

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 C: Superorder Holocephali 1: Order Chimaeriformes - Suborder Chimaeroidei - Family Callorhynchidae - Subfamily Callorhynchinae - Genus: *Callorhynchus*, Family Chimaeridae - Genera: *Chimaera* and *Hydrolagus*, Family Rhinochimaeridae - Genera: *Harriotta*, *Neoharriotta*, and *Rhinochimaera*.

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Abstract

Part C of this series describes and illustrates with SEM or macrophotos the morphology of the tooth plates, the spines of the first dorsal fin and frontal tenacula of extant holocephalan genera. A differential diagnosis and systematic conclusions are summarized in the results.

Key words: Holocephali - Chimaeriformes - Chimaeroidei - Callorhynchidae - Chimaeridae - Rhinochimaeridae - Odontology.

Résumé

Dans la partie C de cette série, la morphologie des plaques dentaires, ainsi que celle de l'épine de la nageoire dorsale et de l'appareil frontal ténaculaire des six genres récents d'Holocéphales sont décrites et figurées (macrophotos ou clichés MEB). Diagnose différentielle et conclusions systématiques sont présentées dans les conclusions.

Mots-clés: Holocephali - Chimaeriformes - Chimaeroidei - Callorhynchidae - Chimaeridae - Rhinochimaeridae - Odologie.

Kurzfassung

Teil C dieser Serie beschreibt und illustriert durch REM oder macrophotos die Morphologie der Zahnplatten, die Stacheln der erste dorsaler Flosse und Stirnklasper von holocephaler rezente Gattungen. Eine Differentialdiagnose und systematische Schlussfolgerung fassen die Ergebnisse zusammen.

Schlüsselwörter: Holocephali - Chimaeriformes - Chimaeroidei - Callorhynchidae - Chimaeridae - Rhinochimaeridae - Odologie.

Part C: Holocephali 1: Order: Chimaeriformes - Suborder: Chimaeroidei

General introduction

Part C of this series comprises the Holocephali. Like the Selachii and Batomorphii, the taxa of this superorder also possess a cartilaginous endoskeleton. However, holocephalan teeth are not regularly shed like Selachii and Batomorphii but form slowly and permanently growing, fused, massive tooth plates in upper and lower jaws.

The Holocephali are subdivided into the three orders Cochliodontiformes, Menaspiformes and Chimaeriformes (STAHL 1999). The first two orders are only represented by extinct taxa. The order Chimaeriformes comprises the suborders Echinochimaeroidei, Squalorajoidei, Myriacanthoidei, Chimaeropsodei and Chimaeroidei. The latter only are represented by both extinct and extant taxa, the others only by extinct taxa. The Chimaeroidei comprise the families Rhinochimaeridae, Chimaeridae and Callorhynchidae. The latter are subdivided after STAHL (1999) into the subfamilies Callorhynchinae and Edaphodontinae. Edaphodontinae comprise extinct taxa only and, like all other extinct taxa, are not included in this study.

If available, the dorsal fin spines and the frontal tenacula (a feature only) are described and illustrated as well.

The authors will not draw any nomenclatorially valid conclusions.

The full bibliographical reference for each species will be given in the descriptive section and not be repeated under literature references.

Terminology

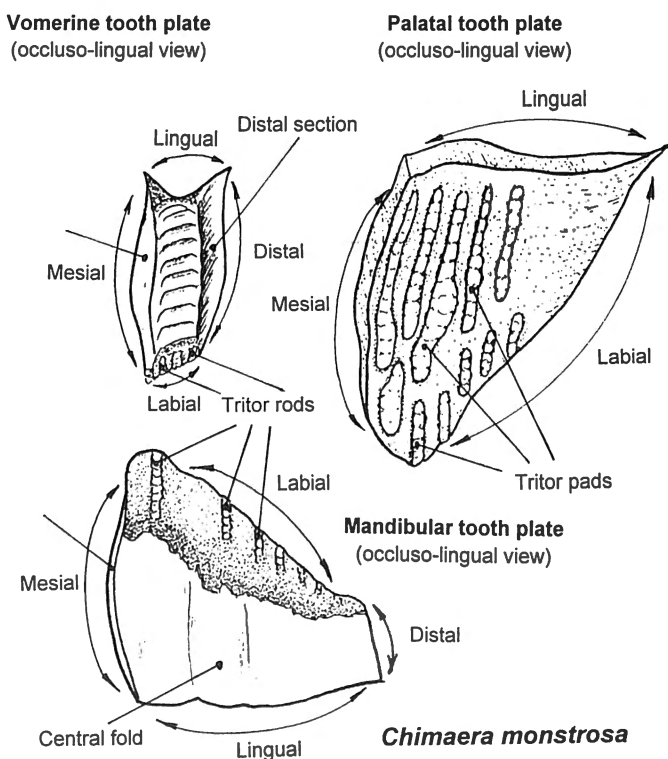
The following terminology is used in this issue for describing the tooth plates:

- Vomerine tooth plate = Upper anterior tooth plate.
 Palatal tooth plate = Upper posterior tooth plate.
 Mandibular tooth plate = Lower tooth plate.
 Tritor rods = Thin inner columns of hypermineralized tissue.
 Tritor pads = Rounded or oval external tips of internal tritor rods on the occlusal surface, longitudinally abraded tritor rods on the lingual surface, or hypermineralized tissue of the central ridge of mandibular tooth plates.

Generally, the terminology used by PATTERSON (1992) is used. However, extant chimaeroids have additional features that are added below:

The distal margin is introduced as a fourth margin, which is often lost due to abrasion; lingual and labial margins join in a distal angle in such cases. Symphyseal border is replaced by mesial margin. Palatal tooth plates have no symphyseal margin, and mesial margin applies to all types of tooth plates. Further, 'mesial' commonly used as the opposite of 'distal'.

For the lingual face, two additional terms are introduced here:



Text figure 1 – Description of the odontological, spine of the first dorsal fin and tenaculum characters

MESIAL SECTION

This is the part of the lingual face forming the symphyseal connection with the opposite vomerine or mandibular tooth plate, respectively.

DISTAL SECTION

This is the part interlocking of the two vomerine and the palatal tooth plates, respectively. (See textfigure 1 below)

Family: Callorhynchidae GARMAN, 1901

Subfamily: Callorhynchinae STAHL, 1999

INTRODUCTION

The Callorhynchinae comprise seven genera, of which only *Callorhynchus* is represented by living species.

Genus: *Callorhynchus* LACEPEDE, 1798

This genus is represented by four extinct species (STAHL, 1999) and the three extant species (DIDIER, 1995) *C. capensis*, *C. milii* and the type species *C. callorhynchus*. Species of this genus possess an additional patch of dermal denticles opposite those of the frontal tenaculum, directly attached to the skull integument. These denticles are equal to those of the frontal tenaculum and are not additionally described but well illustrated on plates 1, 3 and 5. This phenomenon seems to be unique for the extant Holocephali; in the legend of the plates the proposed appellation is *tenacular complex*.

Lacking material of the type species, *C. capensis* and *C. milii* are used for descriptions and illustrations.

Material

The following 4 specimen of 2 species were examined:

Callorhynchus milii
 ANSP 177821 Tooth plates, no data
 IRSNB R.3455 ♂ 78 cm t.l.
 IRSNB R.348 jaws, no data

Callorhynchus capensis
 Coll. Pierre Coupez ♂ skull, claspers and dorsal fin

Callorhynchus milii BORY & SAINT VINCENT, 1823
 (Plates 1 and 2)

Callorhynchus milii BORY & SAINT VINCENT 1823 -
 Dictionnaire classique d'Histoire naturelle. Rey et Gravier.
 Paris. vol.3, 62, pl.5.

HETERODONTY

The dentition is dignathic heterodont. Having a single specimen available only, neither sexual nor ontogenetic heterodonty could be examined.

VOMERINE TOOTH PLATE

The more or less lozenge-shaped plate is about three times as high as broad. The labial surface is undulated and bent lingually from the labial margin towards the lingual margin. The lingual surface possesses an additional mesial and distal section. The narrow mesial section is smooth and flat for linking with the opposite vomerine plate. The uppermost part of the broader, concave main section is always abraded, presenting a single internal mesial tritor rod along the mesial margin. The narrow, smooth distal section is slightly concave, forming an interlock with the palatal tooth plate.

PALATAL TOOTH PLATE

The plate is of more or less trapezoid shape. The distal margin is narrow and about one-third the length of the mesial one. The mesial margin is slightly arched, both labial and lingual margins are more or less straight, and the labial one has a flattened tip. The labial surface presents a large, deep depression in which the jaw part fits. A relatively narrow enameloid-like band is present along the upper mesial, labial and distal margins.

The lingual surface is slightly undulated and presents a large, broad and semi-circular tritor pad that is bifurcated toward the labial margin.

MANDIBULAR TOOTH PLATE

These more or less lozenge-shaped plates have a distal margin that is less than half as long as the mesial one. The mesial margin is straight and its surface is concave. The distal margin is also straight, but the labial one is arched. The lingual margin is slightly undulated. The labial surface presents a large, deep depression in which the jaw part fits. A relatively narrow enameloid-like band is present along the upper mesial, labial and distal margins. The lingual surface presents a mesial section forming the connection with the opposite mandibular plate. The surface is largely undulated due to the presence of a relatively broad central ridge. The part at the labial margin, along the cutting edge of the lingual surface is lost due to abrasion, with only a large, semi-circular central tritor pad remaining.

Callorhynchus capensis DUMÉRIL, 1865
(Plates 3 to 5)

Callorhynchus capensis DUMÉRIL, 1865. Histoire naturelle des poissons ou Ichthyologie générale. Edwards, George, Paris. Vol 1, 695, pl. 13, figs 5, 5a.

The dorsal fin spine possesses a sharp mesial ridge, which is serrated more or less regularly over three-quarters of its length. The tips of the serration is upturned and become shorter toward spine's tip.

The distal face is a relatively shallow, broad central groove. The lateral margins bears minute tubercles, with their tips downturned, along spine's the upper half. The lateral surfaces are convex in cross-section. The interior of the spine is hollow.

FRONTAL TENACULUM DENTICLES

The frontal tenaculum bears approximately a hundred dermal denticles on its bulbous distal part, which are set in fourteen more or less regular longitudinal rows. The size of the denticles diminishes toward the tenaculum's sides. Each dermal denticle consists of a flat, semi/oval, radiated basal plate and a hook-like cusp in the center on top. The cusp lacks cutting edges and is smooth. The basal surface each denticle of the semi-oval shaped flange is funnel shaped with a central aperture.

