supporting the validity of *Hexanchus vitulus* SPRINGER & WALLER, 1969 as the third species of the genus *Hexanchus* RAFINESQUE, 1810, and suggesting intrafamilial reordering of the Hexanchidae.

by J. HERMAN, M. HOVESTADT-EULER and D.C. HOVESTADT

Abstract

The tooth morphology of all hexanchid species, including the controversial species *Hexanchus nakamurai* and *H. vitulus*, is re-examined and illustrated. Odontologically *Hexanchus nakamurai* is clearly distinct from *H. vitulus*.
An odontological determination key to all hexanchid species is given. The odontological results presented suggest another intrafamilial ordering of the taxa than by the number of branchial arches, which seem to be less important.
Key-words : Elasmobranchii - Selachii - Hexanchidae - Systematics - Taxonomy - Odontology.

Résumé

La morphologie dentaire de tous les Hexanchidae, et en particulier celle d'*Hexanchus nakamurai* et de *H. vitulus*, espèces dont la validité restait controversée, est réexaminée et figurée. Cette dernière espèce est odontologiquement distinguable d'*Hexanchus nakamurai*.
Une clef de détermination odontologique de tous les Hexanchidae est proposée. Les résultats de la présente étude odontologique suggèrent des relations différentes entre les taxa de cette famille, autres que celles avancées sur base du nombre de fentes branchiales dont l'importance semble très relative.
Mots-clés : Elasmobranchii - Selachii - Hexanchidae - Systématique - Taxonomie - Odontologie.

Kurzfassung

Die Zahnmorphologie aller hexanchiden Arten, einschliesslich der strittigen *Hexanchus nakamurai* und *H. vitulus* wird überprüft und illustriert. Odontologisch ist *Hexanchus nakamurai* deutlich von *H. vitulus* zu unterscheiden.
Für alle Arten der Hexanchidae wird ein odontologischer Bestimmungsschlüssel vorgestellt. Die dargestellten odontologischen Ergebnisse legen eine andere intrafamiliäre Gruppierung der Arten als die bisherige nach Zahl der Kiemenbögen, die anscheinend weniger relevant ist.
Schüsselwörter : Elasmobranchii - Selachii - Hexanchidae - Systematik - Taxonomie - Odontologie.

Introduction

An addendum to Part A, No. 1, Family Hexanchidae is presented to further elucidate odontological characters of the three genera and their interrelationships. New arguments are provided, that *Hexanchus vitulus* appears to be a valid third species of the genus. Although, the aim of this series is to illustrate and describe micro-teeth only, in the present case the odontological characters of anterior and lateral macro-teeth were added to those of the posterior micro-teeth to provide full information.
TENG (1962) distinguished a new subspecies *Hexanchus griseus nakamurai* as a second form within the genus, and SPRINGER & WALLER (1969) described a new species *H. vitulus*. Variously the originally subspecies *nakamurai* of *H. griseus* has been synonymized by authors either with *H. griseus*, or with the more recently described *H. vitulus*. TANIUCHI & TACHIKAWA (1991) resurrected *nakamurai* at species rank and synonymized *H. vitulus* with the latter. However, in their diagnoses neither TENG, nor SPRINGER & WALLER had included odontological information, and neither was such given

by TANIUCHI & TACHIKAWA. Since tooth samples and odontological information of all three forms became available, investigational results support the validity of all three species of *Hexanchus*. It also turned out, that the paratype of *H. vitulus* happens to be a specimen of *H. nakamurai*.

A comparison of photographs of the jaw dentition of *H. vitulus* holotype (USNM 200674) and the jaws of *H. vitulus* (ORI 2822) from off Natal, as illustrated by BASS, D'AUBREY & KISTNASAMY (1975), revealed conformable tooth morphology. The jaws of another male specimen (RUSI 6897), having been caught in a shark net off Park Rynie and also mentioned by the latter authors, were also examined and had the same dentition as both specimens mentioned above.

Furthermore, we compared jaw photographs of the *H. vitulus* paratype (USNM 200675), jaws of Japanese specimen (FUMT P.10859) from off Ogasawara Islands (TANIUCHI & TACHIKAWA, 1991), jaws of a male (AMNH 33475) and female (AMNH 29830) (both without data), and a jaw of a Caribbean specimen (uncat.) at the Institut des Sciences Naturelles de Belgique, Brussels, which all were determined as *H. vitulus*. They all showed conformable tooth morphology too but clearly differed in odontological characters from those of the *H. vitulus* holotype and both African specimens of this species mentioned above.

The tooth morphology of the hexanchid-species *H. griseus, H. vitulus* and *H. nakamurai* is here described, illustrated and compared.

The illustrations in BASS, D'AUBREY & KISTNASAMY, 1975 are used for further comparison of the species of *Hexanchus* with *Heptranchias perlo* and *Notorhynchus cepedianus* and to illustrate general odontological characters.

The authors will here not draw any nomenclatorially valid conclusions. 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.

Materials and method

The following 35 specimens of 5 species were examined :

Hexanchus griseus		
Coll. Herman	♀	2700 mm. TL. (jaws)
Coll. Herman	♀	1270 mm. TL. (jaws)
Coll. Herman	♀	1190 mm. TL. (jaws)
Coll. Herman	♀	1100 mm. TL. (jaws)
Coll. Herman	♀	1050 mm. TL. (jaws)
Coll. Herman	♀	890 mm. TL. (jaws)
Coll. Herman	♀	780 mm. TL. (jaws)
Coll. Herman	♂	1220 mm. TL. (jaws)
Coll. Herman	♂	890 mm. TL. (jaws)
Coll. Herman	♂	670 mm. TL. (jaws)
Coll. Hovestadt	♀	3150 mm. TL. (jaws)
Coll. Hovestadt	♀	2190 mm. TL. (jaws)
Coll. Hovestadt	♀	1150 mm. TL. (jaws)
Coll. Hovestadt	♀	1140 mm. TL. (jaws)
Coll. Hovestadt	♀	720 mm. TL. (jaws)
Coll. Hovestadt	♂	2050 mm. TL. (jaws)
Coll. Hovestadt	♂	1530 mm. TL. (jaws)
Coll. Hovestadt	♂	1180 mm. TL. (jaws)
Coll. Hovestadt	♂	1180 mm. TL. (jaws)
Coll. Hovestadt	♂	1160 mm. TL. (jaws)
Coll. Hovestadt	♂	920 mm. TL. (jaws)
Coll. Hovestadt	♂	800 mm. TL. (jaws)
Hexanchus vitulus		
Holotype USNM 200674	♂	1480 mm. TL. (photographs)
Paratype USMN 200675	♀	1420 mm TL. (photographs)
ORI 2822	♂	1550 mm. TL. (jaws)
RUSI 6897	♂	1550 mm. TL. (jaws)
Hexanchus nakamurai		
FUMT-P10643	♀	958 mm. TL. (posterior upper and lower teeth)
FUMT-P10859	♂	1171 mm. TL (symphysial, parasymphysial and lateral upper and lower teeth)
AMNH 33475	♂	1100 mm. TL. (jaws)
AMNH 29830	♀	1575 mm. TL. (jaws)
IRSNB uncat.	?	No data (jaws)
Notorhynchus cepedianus		
Coll. Vanderhoeft	♂	2400 mm. TL. (jaws)
Heptranchias perlo		
Coll. Herman	♂	1150 mm. TL. (jaws)
Coll. Herman	♀	1200 mm. TL. (jaws)
Coll. Hovestadt	♀	1220 mm. TL. (jaws)

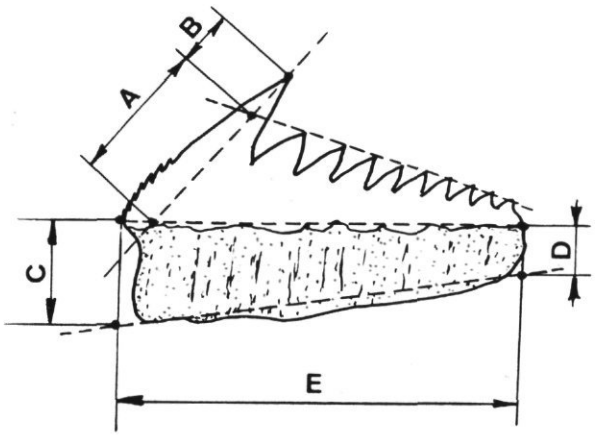
The odontological differences are mainly documented by the biometrical results of the lower lateral teeth. Textfigure 1 shows the four artificial lines resulting in five measurements :

1 : cusplet apex line
— connecting as straight line all cusplet apices.