Family: Chimaeridae BONAPARTE, 1831

INTRODUCTION

The Chimaeridae comprises three genera, with *Chimaera* represented by extinct as well as extant species, and *Hydrolagus* represented by extant species only.

Genus: *Chimaera* LINNAEUS, 1758

This genus is represented by nine extinct species (STAHL, 1999) and the six extant species (DIDIER, 1995) *C. cubana*, *C. owstoni*, *C. jordani*, *C. phantasma*, *C. pseudomonstrosa* and the type species *C. monstrosa*.

Material

The following 13 specimen of the type species were examined:

Chimaera monstrosa

Coll.Herman	♀	55 cm tl.
Coll.Herman	♀	58 cm tl.
Coll.Herman	♂	56 cm tl.
Coll.Herman	♂	61 cm tl.
Coll.Hovestadt	♂	50 cm TL
Coll.Hovestadt	♂	44 cm TL
Coll.Hovestadt	♀	95 cm TL
Coll.Hovestadt	♀	75 cm TL
Coll.Hovestadt	♀	45 cm TL
Coll.Hovestadt	♀	45 cm TL
Coll.Hovestadt	♀	40 cm TL
Coll.Hovestadt	♀	40 cm TL
Coll.Hovestadt	♀	10.5 cm TL

Chimaera monstrosa LINNAEUS, 1758
(Plates 6 to 8)

Chimaera monstrosa LINNAEUS, 1758. Systema Natura. ed. X, tome 1, 824 pp. Nantes & Pisces: 230 - 338.

HETERODONTY

The dentition is dignathic heterodont. Neither sexual nor ontogenetic heterodonty was found.

VOMERINE TOOTH PLATE

The more or less rectangular plate is about twice as high as broad and a little twisted around its vertical axis. The labial

surface is bent from the labial margin towards the lingual margin. Vertical striae, oriented almost parallel, are present, formed by the tips of the internal tritor rods at this surface. The lingual surface is subdivided into mesial and distal subsections. The narrow mesial section is smooth and flat to link with the opposite vomerine plate. The relatively broad main section bears well-developed, horizontal ridges, of which the mesial and distal edges of which are bent labially, so that each ridge is of trapezoid shape. The surface between these ridges slopes from the top of each ridge to the base of the previous one. Along the labial the cutting edge of the main section the surface is strongly abraded, leaving five to six tritor rods visible that lay against the labial surface. The narrow, smooth distal section is slightly concave and interlocks with the palatal tooth plate.

PALATAL TOOTH PLATE

The plate appears more or less trapezoid or triangular, depending on the presence or absence of a distal margin. This margin is often indistinct due to abrasion, with a distal angle remaining only. The mesial margin is arched, and the labial and lingual margins are slightly sigmoid and joining in a distal angle. The labial surface is bent linguallly from the labial margin toward lingual margin.

The slightly undulated lingual surface bears up to six short tritor pads along the labial margin and up to five more larger elongated mesio-lingual ones. The latter are lined up almost parallel from the mesial margin toward the distal angle. Tritor pads are absent closer to the distal angle. If the lingual surface is less abraded, the tritor rods are visible through the thin enameloid-like surface layer, in which case elongated, mesio-lingually directed tritor pads are absent.

MANDIBULAR TOOTH PLATE

The distal margin of this more or less trapezoid plate is less than half the length of the mesial one. The mesial margin is arched, the distal and labial ones more or less straight. The mesial and labial margins join in a rounded angle. The lingual margin is slightly undulated. The labial surface is slightly convex and bent mesio-distally, with the mesial part bent stronger than the distal one. Vertical striae, in almost parallel arrangement, result from the tips of the internal tritor rods that lay against this surface. The mesial section of the lingual surface presents is narrow, smooth and flat, to form the link with the opposite mandibular plate. The remaining surface is undulated due to the presence of a relatively broad central ridge. Along the labial cutting edge the lingual surface is strongly abraded, leaving six distal and a mesial tritor rod visible, that lay against the labial surface, and the tritor pad that supports the central ridge.

The dorsal fin spine possesses three sharp, distinct, mesial ridges, of which at spine's base the central one is approximately three times higher than the lateral ones. The distance at spine's base between the central ridge and each lateral ridge almost equals the height of the central ridge but narrows as the spine tapers toward its apex. The height of the central ridge diminishes toward the apex, and the three ridges join to become one ridge close to the apex.

The distal face is a relatively shallow central furrow. Its lateral margins bear tubercles, with their tips downturned, along the spine's upper half. The lateral surfaces are convex in cross-section. The interior part of the spine is hollow.

FRONTAL TENACULUM DERMAL DENTICLES

The frontal tenaculum bears approximately 70 dermal denticles on its bulbous distal part, arranged in a patch of ten more or less regular longitudinal rows. The size of the denticles diminishes toward tenaculum's sides. Each denticle consists of a more or less flat, semi-oval, radiated basal plate with a hook-like cusp on top. The basal face of each dermal denticle is funnel shaped with a central aperture.

Most of the elongated, curved cusps have a central and two lateral cutting edges and smooth surfaces.

Genus: *Hydrolagus* GILL, 1862

This genus comprises 17 extant species (DIDIER, 1995): *H. affinis*, *H. africanum*, *H. alberti*, *H. barbouri*, *H. colliei*, *H. deani*, *H. eidolon*, *H. lemures*, *H. macrophthalmus*, *H. media*, *H. mirabilis*, *H. novaezealandiae*, *H. ogilbyi*, *H. purpurescens*, *H. waiti*, the type species *H. mitsukuri* and the lately decribed *H. pallidus*. Lacking material of the type species the latter species was selected for description and illustration.

Material

20 specimen of 5 species were examined:

<i>Hydrolagus affinis</i>		
Coll. Hovestadt	♂	80+ cm tl.
<i>Hydrolagus mirabilis</i>		
Coll. Herman	♂	68 cm tl.
Coll. Herman	♂	75 cm tl.
Coll. Herman	♂	74 cm tl.
Coll. Herman	♂	72 cm tl.
Coll. Herman	♂	70 cm tl.
Coll. Herman	♂	69 cm tl.
Coll. Herman	♂	68 cm tl.
Coll. Herman	♀	65 cm tl.
Coll. Herman	♀	68 cm tl.
Coll. Herman	♀	70 cm tl.
Coll. Herman	♀	72 cm tl.
Coll. Herman	♀	75 cm tl.
Coll. Hovestadt	♀	74 cm tl.
Coll. Hovestadt	♀	72 cm tl.
<i>Hydrolagus pallidus</i>		
Coll. Hovestadt	?	100+ cm tl.
Coll. Hovestadt	♂	100+ cm tl.
Coll. Hovestadt	♀	130+ cm tl.

Hydrolagus novaezealandiae
ANSP 177870 No data

Hydrolagus sp.
ANSP 177869 No data

Hydrolagus pallidus HARDY & STEHMANN, 1990
(Plates 9 and 10)

Hydrolagus pallidus HARDY & STEHMANN, 1990. A new deep-water ghost shark, *Hydrolagus pallidus* n.sp. (Holocephali, Chimaeridae), from the Eastern North Atlantic, and redescription of *Hydrolagus affinis* (BRITO CAPELLO, 1867). Archiv für Fisch Wissenschaft 40 (3): 229-248.

HETERODONTY

The dentition is dignathic heterodont. Neither sexual nor ontogenetic heterodonty was found.

VOMERINE TOOTH PLATE

The more or less rectangular plate is about twice as high as broad and a little twisted around its vertical axis. The labial surface is bent from the labial margin toward the lingual margin. Vertical striae, oriented almost parallel, are present formed by five to six internal tritor rods that lay against this surface. The lingual surface is subdivided into mesial and distal subsections. The narrow mesial section is smooth and flat, forming the link with the opposite vomerine plate. The relatively broad main section bears poorly developed horizontal ridges. A large part at the labial side, along the cutting edge of the surface of the main section is strongly abraded, leaving five or six tritor rods visible that lay against the labial surface. The narrow, smooth distal section is slightly concave and interlocks with the palatal tooth plate.

PALATAL TOOTH PLATE

This plate is more or less trapezoid. The mesial margin is slightly arched, the lingual margin slightly sigmoid and the distal one straight and about half the length of the mesial one. The labial margin is structured by large indentations between tritor rods, probably caused by abrasion. The labial surface is bent from the labial margin toward the lingual margin. The slightly undulated lingual surface bears up to six small tritor pads along the labial margin. Larger elongated mesio-lingual pads are absent.

MANDIBULAR TOOTH PLATE

The distal margin of the more or less trapezoid plate is about half the length of the mesial one. The mesial margin is slightly arched, the distal and lingual ones are more or less straight. The labial margin is structured by broad indentations between the tritor rods, probably caused by abrasions. The lingual margin is slightly undulated. The labial surface is slightly convex and bent mesio-distally, with the mesial part stronger bent than the distal one. Vertical striae in almost parallel arrangement result from the internal tritor rods that lay against this surface. The mesial section of the lingual surface is narrow, smooth and flat to form the link with the opposite mandibular plate. The remaining lingual surface is undulated due to the presence of a relatively broad central ridge. The labial margin along the cutting edge of the lingual surface is strongly abraded leaving six distal and one larger mesial tritor rod visible that lay against the labial surface.

The dorsal fin spine possesses three sharp, distinct, mesial ridges, of which at spine's base the central one is approximately three times higher than the lateral ones. The distance at spine's base between the central ridge and each lateral ridge almost equals the height of the central ridge but narrows as the spine tapers toward its apex. The height of the central ridge diminishes toward the apex, and the three ridges join to become one ridge close to the apex. Small tubercles with upward pointed tips are found on the lower section of the central ridge.

The distal face is a relatively shallow central furrow. Its lateral margins bear tubercles, with their tips downturned, along the spine's upper half. The lateral surfaces are convex in cross-section. The interior part of the spine is hollow.

FRONTAL TENACULUM DERMAL DENTICLES

The frontal tenaculum bears approximately 70 dermal denticles on its bulbous distal part, arranged in a patch of ten more or less regular longitudinal rows. The size of the denticles diminishes toward tenaculum's sides. Each denticle consists of a more or less flat, semi-oval, radiated basal plate with a hook-like cusp on top. The basal face of each dermal denticle is funnel shaped with a central aperture.

Some of the elongated, curved cusps have a central and two lateral cutting edges and smooth surfaces.

Family: Rhinochimaeridae BONAPARTE, 1831

INTRODUCTION

The Rhinochimaeridae comprise six extinct and the three extant genera *Harriotta*, *Neoharriotta* and *Rhinochimaera*.

Genus: *Harriotta* GOODE & BEAN, 1895

This genus is represented by one extinct species (STAHL, 1999) and the two extant species (DIDIER, 1995) *H. haeckeli* and the type species *H. raleighana*. Dorsal fin spine and frontal tenaculum were lacking for description and illustration.

MATERIAL

The following 4 specimen of 1 species were examined:

Harriotta raleighana

Coll. Hovestadt	♂	98 cm tl.
Coll. Hovestadt	♀	71 cm tl.
ANSP 177811		no data
Coll. Mailliot	♂	75 cm tl.

Harriotta raleighana GOODE & BEAN, 1895
(Plates 12, 13 and 20)

Harriotta raleighana GOODE & BEAN, 1895. Scientific results of explorations by the U.S. fish commission steamer 'Albatros'. No.30. On *Hariotta*, a new type of chimaeroid fish from the deeper waters of the northwestern Atlantic. Proceedings of the United States National Museum 17 (1014): 471-473.

HETERODONTY

The dentition is dignathic heterodont. Neither sexual nor ontogenetic heterodonty were found.

VOMERINE TOOTH PLATE

The plate is mesially enlarged. The mesial edge of the labial margin forms a very sharp angle (about 20°) with the mesial margin, forming a hook-shaped cutting edge with the arched mesial margin. The labial cutting edge abruptly bends horizontally and finally forms a rounded junction with the distal margin, which is slightly arched. The lingual margin is straight.

The plate is a little twisted around its vertical axis. The labial surface is bent from the labial margin towards the lingual one. Vertical striae, oriented almost parallel, are present formed by five to six internal tritor rods that lay against this surface. The lingual surface is subdivided into mesial and distal subsections. The narrow mesial section is smooth and flat, forming the link with the opposite vomerine plate. The relatively broad main section is convex and smooth. With the exception of the mesial part, a large part at the labial side, along the cutting edge of the surface of the main section is strongly abraded, leaving up to ten tritor rods visible that lay against the labial surface. The narrow, smooth distal section is slightly concave and interlocks with the palatal tooth plate.

PALATAL TOOTH PLATE

This plate is more or less trapezoid. The mesial margin is slightly arched, the lingual margin slightly sigmoid and the distal one straight and about one-quarter the length of the mesial margin. The labial surface is bent lingually from the labial margin towards lingual one.

The slightly undulated lingual surface bears up to seven distinct tritor pads along the labial margin. Several tritor pads are merged in the mesio-mid section several, forming a large convex surface.

MANDIBULAR TOOTH PLATE

The more or less trapezoid plate has a distal margin that is about one-fifth of the length of the mesial one. The mesial margin is slightly arched, the distal and lingual ones are more or less straight.

The labial margin is structured by a few rounded indentations between the tritor rods, probably caused by abrasions. The lingual margin is slightly undulated. The labial surface is slightly convex and bent mesio-distally, with the mesial part stronger bent than the distal one. Vertical striae in almost parallel arrangement result from the internal tritor rods that lay against this surface. The mesial section of the lingual surface is narrow, smooth and flat to form the link with the opposite mandibular plate. The remaining lingual surface is undulated due to the presence of a relatively broad central ridge, which is supported by a large tritor pad. The labial margin along the cutting edge of the lingual surface, is strongly abraded, leaving five distal and three larger mesial tritor rod visible that lay against the labial surface.

The dorsal fin spine possesses one sharp mesial ridge that diminishes in height toward the apex. Minute knobs are

present at each side of the ridge up to half the spine's length. The distal face is slightly concave or almost flat, with a low central ridge at the lower half of the spine. Its lateral margins bear minute tubercles, with their tips downturned, along the spine's upper two-third part. The lateral surfaces are convex in cross-section. The interior part of the spine is hollow.

FRONTAL TENACULUM DERMAL DENTICLES

The frontal tenaculum is three as long as broad and bears approximately dermal denticles on its bulbous distal part, arranged in a patch of eight more or less regular longitudinal rows. The size of the denticles diminishes toward tenaculum's sides. Each denticle consists of a hook-like cusp on top. The basal face of each dermal denticle is funnel shaped with a central aperture.

Cutting edges on the elongated arched cusp are present at each side and surfaces are smooth.

Genus: *Neoharriotta* BIGELOW & SCHROEDER, 1950

This genus comprises the three extant species (DIDIER, 1995), *N. carri* and *N. pumila* and the type species *N. pinnata*. Lacking material of the type species, *N. pumila* is used for description and illustration. Dorsal fin spine and frontal tenaculum were lacking for description and illustration.

MATERIAL

The following 1 specimen of 1 species were examined:

Neoharriotta pumila
ANSP 172538 (Paratype) ♂ 21 cm tl., isolated tooth plates only.

Neoharriotta pumila DIDIER & STEHMANN, 1996 (Plate 14)

Neoharriotta pumila DIDIER & STEHMANN 1996.
Neoharriotta pumila, a new species of Longnose Chimaera from the Northwestern Indian Ocean (Pisces, Holocephali, Rhinochimaeridae). *Copeia* 1996 (4): 955-965.

HETERODONTY

The dentition is dignathic heterodont. Sexual or ontogenetic heterodonty could not be examined with only a single specimen available.

VOMERINE TOOTH PLATE

The plate is more or less quadrangular. The plate is a little twisted around its vertical axis. The labial surface is bent from the labial margin toward the lingual margin.

Vertical striae, oriented almost parallel, are present formed by the internal tritor rods that lay against this surface. The lingual surface is subdivided into mesial and distal subsections. The narrow mesial section is smooth and flat, forming the link with the opposite vomerine plate. The relatively broad main section is convex and smooth. A large part at the

labial side, along the cutting edge of the surface of the main section is strongly abraded, leaving nine tritor rods visible that lay against the labial surface and additionally five mesial ones. The narrow, smooth distal section is slightly concave and interlocks with the palatal tooth plate.

PALATAL TOOTH PLATE

This plate is more or less trapezoid. Its mesial, lingual and distal margins are straight and the distal one is one third of the length of the mesial margin only. The labial margin is straight with a flattened tip. The labial surface is bent from the labial margin towards lingual one.

The slightly undulated lingual surface bears up to ten, small, distally located tritor rods, a large one merged with the tritor pad of the central ridge and three smaller tritor pads that are mesially, all located along the labial margin.

MANDIBULAR TOOTH PLATE

The distal margin of this lozenge-shaped plate is about half the length of the mesial one. The mesial and distal margins are straight, the lingual one is arched. The labial margin is structured by rounded indentations between the tritor rods, probably caused by abrasions. The lingual margin is undulated, due to a well-developed central ridge. The labial surface is slightly convex and bent mesio-distally, with the mesial part stronger bent than the distal one. Vertical striae in almost parallel arrangement result from the internal tritor rods that lay against this surface. The mesial section of the lingual surface is narrow, smooth and flat to form the link with the opposite mandibular plate. The remaining lingual surface is strongly undulated due to the presence of a relatively broad central ridge. The labial margin along the cutting edge of the lingual surface is strongly abraded, leaving nine small mesial, one large central and four smaller tritor rod visible that lay against the labial surface. The central tritor rod is merged the large tritor pad that supports the central ridge.

Genus: *Rhinochimaera* GARMAN 1901

This genus comprises the three extant species (DIDIER, 1995) *R. atlantica*, *R. africana* and the type species *R. pacifica*. Lacking sufficient material of the type species, *R. atlantica* was used for description and illustration.

MATERIAL

The following 14 specimen of 2 species were examined:

Rhinochimaera atlantica

Coll. Herman	♀	120 cm tl.
Coll. Herman	♀	125 cm tl.
Coll. Herman	♀	135 cm tl.
Coll. Herman	♀	139 cm tl.
Coll. Herman	♂	100 cm tl.
Coll. Hovestadt	♂	100 cm tl.
Coll. Hovestadt	♂	100 cm tl.
Coll. Hovestadt	♂	100 cm tl.
Coll. Hovestadt	♂	100 cm tl.
Coll. Hovestadt	♀	120 cm tl.

Coll. Hovestadt	♀	120 cm tl.
Coll. Hovestadt	♀	150 cm tl.
Coll. Hovestadt	♀	150 cm tl.

Rhinochimaera pacifica

ANSP 177812 No data

Rhinochimaera atlantica HOLT & BYRNE, 1909 (Plates 15 to 19)

Rhinochimaera atlantica HOLT & BYRNE, 1909. Preliminary note on some fishes from the Irish Atlantic slope. *Annals and Magazine of Natural History*, series 8, 3: 279-280.

HETERODONTY

The dentition is dignathic heterodont. Neither sexual nor ontogenetic heterodonty was found.

VOMERINE TOOTH PLATE

This plate has an arched mesial margin. The mesial edge of the labial margin makes a sharp angle (about 60°) with the mesial margin. The labial cutting edge gradually slopes towards the distal angle. The lingual margin is straight.

The labial surface is bent from the labial margin towards the lingual margin. Neither tritor rods nor tritor pads are present. The lingual surface is subdivided into mesial and distal subsections. The narrow mesial section is smooth and flat, forming the link with the opposite vomerine plate. The relatively broad main section is convex and smooth. A large part at the labial side, along the cutting edge of the surface of the main section is strongly abraded, leaving nine tritor rods visible that lay against the labial surface and additionally five mesial ones. The narrow, smooth distal section is slightly concave and interlocks with the palatal tooth plate.

PALATAL TOOTH PLATE

The plate is triangular. The mesial margin is slightly arched and joins the lingual margin in a rounded angle. The slightly arched lingual margin joins the labial one in a sharp angle of about 20°. The lingual and mesial margins join in an angle of about 30°. The labial surface is bent from the labial margin towards lingual margin. The concave lingual surface is smooth and bent from the labial margin toward lingual margin. Tritor rods and tritor pads are absent.

MANDIBULAR TOOTH PLATE

The plate is triangular. The mesial margin is straight and joins the lingual margin in a rounded angle. The lingual margin joins the labial one in a sharp angle of about 30°. The lingual and mesial margins join in an angle of about 30°. The labial surface is bent from the labial margin toward lingual margin. The concave lingual surface is smooth and bent from the labial margin toward lingual margin. Tritor rods and tritor pads are absent.

The dorsal fin spine possesses one sharp mesial ridge that diminishes in height toward the apex.

The distal face is a relatively shallow, broad central furrow.

Its lateral margins bear minute tubercles, with their tips downturned, along the spine's lower half. The lateral surfaces are convex in cross-section. The interior part of the spine is hollow.