2 : crown base line
— connecting extreme mesial and distal edges of tooth along crown-root junction.

3 : root base line
— connecting extreme mesial and distal lower edges of root, and may cut through median lower part of root.
4 : principal cusp dividing line
— from tip of principal cusp along about midline of its exposed upper part, and not connecting to a fixed lower point.

The corresponding standard measurements are accordingly :
A : maximum cusplet height - distance between points of intersection of lines 1 and 2 with line 4.
B : exceeding length of principal cusp - distance between tip of principal cusp and point of intersection of lines 1 and 4.
C : mesial length of root - perpendicular distance between lines 2 and 3 at extreme upper mesial edge of root.
E : maximum length of crown - distance between extreme mesial and distal edges of crown, i.e. points of line 2.



Textfigure 1. – *Biometrical criterions.*

Family : Hexanchidae

After COMPAGNO (1984), the family Hexanchidae comprises three genera : *Notorhynchus,* monotypic with the type species *Notorhynchus cepedianus* (PERON,1807), *Heptranchias,* monotypic with the type species *Heptranchias perlo* (BONNATERRE, 1788) and *Hexanchus* with the type species *Hexanchus griseus* (BONNATERRE, 1788) and *Hexanchus vitulus* SPRINGER & WALLER, 1969. *Hexanchus nakamurai* TENG, 1962 resurrected as a senior synonym of *H. vitulus* by TANIUCHI & TACHIKAWA (1991).

HETERODONTY

Disregarding the commissural teeth, hexanchid dentition is in general gradient dignathic heterodont.
The dentition of an upper jaw half consists of two anterior rows (including the parasymphysial one), seven lateral rows (with the exception of five rows in *N. cepedianus*) and eight to fourteen commissural rows.
The dentition of a lower jaw presents one symphysial row, five lateral rows in *Heptranchias perlo, Hexanchus vitulus* and *H. nakamurai,* but six in *Hexanchus griseus* and *Notorhynchus cepedianus* and three to thirteen commissural rows.
The anterior and lateral teeth of both upper and lower jaws are strongly compressed in inner-outer direction with a narrow anaulacorhizid root. Commissural teeth of both upper and lower jaws are always irregularly shaped and show flattened crown, mostly presenting a median keel, and an anaulacorhizid, relatively wide root. Due to their inactive function, they are irregularly shaped and numbered, and rest as rudimentary remains. However, their crown possesses an inner and outer ornamentation, which is characteristic for its genus (Hovestadt, Hovestadt & Smith, 1983; Herman, Hovestadt & Hovestadt-Euler,1987).
Sexual heterodonty does not exist, but ontogenetic heterodonty is given by lower number of cusplets in lateral teeth of upper and lower jaws.

DESCRIPTION OF THE ODONTOLOGICAL CHARACTERS

The description of the odontological characters will here only consider anterior and lateral teeth of upper and lower jaws of *Heptranchias perlo, Hexanchus griseus* and *Notorhynchus cepedianus.* Commissural teeth were already described in Part A, No. 1 of this series.

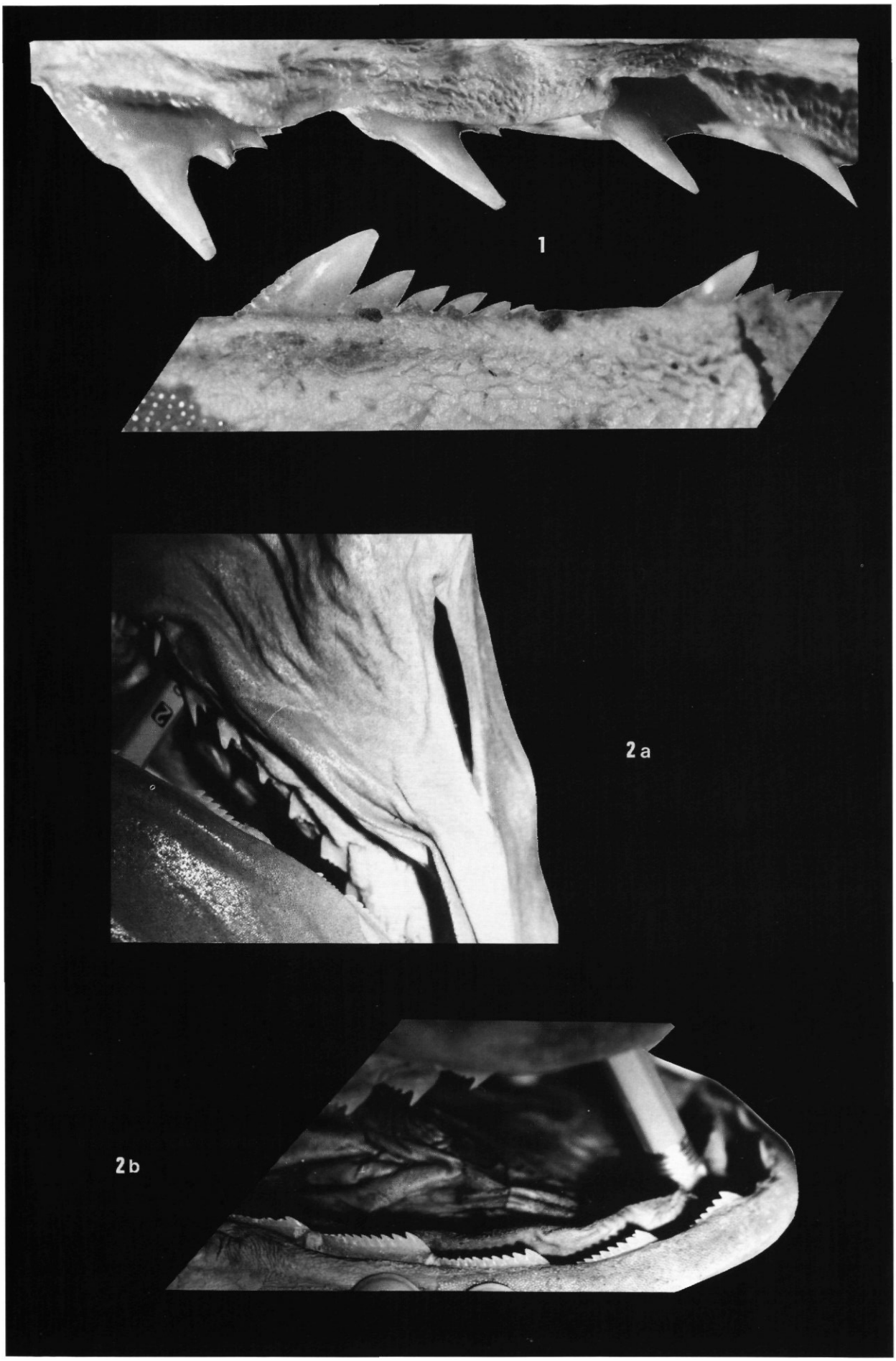
Genus : *Heptranchias* RAFINESQUE, 1810

Heptranchias perlo (BONNATERRE,1788)

Squalus perlo, Bonnaterre, 1788, Tableau encyclopédique et méthodique des trois règnes de la nature. Paris, p. 10.

UPPER JAW

The crown of anterior and lateral teeth has an elongated principal cusp, which is inclined distally and sigmoidal in both anterior teeth and slightly bent in lateral ones. The crown height diminishes toward the commissure. The size of the root remains more or less equal throughout.
The mesial cutting edge of the anterior teeth is smooth, whereas lateral teeth bear two or three mesially directed



Textplate. – Hexanchus vitulus *Springer & Waller, 1969.*
1. Holotype, USNM 200674, ♂ 1480 mm tl., Bahamas USA; some upper and lower teeth.
2. Paratype, USNM 200765 ♀ 1420 mm tl., Bahamas USA; left (a) and right side views (b) of the jaws.

cusplets at the base. The number of cusplets increases toward the commissure. The orientation of the distal cutting edge follows more or less the angle of the principal cusp, curves distally just before reaching the base of the crown, to form a blade on anterior teeth. One to four distally directed cusplets are present on lateral teeth, their number increasing toward the commissure.
The flattened root is anaulacorhizid and subquadrangular in shape.
The principal cusp and cusplets are slightly convex and smooth on outer surface, stronger convex and smooth on inner surface.
An inner or outer ornamentation is absent.
The inner part of the root is divided by a protuberating, transverse ridge just below the crown-root junction. One or two vertically elongated apertures may be present on the lower part, which in fact are side-long opened vertical canals, being part of the vascularization system (HOVESTADT & HOVESTADT-Euler, 1993). Minute foramina are scattered all over the lower part of the root.

LOWER JAW

The principal cusp of the symphysial tooth is erect and flanked by two pairs of cusplets, of which the outer ones are very low. The crown of the lateral teeth bears an elongated, distally inclined principal cusp with two or three well developed mesial cusplets, three to five, more or less equally large, distal cusplets and one or two lower cusplets at the extreme distal edge. The dimensions of A and B (textfigure 1) are equal sized, which show the extreme height difference between the principal cusp and cusplet apex line.
The principal cusp becomes stronger inclined toward the commissure, and the number of distal cusplets decreases.
The mesial and distal cutting edges of principal cusp and cusplets are smooth.
The flattened root is anaulacorhizid and more or less quadrangularly shaped, becoming wider in teeth toward the commissure. From the crown-root junction downward the root is constricted at the mesial edge. The root height C at the mesial part is slightly higher than at the distal part D. The dimensions of C are 25 to 28 % of the total tooth width E.
The principal cusp and cusplets are slightly convex and smooth in outer view, but more convex and also smooth in inner view.
An inner and outer ornamentation is absent.
The inner part of the root is divided by a protuberating. transversal ridge, just below the crown-root junction. On the lower part one or two, vertically elongated apertures can be present. Minute foramina are scattered all over the lower part of the root.

Genus : *Hexanchus* RAFINESQUE,1810

Hexanchus griseus (BONNATERRE,1788)
(Plates 1 & 2)

Squalus griseus BONNATERRE, 1788. Tableau encyclopédique et méthodique des trois règnes de la nature. Paris, p. 9.

A juvenile specimen was selected for comparison with specimens equally small as *H. vitulus* and *H. nakamurai*.

UPPER JAW

The crown of anterior and lateral teeth has an elongated principal cusp, which is slightly bent distally. The crown height diminishes toward the commissure. However, the size of the root remains nearly equal in the first five tooth rows and becomes slightly wider only from the sixth tooth row onward.
The mesial cutting edge of the anterior and lateral teeth is smooth. A poorly developed, distally directed, cusplet may be present. The distal cutting edge follows more or less the angle of the principal cusp, and curves distally just before reaching the base of the crown, forming a blade on anterior first two lateral teeth. On the following, lateral teeth one or two, distally directed cusplets are present. (In adult specimens all laterals have one to four distal cusplets)
The flattened root is anaulacorhizid and subquadrangular in shape.
The principal cusp and cusplets are slightly convex and smooth on outer surface, more convex and also smooth on inner surface.
An inner or outer ornamentation is absent.
The inner part of the root is divided by a protuberating, transversal ridge, just below the crown-root junction. On the lower part one or two, vertically elongated apertures can be present. Minute foramina are scattered all over the lower part of the root.

LOWER JAW

The principal cusp of the symphysial tooth can be extremely bent distally or mesially (this is undefined), flanked by a pair of cusplets, of which the ones at the extreme edges are very low. The crown of the lateral teeth presents a low principal cusp, which is distally oblique. Mesial cusplets or serration are absent. Three to five, distal cusplets (seven to nine in adult specimens) are present, which gradually diminish in height. The very low height difference between the principal cusp and the first cusplet makes B (textfigure 1) absent, which means, that the apex of the crown is in line with the cusplet apex line.
The principal cusp becomes more oblique and the number of distal cusplets slightly decreases closer toward the commissure.

The mesial and distal cutting edges of the cusplets are smooth.
The flattened root is anaulacorhizid and more or less quadrangularly shaped, becoming wider on positions closer to the commissure. From the crow-root junction downward the root is constricted at the mesial edge. The root height C at the mesial part is slightly higher than at the distal part D. The dimensions of C are 40 to 44 % of the total tooth width E.
The principal cusp and cusplets are slightly convex and smooth in outer view, but more convex and also smooth in inner view.
An inner and outer ornamentation is absent.
The inner part of the root is divided by a protuberating, transversal ridge, just below the crown-root junction. On the lower part one or two, vertically elongated apertures can be present, Minute foramina are scattered all over the lower part of the root.

Hexanchus nakamurai TENG,1962
(Plates 3, 4 & 5)

Hexanchus nakamurai TENG, 1962. Classification and distribution of the Chondrichthyes of Taiwan. Ogawa print. Maizuru, pp. 304.

UPPER JAW

The crown of anterior and lateral teeth has an elongated principal cusp, which is slightly bent distally. The crown height diminishes toward the commissure. However, the size of the root gradually becomes slightly wider toward the commissure.
The mesial cutting edge of both anterior teeth is smooth, whereas that of the first two lateral teeth is slightly serrated. The remaining lateral teeth have smooth mesial cutting edges. The orientation of the distal cutting edge follows more or less the angle of the principal cusp, curves distally just before reaching the base of the crown to form a blade on anterior first two lateral teeth. One to three distally cusplets are present on the following lateral teeth.
The flattened root is anaulacorhizid and subquadrangular in shape.
The principal cusp and cusplets are slightly convex and smooth on outer surface, but more convex and also smooth on inner surface.
An inner or outer ornamentation is absent.
The inner part of the root is divided by a protuberating, transversal ridge, just below the crown-root junction. On the lower part one or two, vertically elongated apertures can be present. Minute foramina are scattered all over the lower part of the root.