FRONTAL TENACULUM DERMAL DENTICLES

The frontal tenaculum bears approximately 80 dermal denticles on its bulbous distal part, arranged in a patch of ten more or less regular longitudinal rows. The size of the denticles diminishes toward tenaculum's sides. Each denticle consists of a more or less flat, semi-oval, radiated basal plate with a hook-like cusp on top. The basal face of each dermal denticle is funnel shaped with a central aperture.

Cutting edges on elongated arched cusps are absent and surfaces are smooth.

Differential diagnosis

TOOTH PLATES

Although some extinct species have a different configuration, the six extant chimaeroid genera all possess a pair of vomerine and palatal plates in the upper jaw and a pair of mandibular plates in the lower jaw.

The most significant morphologically distinctive features of the genera are summarized in table 1.

The tooth plate morphology of *Rhinochimaera* differs strongly from the remaining five genera by the extraordinary shape of vomerine, palatal and mandibular tooth plates. The palatal and mandibular plates have one sharp, more or less straight labial margin, without any indentation between tritor rods and tritor pads, and tritor pads are absent on vomerine, palatal and mandibular plates.

Callorhynchus is distinguished from *Chimaera*, *Hydrolagus*, *Harriotta* and *Neoharriotta* by a vomerine plate with a single mesial tritor rod only, a palatal plate with a single bifurcated tritor pad and a mandibular plate with a single semi-circular tritor pad. Further, the palatal and mandibular plates have a unique deep depression on the labial surface.

There are no significantly morphological differences between *Chimaera* and *Hydrolagus*. However, both can be distinguished from *Harriotta* and *Neoharriotta* by a vomerine plate with a low number of tritor rods (five) and a lingual surface with well-developed horizontal ridges; further by a palatal plate with six distal and five mesial tritor pads and a mandibular plate with six distal and a single mesial tritor rod. Both *Harriotta* and *Neoharriotta* lack horizontal ridges on the lingual surface of the vomerine plate. However, *Harriotta* has a vomerine plate with up to ten tritor rods with the most mesial one forming a hook-like extension, whilst that of *Neoharriotta* has nine distal and five mesial tritor rods and lacks a hook-like extension. Their palatal plates differ, in that *Harriotta* has seven small plus a large mesio-mid tritor pad, whereas *Neoharriotta* shows up to ten small distal, a central and three smaller mesial tritor rods. Further, *Harriotta* and *Neoharriotta* can be distinguished by their mandibular plates, on which *Harriotta* has five distal and three larger tritor rods, whereas *Neoharriotta* has up to ten small distal, a large central and four smaller mesial tritor rods.

DORSAL FIN SPINES

Although such material of *Neoharriotta* was lacking, significant intergeneric differences were noted in the other genera. Generally, the dorsal fin spine has a central ridge at the mesial face and convex lateral faces. *Callorhynchus*, *Harriotta* and *Rhinochimaera* share a mesial central ridge and convex lateral faces. They can be distinguished by the distal spine face. *Callorhynchus* possesses tubercles with downturned tips at both lateral margins of spine's the upper third part, *Harriotta* possesses tubercles with downturned tips at both lateral margins of spine's the upper two-third part, and *Rhinochimaera* possesses hardly perceptible tubercles at the lateral margins of the lower spine part. The mesial spine face of both *Chimaera* and *Hydrolagus* possesses three sharp, distinct, mesial ridges, of which at spine's base the central one is approximately three times higher than the lateral ones. The distance at spine's base between the central ridge and each lateral ridge almost equals the height of the central ridge but narrows as the spine tapers toward its apex. The height of the central ridge diminishes toward the apex, and the three ridges join to become one ridge close to the apex. The central ridge of *Chimaera* is smooth, whilst in *Hydrolagus* it has tubercles with upturned tips at spine's lower part. The upper distal spine face of both possesses tubercles with downturned tips on the lateral margins of the spine.

FRONTAL TENACULUM DERMAL DENTICLES

The frontal tenacula of *Callorhynchus*, *Rhinochimaera*, *Harriotta*, *Chimaera* and *Hydrolagus* are similar. They consist of a cartilaginous appendix at the skull's fore head which bears an oval- to circular-shaped patch of dermal denticles at the tip. The denticles are more or less arranged in semi-parallel rows. The numbers of rows, as well as the number of denticles within a row vary in each genus. Each denticle consists of a more or less flat, semi-oval, radiated basal plate with a hook-like cusp on top. The basal face of each dermal denticle is funnel shaped with a central aperture. The elongated, curved cusps of the dermal denticles of *Chimaera* and some of *Hydrolagus* have a central and two lateral cutting edges and smooth surfaces. Those of *Harriotta* only possess lateral cutting edges. Examined specimens of male of *Callorhynchus* present an opposite additional patch of denticles fixed on the skull, forming a tenacular complex. Material of *Neoharriotta* was not available, but illustrated male specimens in the scientific literature are only in possession of a common frontal tenaculum.

Conclusions

Concerning the tooth plate morphology, *Rhinochimaera* differs severely from all other chimaeroid taxa. Among the remaining taxa, *Callorhynchus* shares some general characters like having tritor rods and tritor pads but has unique characteristic features separating it from the other taxa (see differential diagnosis). *Harriotta* share more characters with the remaining taxa than *Callorhynchus* but has an unique shaped vomerine plate. *Neoharriotta*, *Chimaera* and *Hydrolagus* share many characteristic features, and the latter two cannot be separated by tooth plate morphology.

Species	Vomerine plate	Palatal plate	Madibular plate
<i>Callorhinchus</i>	- A single mesial tritor rod - Main lingual surface smooth	- One large bifurcated tritor pad - Deep depression at the labial surface	- One large semi-circular tritor pad - Deep depression at the labial surface
<i>Chimaera</i>	- Five or six tritor rods - Main lingual surface with well developed horizontal ridges	- Six distal and five larger mesial tritor pads - Short or lacking distal margin	- Six distal and one larger mesial tritor rod - Lingual central ridge supported by a large tritor pad
<i>Harriotta</i>	- Up to ten tritor rods with the mesial one with a hook-like extension - Main lingual surface smooth	- Seven distal and one large mesio-mid tritor pad - Short distal margin	- Five distal and three larger mesial tritor rod - Lingual central ridge supported by a large tritor pad
<i>Hydrolagus</i>	- Five or six tritor rods - Main lingual surface with well developed horizontal ridges	- Six distal and five larger mesial tritor pads - Short distal margin	- Six distal and one larger mesial tritor rod - Lingual central ridge supported by a large tritor pad
<i>Neoharriotta</i>	- Nine labial and five mesial tritor rods - Main lingual surface smooth	- Up to ten small distal, one large central and three smaller tritor rods - Lingual central ridge supported by a large tritor pad - Labial surface smooth	- Up to ten small distal, one large central and four smaller tritor rods - Lingual central ridge supported by a large tritor pad - Labial surface smooth
<i>Rhinochimaera</i>	- Tritor rods absent - Main lingual surface smooth	- Tritor rods absent - Main lingual surface smooth - Central ridge absent - Sharp, straight cutting edge	- Tritor rods absent - Main lingual surface smooth - Central ridge absent - Sharp, straight cutting edge

Table 1

Concerning the type of character differences, the following hypothetical phylogenetic interrelationships can be given (see textfigure 2): *Chimaera* and *Hydrolagus* cannot be distinguished and could be considered congeneric. *Rhinochimaera* is clearly different from all other taxa. The remaining taxa *Harriotta*, *Chimaera/Hydrolagus* and *Neoharriotta* may form a subgroup in which *Harriotta* clearly distinguishes.

Dorsal fin spine morphology indicates a closer relationship of *Harriotta*, *Rhinochimaera* and *Callorhinchus* and a separation of these genera from *Chimaera* and *Hydrolagus*. *Neoharriotta* cannot be interpreted due to lacking material.

Frontal clasper morphology presents too little character variation for distinguishing externally between the genera.

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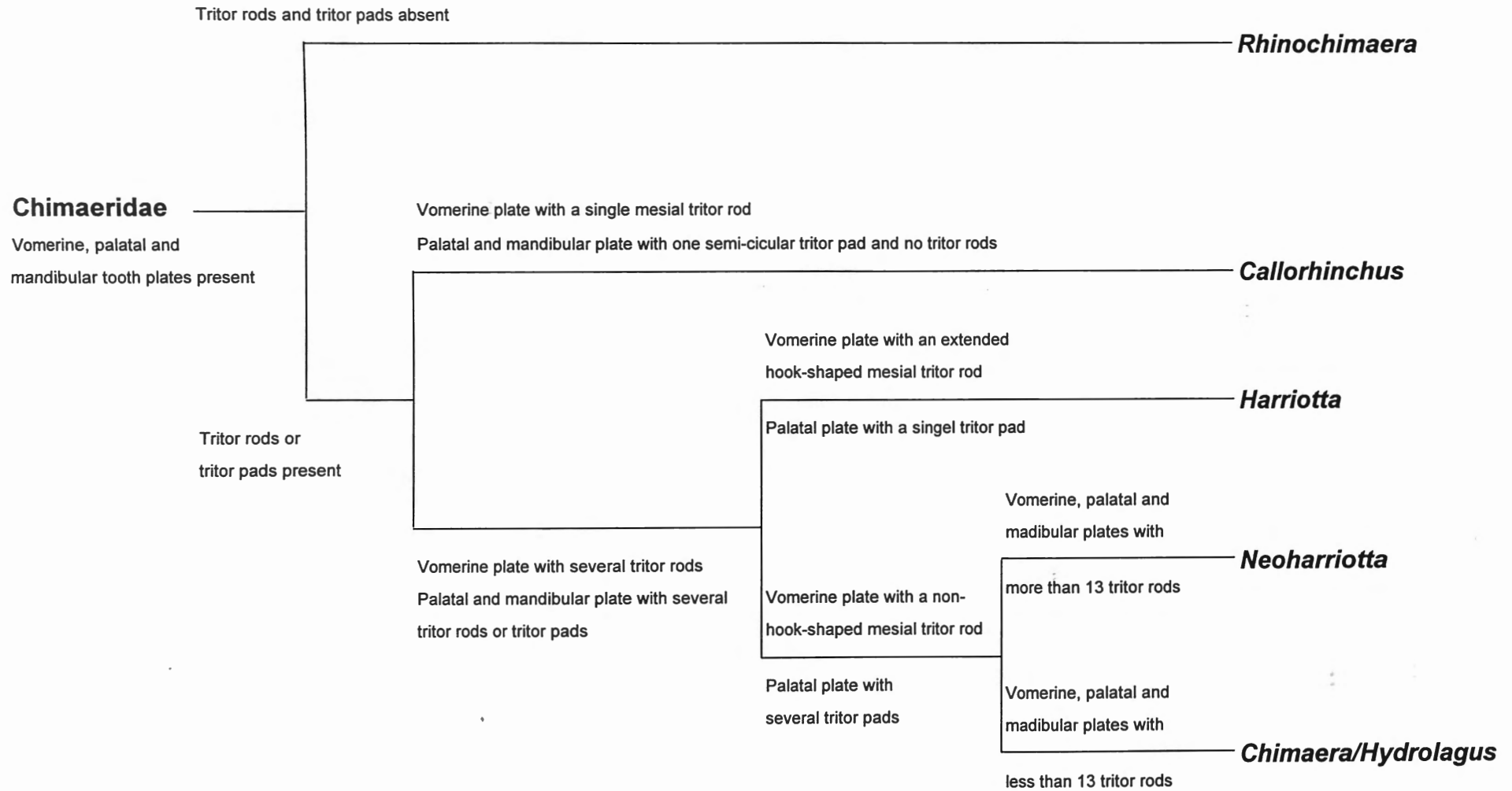
also would like to thank Captain P. GUEGUEN for allowing and helping us to collect specimens and S. MAILLIOT (University Claude Bernard, Lyon, France) for the gift of a *Harriotta* specimen.