LOWER JAW

The principal cusp of the symphysial tooth is more or less erect, flanked by a set of three cusplets. The crown of the lateral teeth presents a low principal cusp, which is distally oblique. The mesial cutting edge of the first two lateral teeth is finely serrated but smooth on the remaining lateral teeth. Seven to eight, distal cusplets are present, which gradually diminish in height. The very low height difference between the principal cusp and the first cusplet makes B (textfigure 1) absent, which means, that the apex of the crown is in line with the cusplet apex line.
The principal cusp becomes slightly more oblique and the number of distal cusplets slightly decreases closer toward the commissure.
The mesial and distal cutting edges of the distal cusplets are smooth.
The flattened root is anaulacorhizid and more or less quadrangularly shaped, becoming wider on positions closer to the commissure. From the crown-root junction downward the root is constricted at the mesial edge. The root height C at the mesial part is slightly higher than at the distal part D. The mesial root height is 22 to 29 % of the maximum crown length E.
The principal cusp and the cusplets are slightly convex and smooth on outer surface but more convex and also smooth on inner surface.
An inner or outer ornamentation is absent.
The inner part of the root is divided by a protuberating, transversal ridge, just below the crown-root junction. On the lower part one or two, vertically elongated apertures can be present. Minute foramina are scattered all over the lower part of the root.

COMMISSURAL TEETH

The morphology of the upper and lower commissural teeth is more or less equal. Possible differences are within their natural range of variation and therefore are not separately described.
The commissural teeth are transversely elongated and low, with a slightly rounded, flattened crown.
A transversal median keel on the crown is mostly absent and the top of the crown consists of a weakly convex surface. The outer face presents extremely coarse and very protuberated, basal costules, that are irregularly bent longitudinally, often forming a coarse reticulation.
The inner face also has coarse costules, which are less developed than the outer ones.
The anaulacorhizid root is basally large and plane to subconcave. The inner and outer face show some irregularly lined-up foramina.

Hexanchus vitulus SPRINGER & WALLER,1969
(Plates 5, 6 & 7., Textplate 1)

Hexanchus vitulus SPRINGER & WALLER, 1969. Bulletin of Marine Science. 19 : 159-174.

UPPER JAW

The crown of anterior and lateral teeth has an elongated principal cusp, which is slightly bent distally. The crown height diminishes toward the commissure. However, the size of the root gradually becomes slightly wider toward the commissure.
The mesial cutting edge of both anteriors is smooth and of the first two laterals slightly serrated. Also the remaining lateral teeth have a weak serration, which is stronger developed in the mid-lateral positions and again is weaker in the teeth toward the commissure. The orientation of the distal cutting edge follows more or less the angle of the principal cusp, and curves distally just before reaching the base of the crown, forming a blade on anterior first two lateral teeth. One to six distally directed cusplets are present on the following lateral teeth, with size of cusplets gradually increasing toward the commissure.
The flattened root is anaulacorhizid and more or less quadrangularly shaped and lower toward the commissure.
The principal cusp and cusplets are slightly convex and smooth on outer surface, but stronger convex and also smooth on inner surface.
An inner or outer ornamentation is absent.
The inner part of the root is divided by a protuberating, transversal ridge, just below the crown-root junction. On the lower part one or two, vertically elongated apertures can be present. Minute foramina are scattered all over the lower part of the root.

LOWER JAW

The principal cusp of the symphysial tooth is more or less erect, flanked by a set of three cusplets. The crown of the lateral teeth presents a high principal cusp, which is distally inclined. The mesial cutting edge of teeth of the first two rows have a coarse serration, becoming poorer developed on teeth of the third and fourth rows and finely has disappeared on teeth of the fifth row. Seven to nine distal cusplets are present, which gradually diminish in height. The great difference in height between the principal cusp and the first cusplet makes B (textfigure 1) 23 to 30 % of A, which means, that the apex of the crown is obviously higher than the cusplet apex line.
The principal cusp becomes slightly more oblique and the number of distal cusplets slightly decreases closer toward the commissure.
The mesial and distal cutting edges of the distal cusplets are smooth.
The flattened root is anaulacorhizid and more or less quadrangularly shaped, becoming wider on positions closer to the commissure. From the crow-root junction downward the root is constricted at the mesial edge. The root height C at the mesial part is slightly higher than at the distal part D. The latter diminishes strongly toward the commissure. The dimensions of C are 22 to 29 % of the total tooth width E.
The principal cusp and cusplets are slightly convex and smooth in outer view, but more convex and also smooth in inner view.
An inner and outer ornamentation is absent.
The inner part of the root is divided by a protuberating, transversely ridge, just below the crown-root junction. On the lower part one or two, vertically elongated apertures can be present. Minute foramina are scattered all over the lower part of the root.

COMMISSURAL TEETH

The morphology of the upper and lower commissural teeth is more or less equal. Possible differences are within their natural range varietion and therefore are not described separately.
The commissural teeth are transversely very elongated and low, with a slightly rounded, flattened cusp.
The rounded to flattened crowns are divided into an inner and outer face by a transversal median keel. The outer face presents coarse, protuberated, basal costules, that are irregularly bent transversely and reach to half way the outer crown surface. Some teeth also present a secondary, fine, poorly developed, reticulated ornamentation between the costules.
The inner face also has coarse costules, which are less developed than the outer ones.
The anaulacorhizid root is basally large and plane to subconcave. The inner and outer face show some irregularly lined-up foramina.

Genus : *Notorhynchus* AYRES, 1855

Notorhynchus cepedianus (PERRON, 1807)

Squalus cepedianus PERRON,1807. Voyages de découverte aux Terres Australes. Tome 1 : 377.

UPPER JAW

The crown of anterior and lateral teeth has an elongated principal cusp, which is slightly inclined distally. The crown height diminishes toward the commissure. The size of the root becomes slightly wider in lateral teeth.
The mesial cutting edge of the anterior and lateral teeth is smooth. However, on the more posterior ones a poorly developed, distally directed, cusplet can be present. The orientation of the distal cutting edge follows more

or less the angle of the principal cusp, and curves distally just before reaching the base of the crown, forming a blade on anterior first two lateral teeth. On the following, lateral teeth one or two, distally directed cusplets are present.
The flattened root is anaulacorhizid and subquadrangular in shape.
The principal cusp and cusplets are slightly convex and smooth on outer surface, stronger convex and also smooth on inner surface.
An inner or outer ornamentation is absent.
The inner part of the root is divided by a protuberating, transversal ridge, just below the crown-root junction. On the lower part one or two, vertically elongated apertures can be present. Minute foramina are scattered all over the lower part of the root.

LOWER JAW

The principal cusp of the symphysial tooth can be extremely bent distally or mesially (this is undefined), flanked by a pair of cusplets. The crown of the lateral teeth presents a low principal cusp, which bents distally. Mesial cusplets are absent, but a rather coarse serration is present on the mesial cutting edge of all lateral teeth. Four distal cusplets are present, which gradually diminish in height distally. Tooth measurement B (textfigure 1) is nearly 0, which means, that the apex of the principal cusp is about level with the cusplet apex line.
The principal cusp becomes stronger inclined toward the commissure.
The mesial and distal cutting edges of the cusplets are smooth.
The flattened root is anaulacorhizid and subquadrangular in shape, becoming wider in teeth toward the commissure. From the crown-root junction downward the root is constricted at the mesial edge. The root height C at the mesial part is slightly higher than the at the distal part D. The dimensions of C are 39 to 45 % of the total tooth width E.
The principal cusp and cusplets are slightly convex and smooth on outer surface, stronger convex and also smooth on inner surface.
An inner or outer ornamentation is absent.
The inner part of the root is divided by a protuberating, transversely ridge, just below the crown-root junction. On the lower part one or two, vertically elongated apertures can be present. Minute foramina are scattered all over the lower part of the root.

Differential diagnosis

UPPER TEETH

The upper teeth of *Hexanchus griseus* and *Notorhynchus cepedianus* have a cusplet-like irregularity on the mesial cutting edge. *Heptranchias perlo* has true mesial cusplets, while *Hexanchus nakamurai* and *Hexanchus vitulus* have a mesial serration. All species bear upper a number of distal cusplets on their upper teeth.

LOWER TEETH

The lower lateral teeth of *Hexanchus griseus*, *Notorhynchus cepedianus* and *Hexanchus nakamurai* have a principal cusp, that does not, or hardly exceed the height of cusplets. However, in *Heptranchias perlo* and *Hexanchus vitulus* the principal cusp is much longer than the cusplet as expressed by the relation of tooth measurements A and B. Only *Heptranchias perlo* possesses true mesial cusplets. *Notorhynchus cepedianus* and *Hexanchus vitulus* have only rather coarse mesial serrations, and *Hexanchus griseus* and *Hexanchus nakamurai* lack mesial cusplets and serrations but show smooth mesial tooth edges.
All species have lower lateral teeth bearing a number of strong distal cusplets.
The height of the root in juvenile *Hexanchus griseus* and *Notorhynchus cepedianus* is equal, and roughly twice as high as that of *Heptranchias perlo*, *Hexanchus nakamurai* and *Hexanchus vitulus*.

COMMISSURAL TEETH

The most significant features of the commissural teeth is the ornamentation of the crown. *Heptranchias perlo*, *Hexanchus griseus* and *Notorhynchus cepedianus* have always a well developed ornamentation (HERMAN, HOVESTADT and HOVESTADT, 1987), which is relatively less developed in *Hexanchus nakamurai* and *Hexanchus vitulus*. The ornamentation of *Hexanchus vitulus* is restricted to very coarse, basal costules only. In *Hexanchus vitulus* the remains of a secondary reticulated ornamentation is absent. The costules on commissural teeth of *Hexanchus nakamurai* more or less merge to form a very coarse, poorly developed reticulation.

Conclusions

Hexanchus nakamurai and *Hexanchus vitulus* are clearly distinguishable by odontological characters. So far, only three specimens of *Hexanchus vitulus* and six of *Hexanchus nakamurai* could be re-identified by the authors. Further *H. vitulus* in various collections are of questionable identity and need to be reexamined.
Also the distribution of *Hexanchus vitulus* and *Hexanchus nakamurai*, and even of *Hexanchus griseus* should be reviewed.
All three species can be separated from each other by their differences in their tooth morphology.

Based on odontological characters the Hexanchidae can be grouped into two lineages :

Group 1	Group 2
UPPER TEETH	
– Mesial serration present	– Mesial serration absent
LOWER TEETH	
– 5 lateral teeth	– 6 lateral teeth
– root low	– root high

The taxonomy of the hexanchid species is traditionally strongly affected by the number of branchial arches, being considered an important systematic character by various authors. However, several authors also doubt the significance of this character (BASS, D'AUBREY & KISTNASAMY, 1975, HERMAN, HOVESTADT & HOVESTADT, 1987). SHIRAI, 1992 investigated the origin of the branchial arches in Hexanchiformes by extensive morphological and anatomical studies and concluded : within Hexanchiformes, *Chlamydoselachus* seems to be descent of a different lineage; *Hexanchus* is more closely related to *Heptranchias*, and two families Hexanchidae and Notorhynchidae can be recognized. These results largely conform with our odontological findings. WARD (1979) already introduced the terms "grisiform" and "vituliform" to separate lower lateral teeth of fossil hexanchid records.

Odontological key to the hexanchid species

(The lower symphysial and the commissural teeth are excluded)

1a Root compressed and high (C ≥ 39 % of E) . . 2

2a 7 or more distal cusplets on lower lateral teeth . . . . . *Hexanchus griseus*

2b Less than 7 distal cusplets on lower lateral teeth 3

3a 5 or more distal cusplets on lower lateral teeth . . . . . *Notorhynchus cepedianus*

3b Less than 5 distal cusplets on lower lateral teeth 4

4a 3 or more distal cusplets on lower lateral teeth (juveniles only) . . . . . *Hexanchus griseus*

4b Less than 3 distal cusplets on lower lateral teeth 5

5a Principal cusp bent distally in upper anterior teeth . . . . . *Hexanchus griseus*

5b Principal cusp distally inclined 6

6a Mesial serrations absent on upper anterior and lateral teeth . . . . . *Notorhynchus cepedianus*

6b Mesial serration present on upper anterior and lateral teeth 7

7a Mesial serrations poorly developed on upper anterior and anterolateral teeth . *Hexanchus vitulus*

7b Mesial serration well developed on upper anterior and anterolateral teeth . . . . . *Hexanchus nakamurai*

1b Root compressed and low (C ≥ 39 % of E) . . 8

8a 3 or more distal cusplets 9

9a Principal cusp of upper anterior and first lateral teeth strongly sigmoidal . *Heptranchias perlo*

9b Principal cusp of upper anterior and first lateral teeth inclined 10

10a Mesial serrations absent on upper latero-posterior teeth 11

11a Mesial cusplets present on upper latero-posterior teeth . . . . . *Heptranchias perlo*

11b Mesial cusplets absent on upper latero-posterior teeth . . . . . *Hexanchus griseus*

10b Mesial serration present on upper latero-posterior teeth 12

12a Serration poorly developed on upper latero-posterior teeth . . . . . *Hexanchus nakamurai*

12b Serration well developed on upper latero-posterior teeth . . . . . *Hexanchus vitulus*

8b Less than 3 cusplets 13

13a Mesial cusplets present on lower lateral teeth . . . . . *Heptranchias perlo*

13b Mesial cusplets absent on lower lateral teeth . 14

14a Mesial serration absent on lower lateral teeth . . . . . *Hexanchus griseus*

14b Mesial serration present on lower lateral teeth . 15

15a Principal cusp clearly exceeds height of cusplets . . . . . *Hexanchus vitulus*

15b Principal cusp does not exceed height of cusplets ..... *Hexanchus nakamurai*

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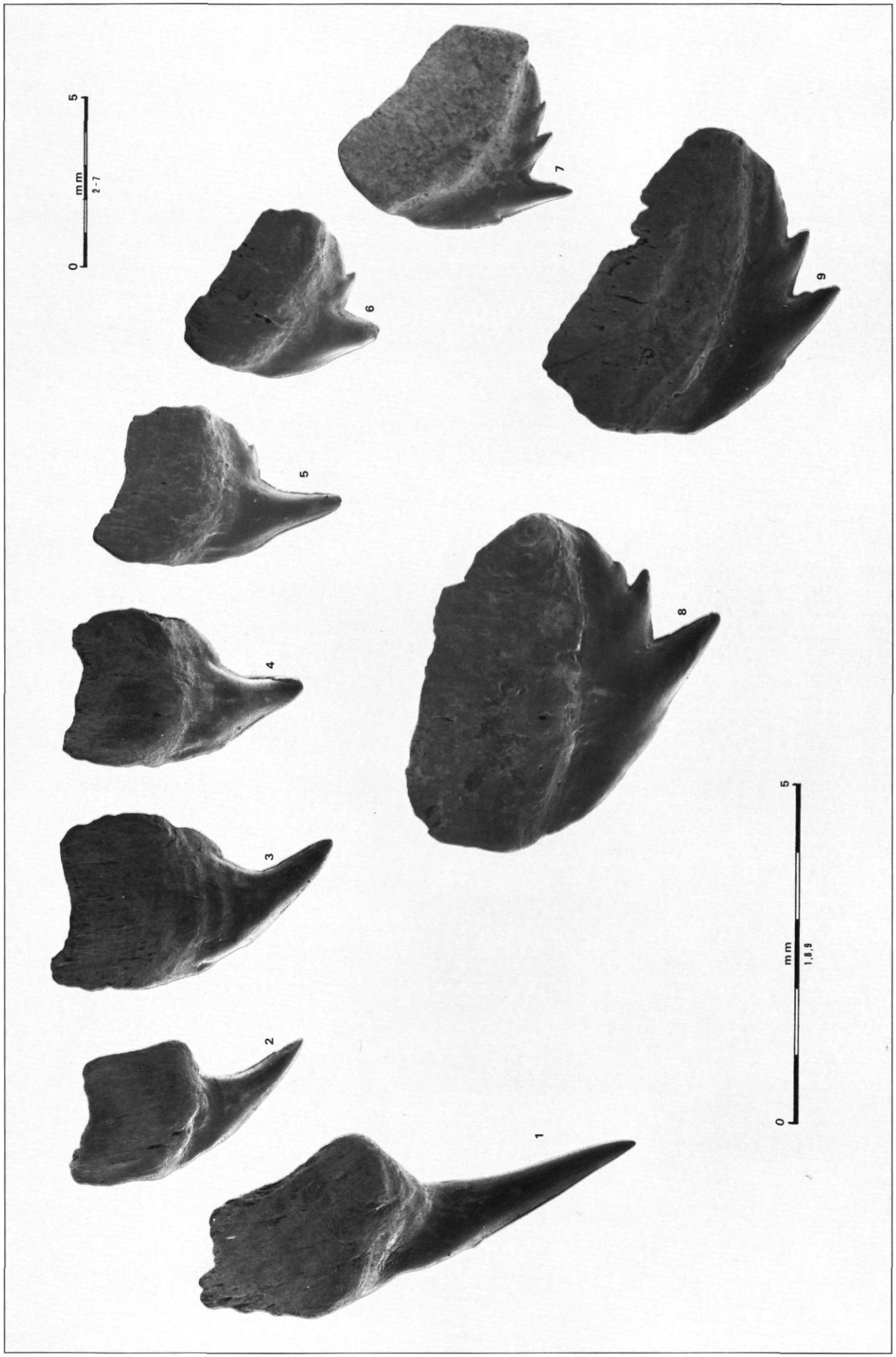