Bibliography

- DIDIER, D.A. 1995. Phylogenetic Systematics of Extant Chimaeroid Fishes (Holocephali, Chimaeroidei). *Novitates, American Museum of Natural History*, 3119: 1-86.
- PATTERSON, C. 1992. Interpretation of the tooth plates of chimaeroid fishes. *Zoological Journal of the Linnean Society*, 106 (1): 33-61.
- STAHL, B.J. 1999. Chondrichthyes III Holocephali. In: Handbook of Paleichthyology Vol.4. *Gustav Springer Verlag, Stuttgart*: 164 pp.

Additional references

- BIGELOW, H.B. & SCHROEDER, W.C. 1953. Fishes of the Western North Atlantic, *Memoir Sears Foundation for marine research*, 1. part 2 : 515 - 562.
- DEAN, B. 1904. Notes on the long-snouted chimaeroid of Japan, *Rhinochimaera (Harriotta) pacifica*. *Journal of the College of Science of the Imperial University of Tokyo* 19.4: 20 pp.



Text figure 2

DEAN, B. 1906. Chimaeroid fishes and their development. *Washington D.C., Carnegie Institution*. 32 : 156 pp.

DIDIER, D.A. 1996. Neoharriotta pumila a new species of long-nose Chimaera from the Northwestern Indian Ocean (Pisces, Holocephali Rhinochimaeridae). *Copeia* 4: 955 - 965.

FOWLER, H. 1941. The fishes of the group Elasmobranchii, Holocephali, Isospondyli, and Ostarophysi, obtained by the United States Bureau of Fisheries steamer «Albatross» in 1907 to 1910, chiefly in the Philippine islands and adjacent seas.

United States National Museum, Bulletin 100, 13, 486-510.

HARDY, S. & STEHMANN, M. 1990. A new deeper-water ghost shark *Hydrolagus pallidus* n.sp. (Holocephali, Chimaeridae) from the eastern North Atlantic and redescription of *Hydrolagus affinis* (Brito Capello, 1867). *Archiv für Fischerei Wissenschaft*. 40, 3 : 229 - 248.

INADA, T. & GOTO, M. 1979. *Rhinochimaera pacifica*, a long-snouted Chimaera (Rhinochimaeridae) in New Zealand waters. *Japanese Journal of Ichthyology*. 25. 4 : 235 - 243.

KARRER, C. 1972. Die Gattung Harriotta GOODE & BEAN, 1895 (Chondrichthyes, Chimaeriformes, Rhinochimaeridae). *Mitteilungen Zoologische Museum Berlin*. 48.1 : 203 - 221.

POLL, M. 1951. Expédition océanographique belge dans les eaux côtières africaines de l'Atlantique sud (1948-1949). Résultats scientifiques. *IRSNB, Bruxelles*, vol IV, fasc. 1, 144-154.

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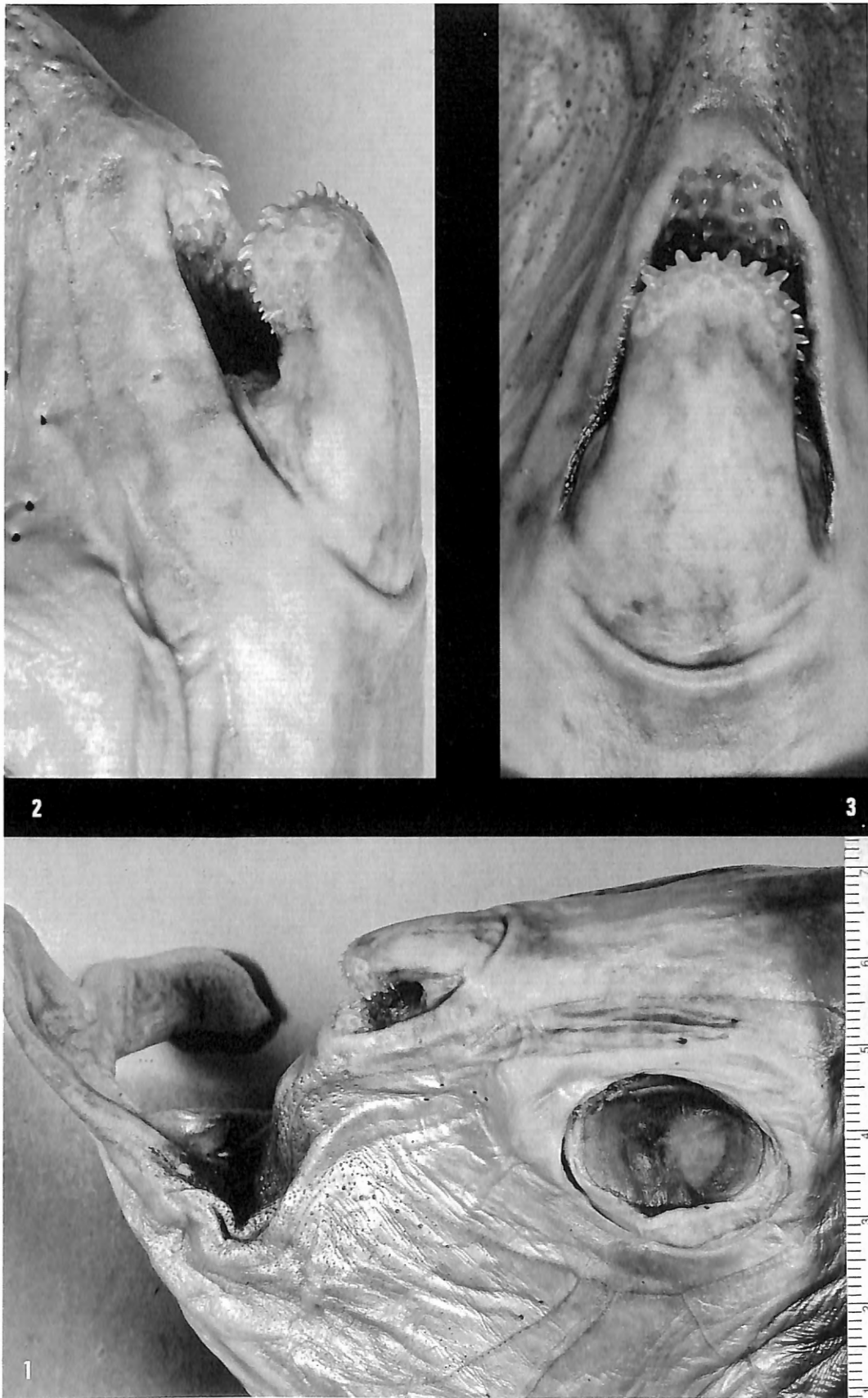


Plate 1. *Callorhynchus milii* BORY & SAINT VINCENT, 1823. Male, 78 cm t.l., off south east Australia, IRSNB, R. 3455, collected in 1874. Fig. 1: partial left lateral view of the head ; details of the frontal *tenaculum complex*: lateral view (fig.2) and dorsal view (fig.3).