Plate 1. – Hexanchus griseus *(BONNATERRE, 1788), ♀ 1140 mm tl., fish-market at La Rochelle. Inner view of the first nine upper teeth.*

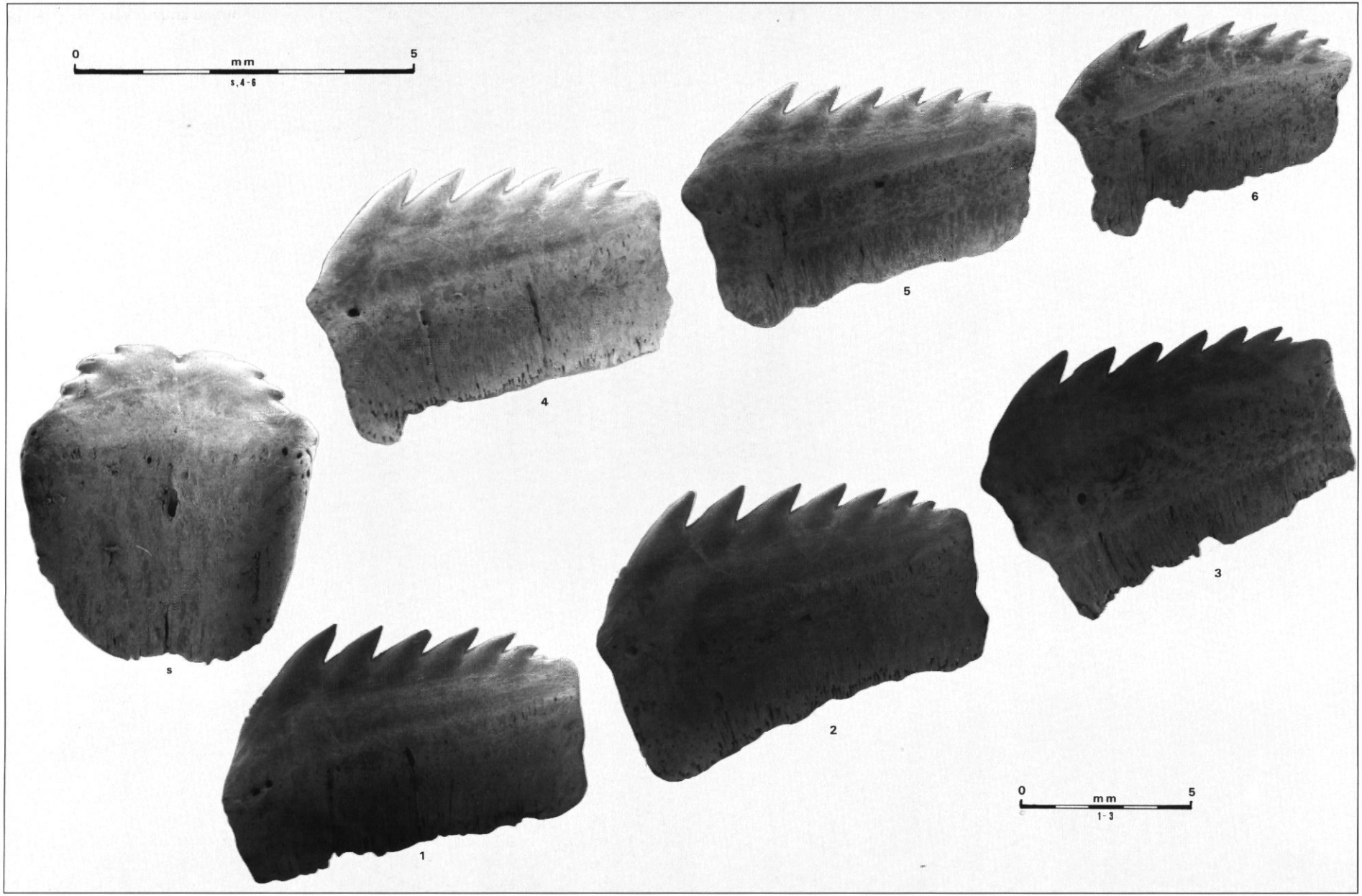

Plate 2. – Hexanchus griseus *(BONNATERRE, 1788), ♀ 1140 mm tl., fish-market at La Rochelle. Inner view of the symphysial and the first six lower teeth.*

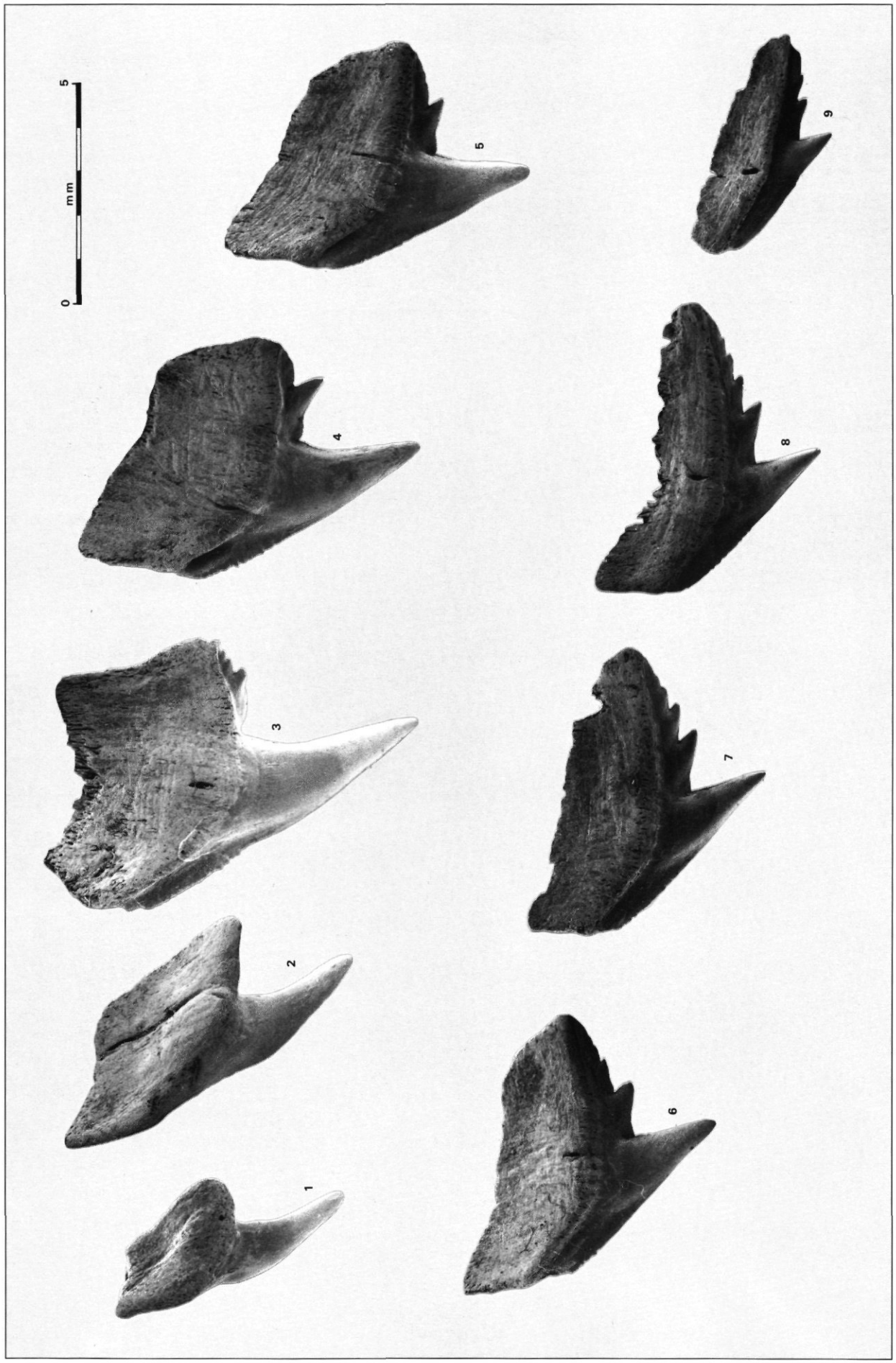

Plate 3. – Hexanchus nakamurai *Teng, 1962, ♂ 1170 mm tl., FUMT.P10859, Taiwan. Inner view of the first nine upper teeth.*

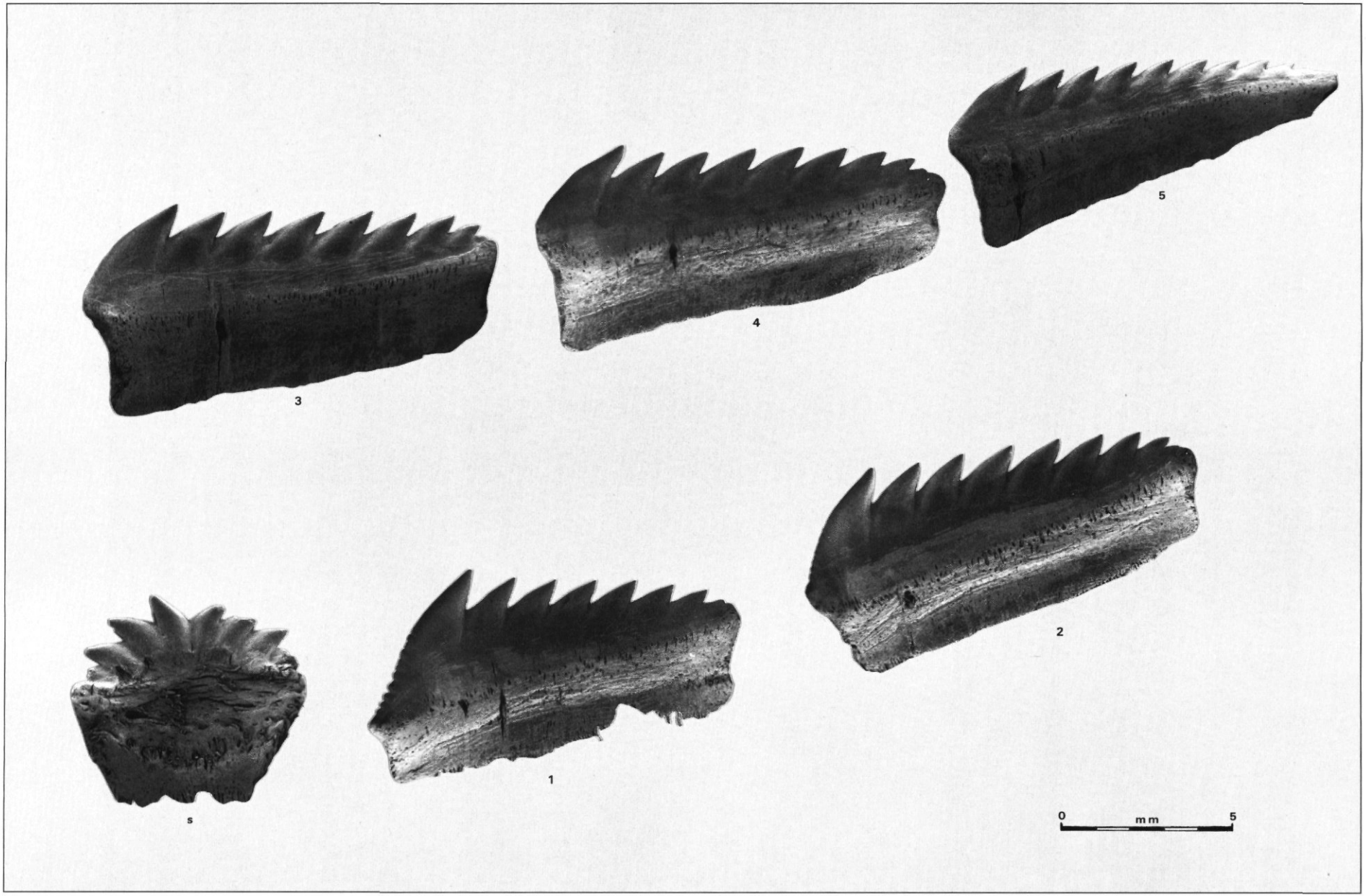

Plate 4. – Hexanchus nakamurai *TENG, 1962, ♂ 1170 mm tl., FUMT.P10859, Taiwan. Inner view of the symphysial and the first five lower teeth.*