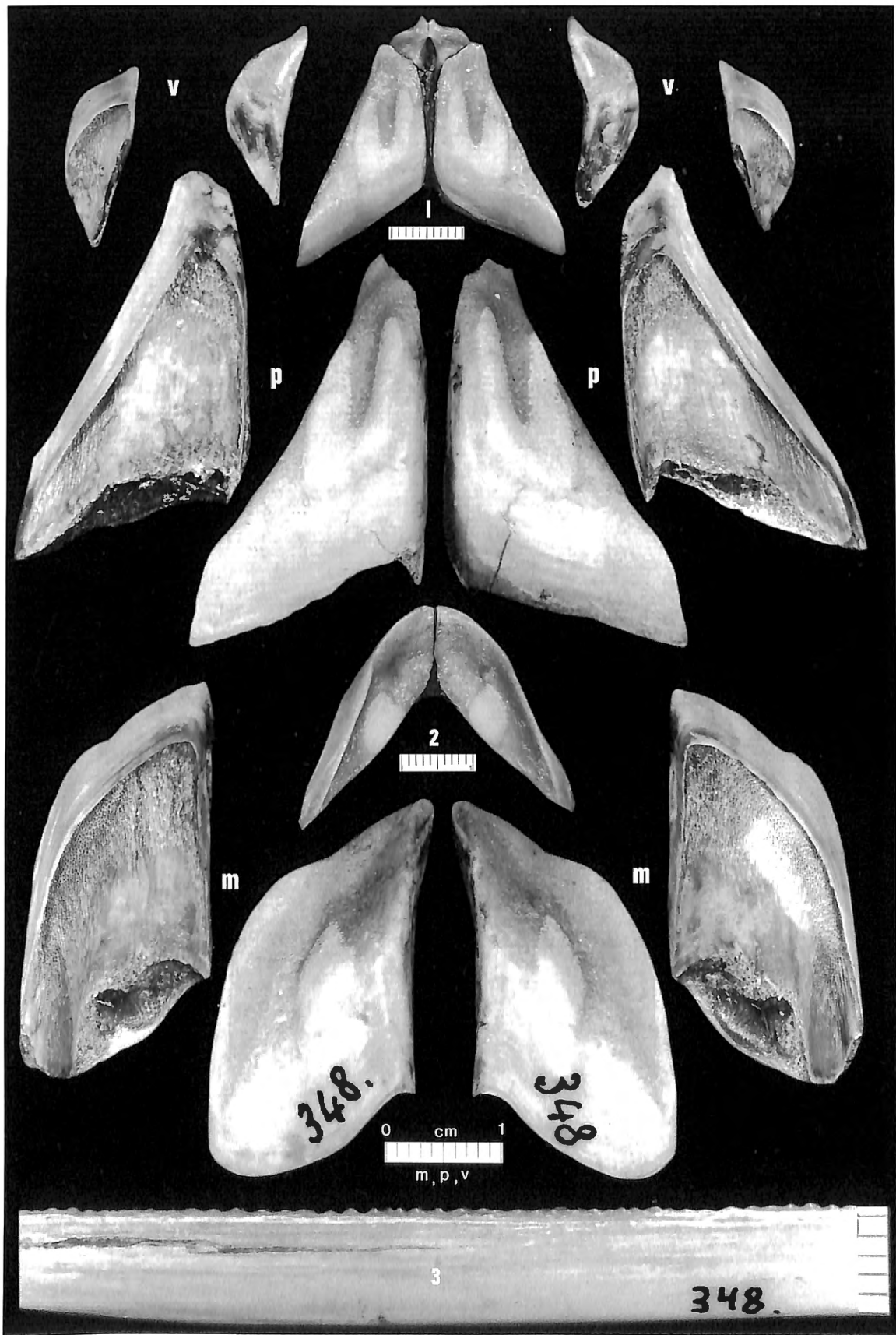


Plate 2. *Callorhynchus milii* BORY & SAINT VINCENT, 1823. Male, 78 cm t.l., off south east Australia, IRSNB R. 348, collected in 1874. Upper (fig.1) and lower (fig.2) jaws, with details of both lingual or functional face and labial with jaw attachment surface growing of their respective vomerine (v), palatine (p) and mandibular (m) dental plates. Fig. 3 shows a part of the left side of the dorsal fin spine.

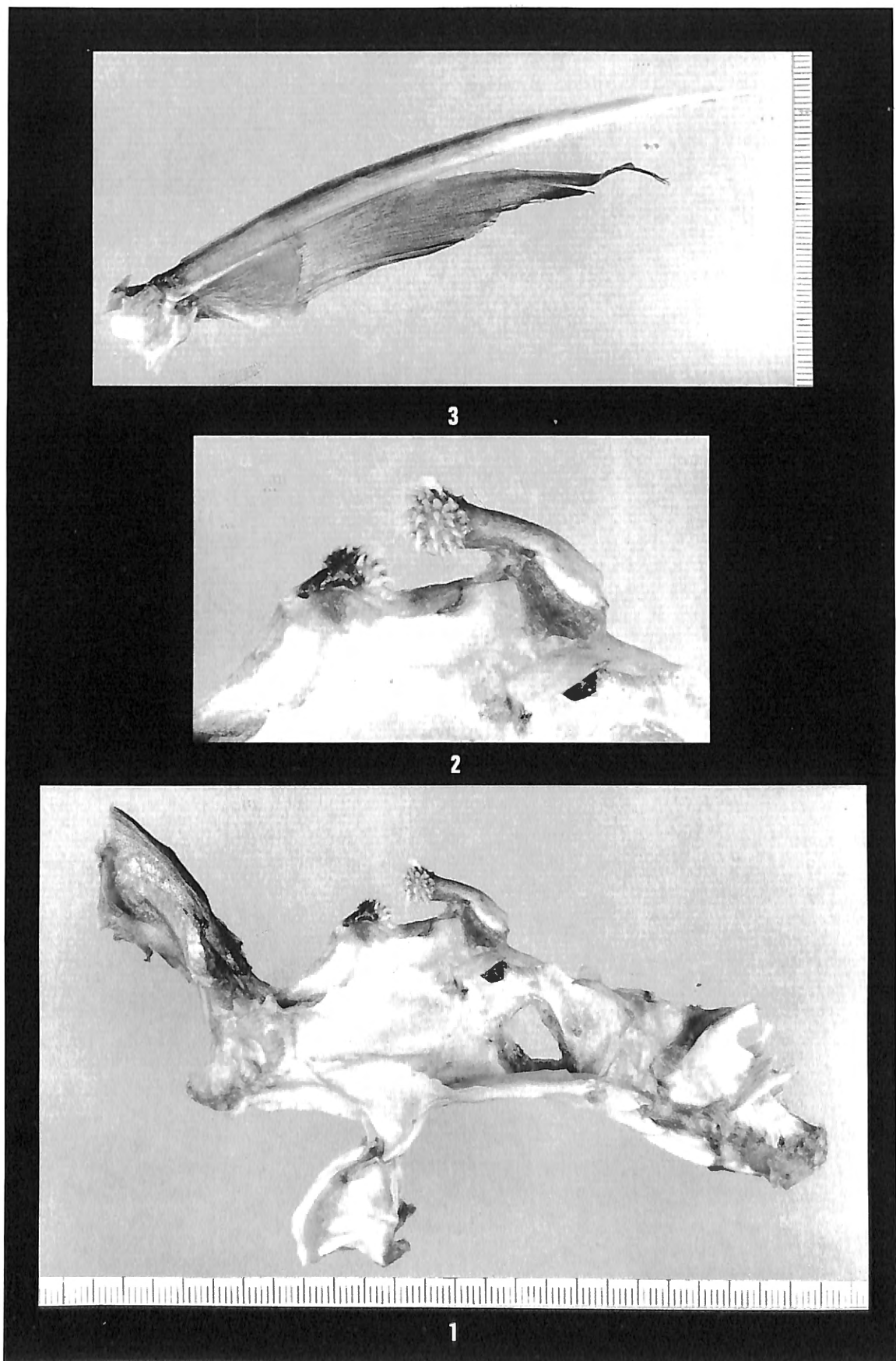


Plate 3. *Callorhynchus capensis* DUMERIL, 1865. Male, estimated total length circa 70 cm, False Bay, South Africa. Coll. P. COUPATEZ. Left side view of the skull (fig.1), detail of the *tenaculum complex* (fig.2) and first dorsal fin spine in connection with the fin (fig.3).

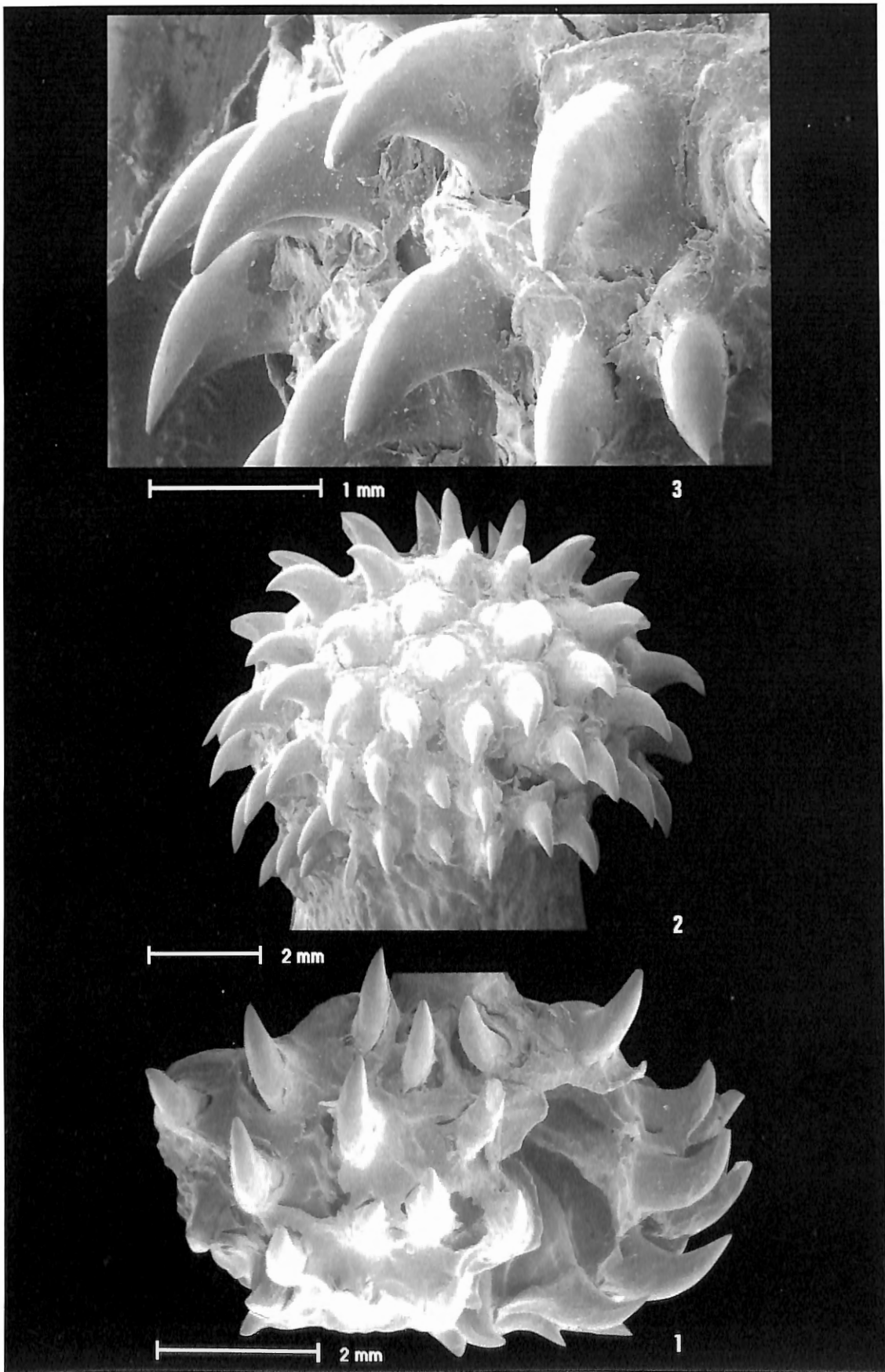


Plate 4. *Callorhynchus capensis* DUMERIL, 1865. Male, estimated total length circa 70 cm, False Bay, South Africa. Coll. P.COUPATEZ. *Tenaculum* complex: «dermal denticles (spinules) within *tenaculum* groove (fig.1), on the *tenaculum* head (fig.2) and close up of the latter (fig.3).

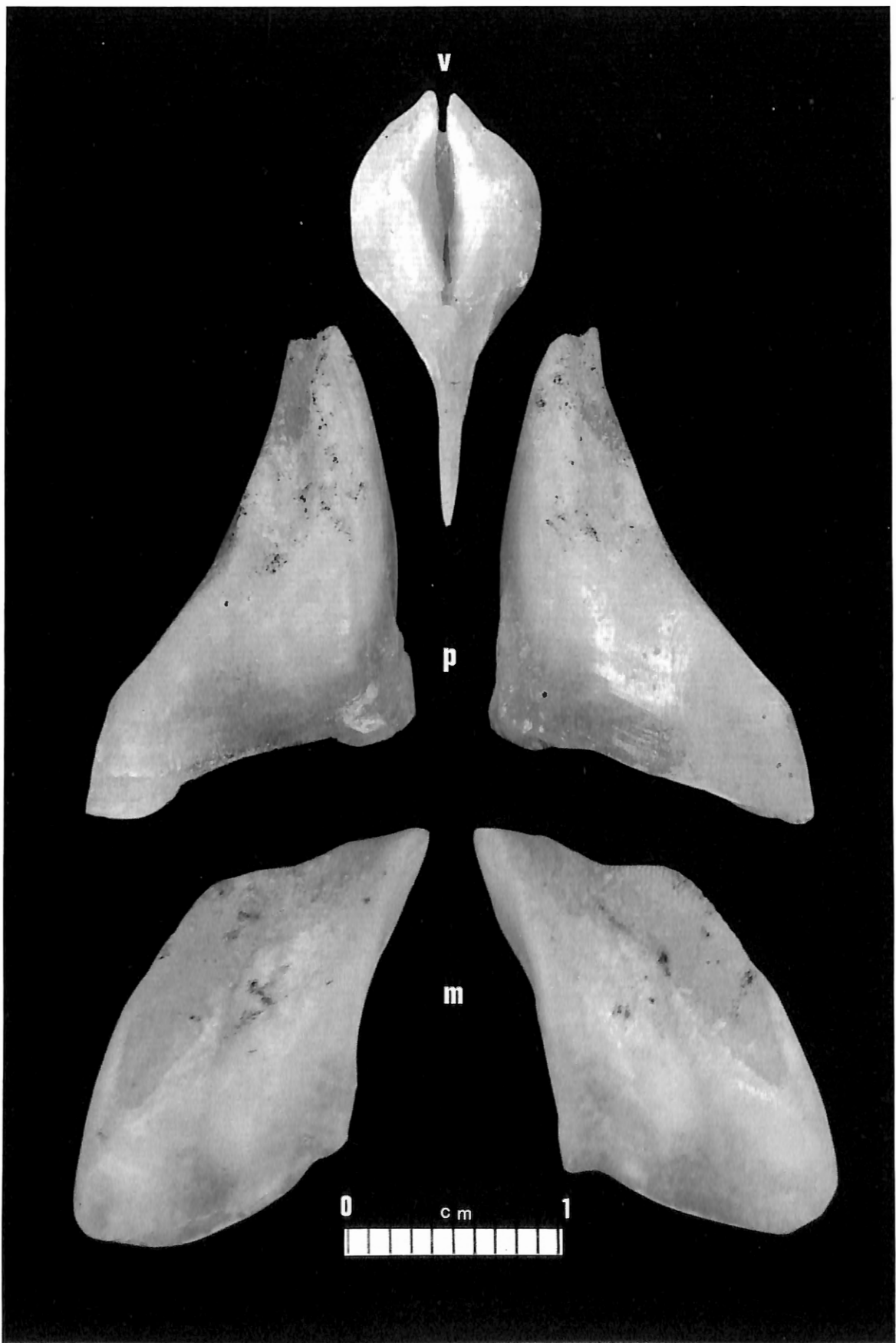


Plate 5. *Callorhynchus capensis* DUMERIL, 1865. Male, estimated total length circa 70 cm, False Bay, South Africa. Coll. P.COUPATEZ. Tooth plates, mandibulars (m), palatals (p) and vomerines (v); the last one are in position on their cartilagineous support.

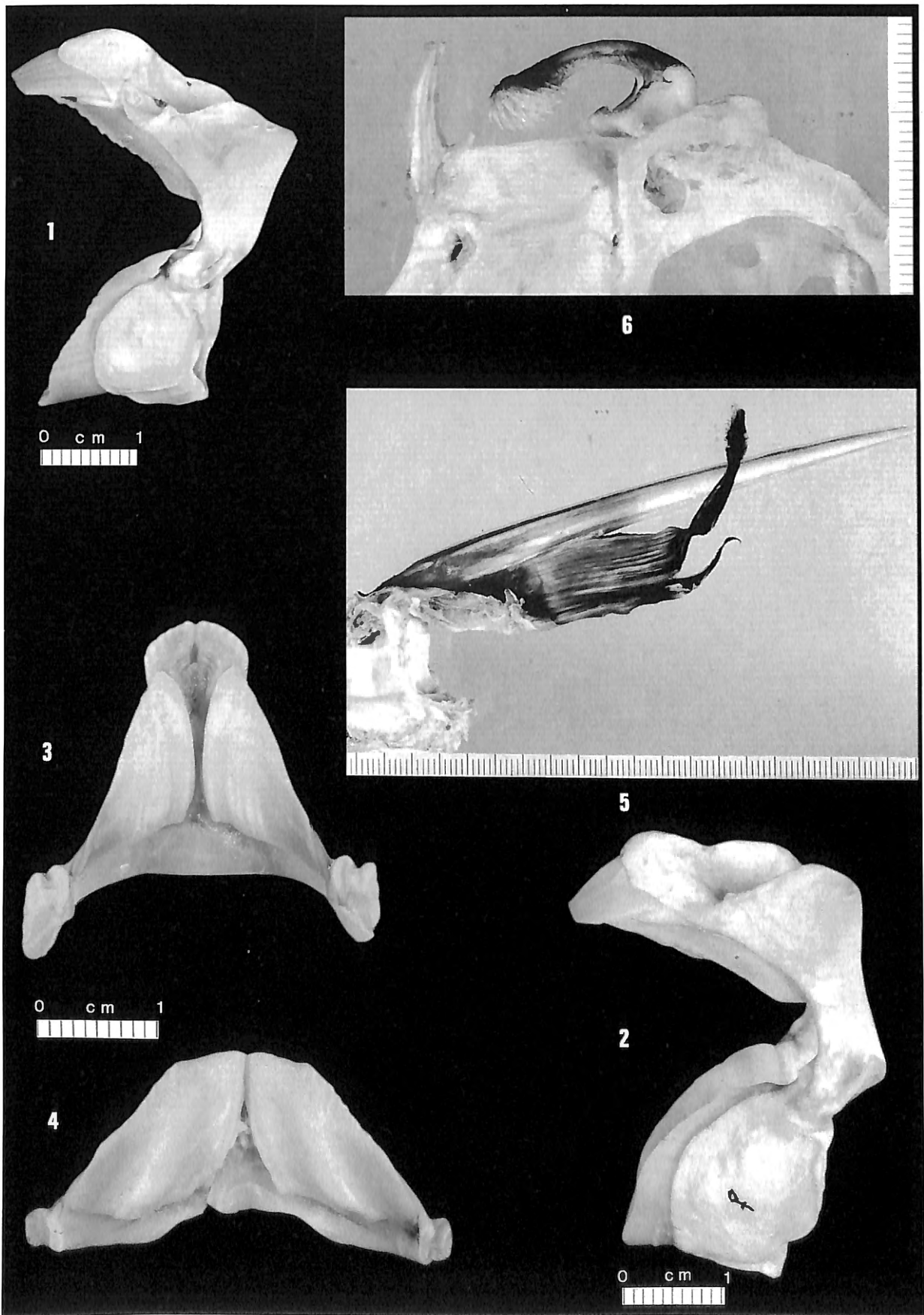


Plate 6. *Chimaera monstrosa* LINNAEUS, 1758. Left side view of the jaws of a male circa 85 cm t.l. (fig.1) and a female circa 95 cm t.l. (fig.2), both from Porcupine Bank, Ireland, upper (fig.3) and lower (fig.4) jaw of a male circa 80 cm t.l. Porcupine Bank, Ireland, first dorsal fin spine and fin of the same male (fig.5) and detail of the frontal *tenaculum* of the same male (fig.6).