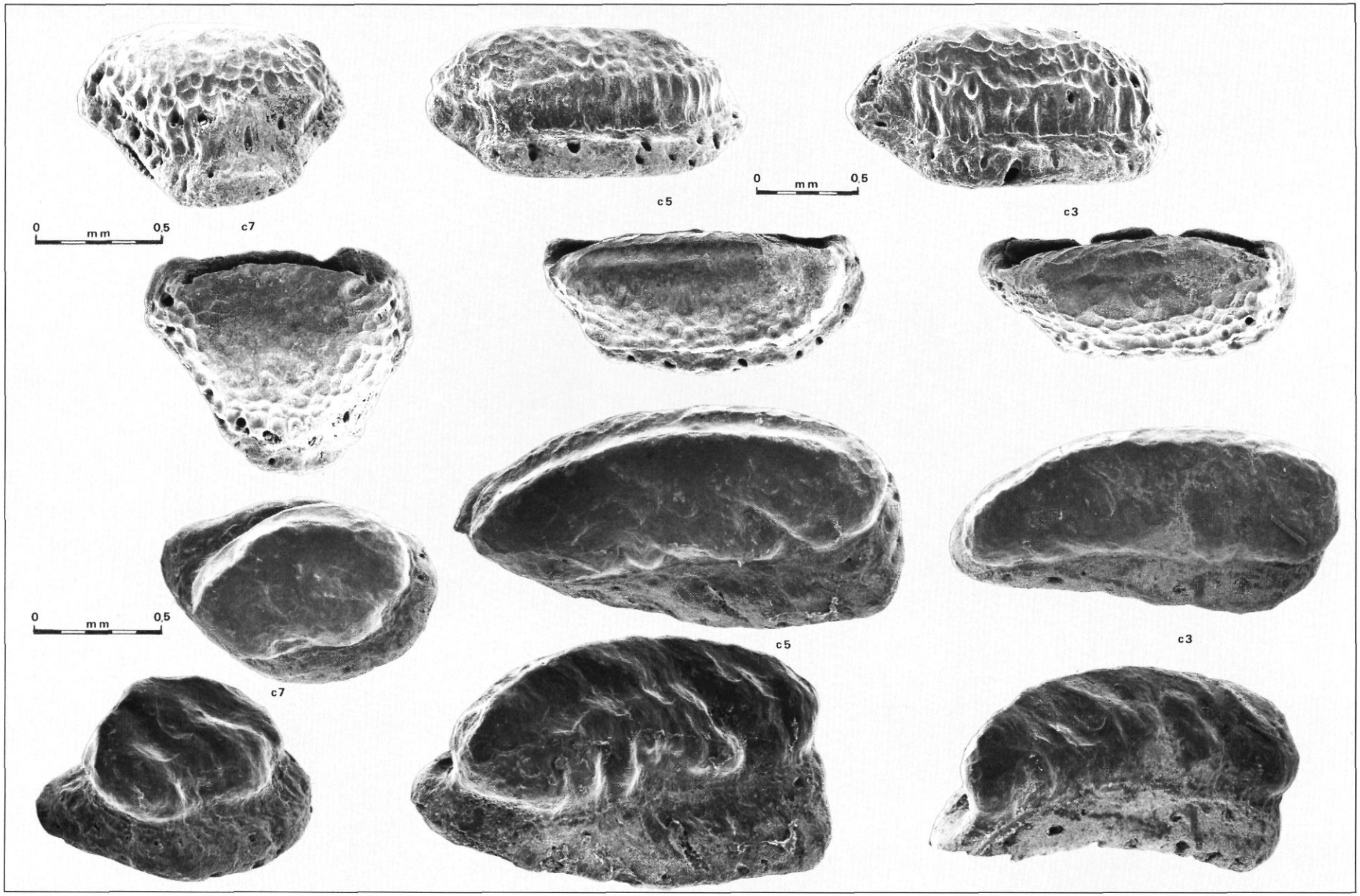

Plate 5. – *Upper part :* Hexanchus nakamurai *TENG, 1962, ♂ 1100 mm tl., AMNH-33475. North-Madagascar. Outer and occlusal views of the third, fifth and seventh right commissural lower teeth.*
Lower part : Hexanchus vitulus SPRINGER & WALLER, *1969, ♂ 1500 mm tl., RUSI-6897, Park Rynie, South Africa. Outer and occlusal views of the third, fifth and seventh right commissural lower teeth.*

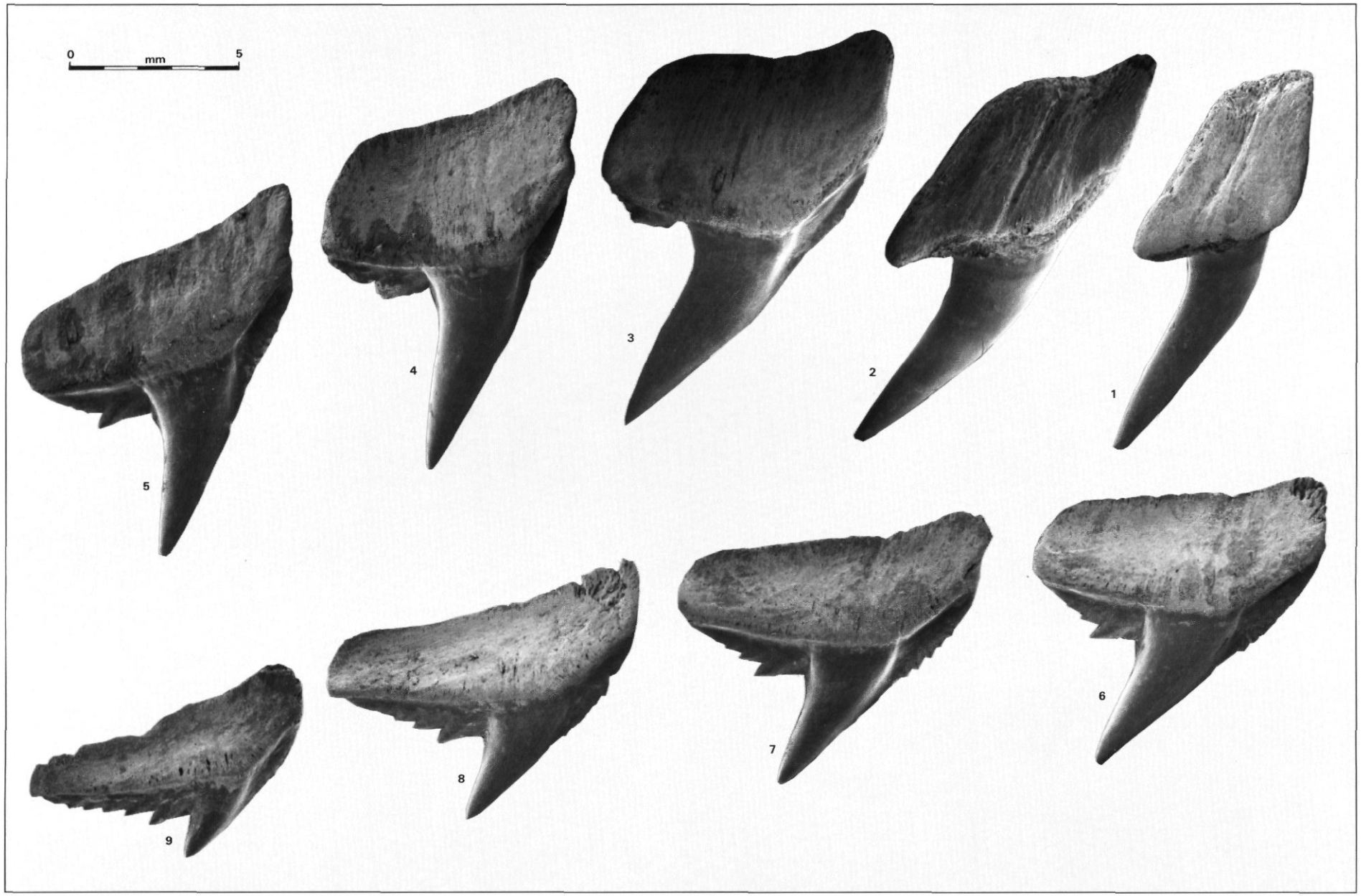

Plate 6. – Hexanchus vitulus *SPRINGER & WALLER, 1969, ♂ 1550 mm tl., RUSI-6897, Park Rynie,South Africa. Inner view of the first nine upper teeth.*

Plate 7. – Hexanchus vitulus *Springer & Waller, 1969, ♂ 1550 mm tl., RUSI-6897, Park Rynie, South Africa. Inner view of the lower symphysial, first, second and fifth teeth.*