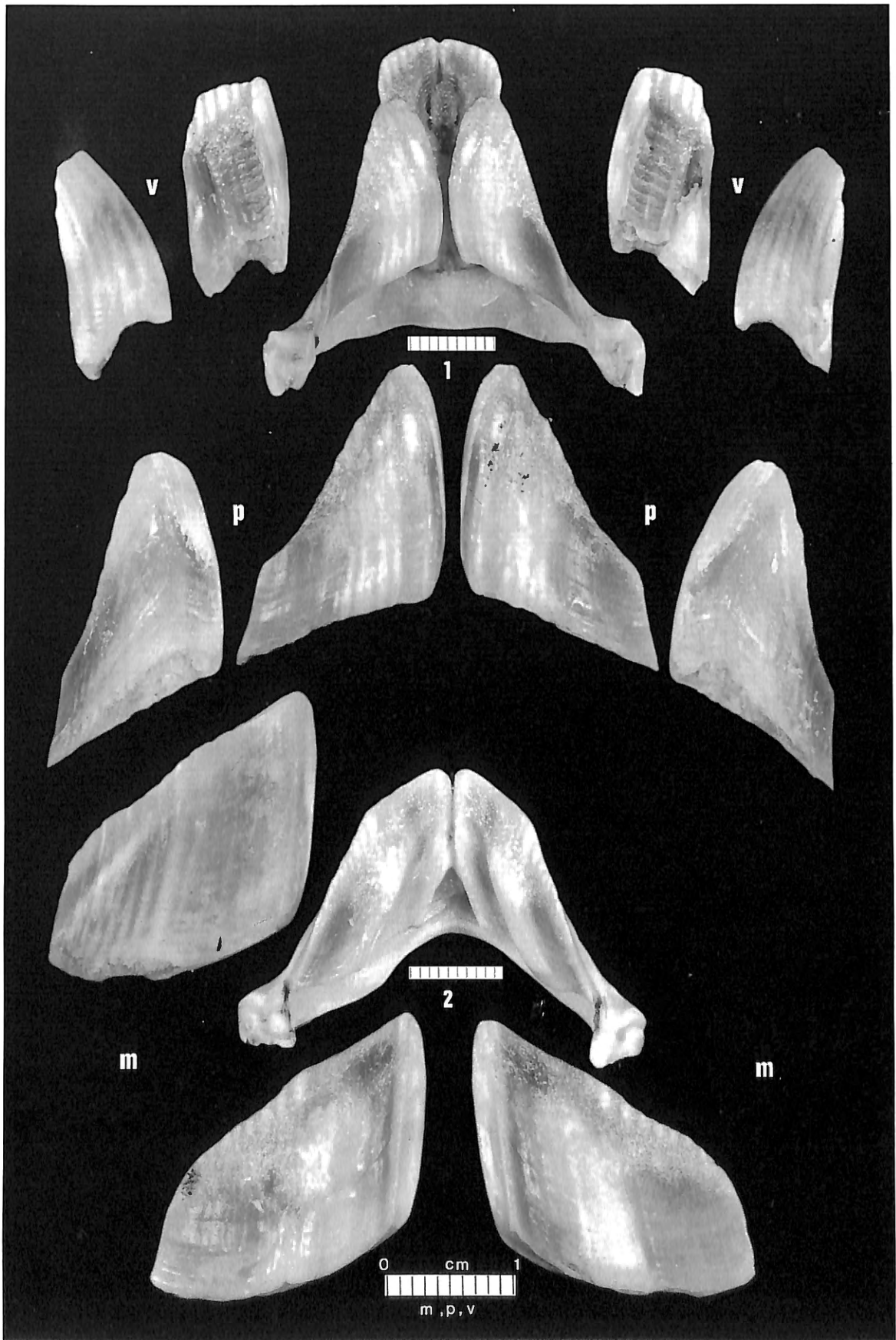


Plate 7. *Chimaera monstrosa* LINNAEUS, 1758. Female circa 100 cm t.l., West Flugga, North East Atlantic, Upper (fig.1) and lower (fig.2) jaws, with details of both lingual or functional, and labial plus attachment surface of their respective vomerine (v), palatine (p) and mandibular (m) dental plates.

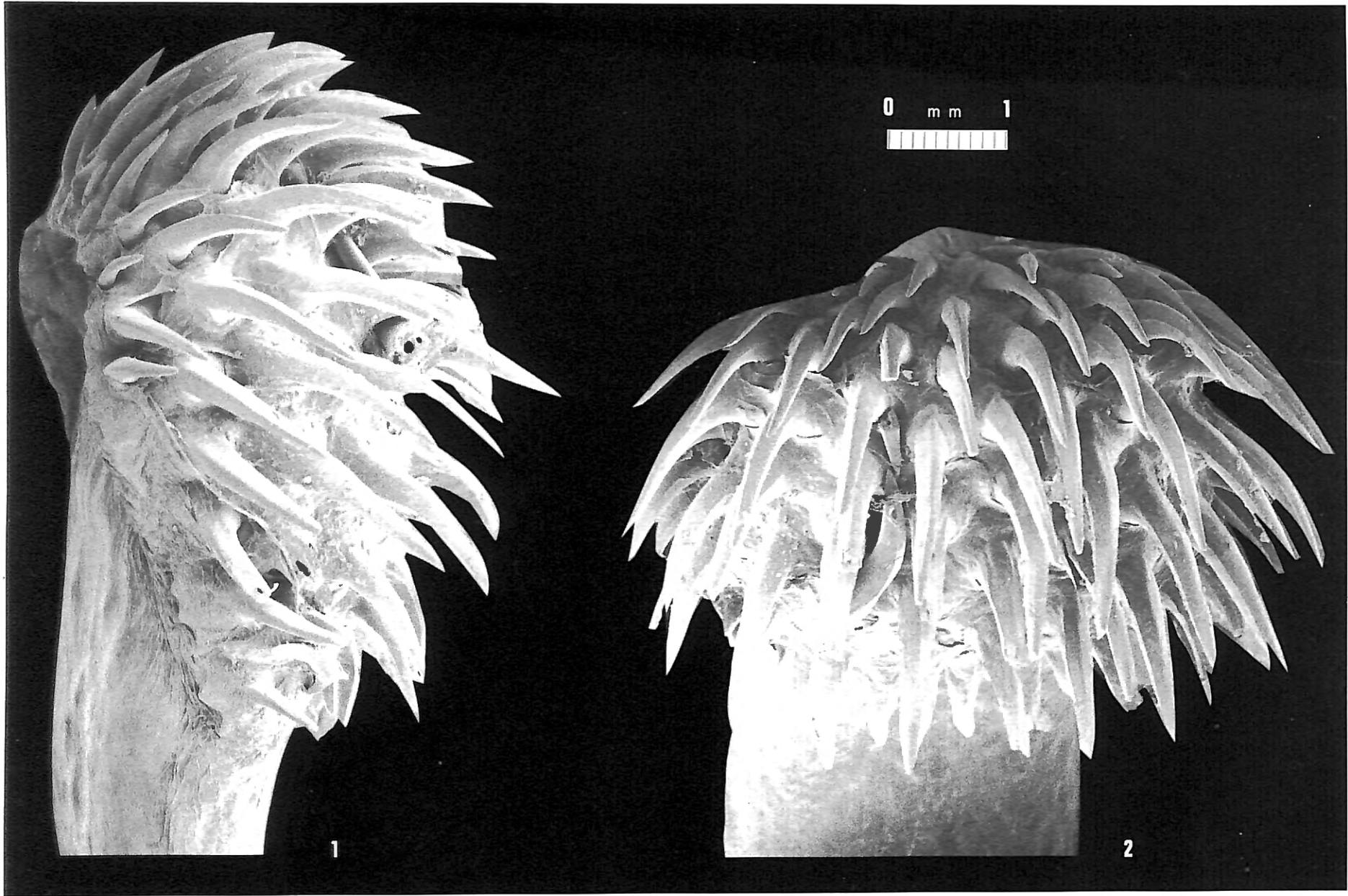


Plate 8. *Chimaera monstrosa* LINNAEUS, 1758. Male circa 30 cm t.l., Southeast Rona, North East Atlantic. Right (fig.1) and front (fig.2) views of the frontal *tenaculum* head.

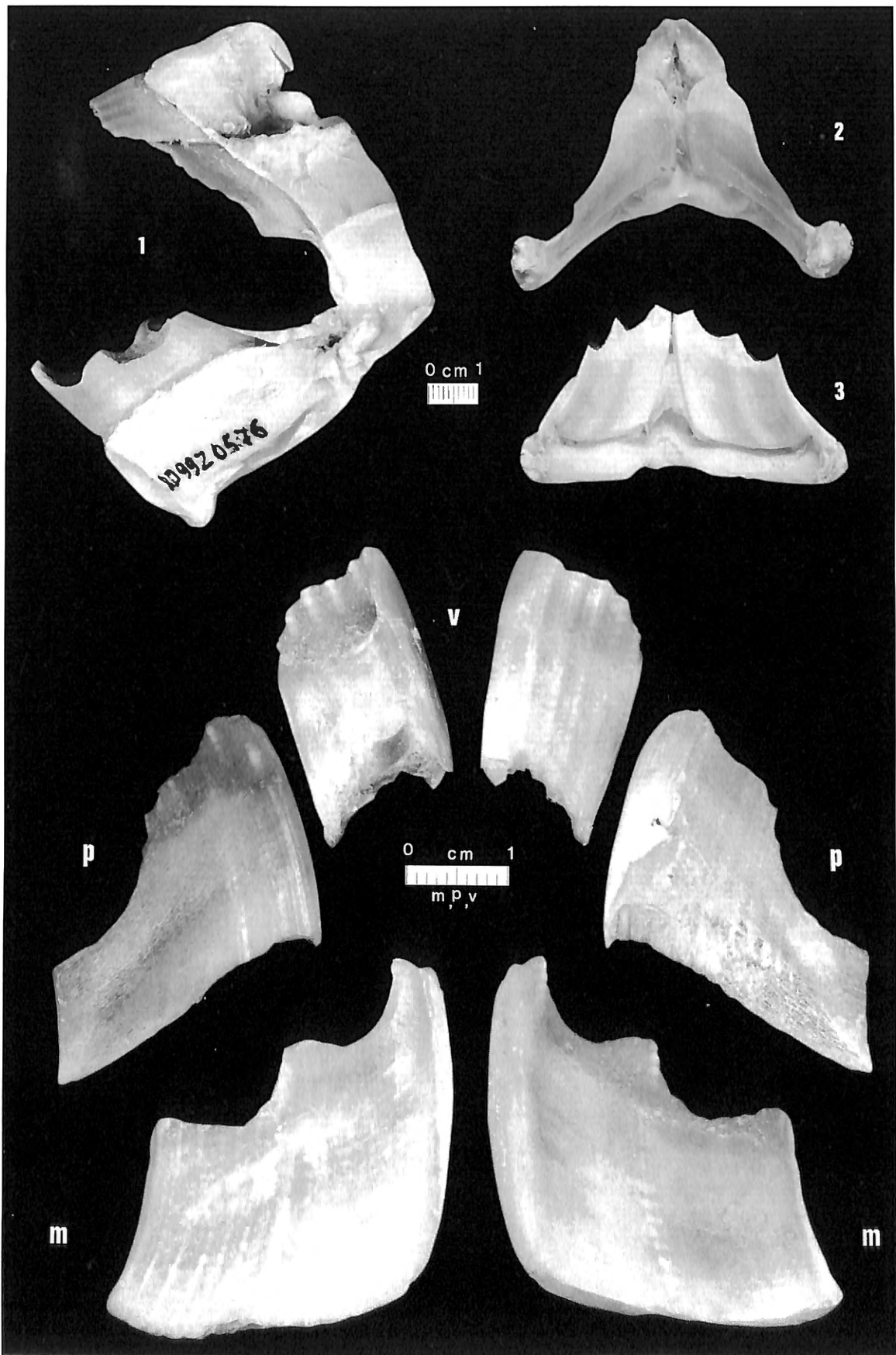


Plate 9. *Hydrolagus pallidus* HARDY & STEHMANN, 1990. Male circa 105 cm t.l., no precise locality data, «North East Atlantic». Left lateral view of the jaws (fig.1), inner view of upper (fig.2) and lower (fig.3) jaws. Lingual and labial views of the three right dental plates (v, p, m).



Plate 10. *Hydrolagus pallidus* HARDY & STEHMANN, 1990. Female circa 120 cm t.l., no precise locality data „North East Atlantic». Left lateral view of the jaws (fig.1), inner view of upper (fig.2) and lower (fig.3) jaws. Lingual and labial views of the three left dental plates (v, p, m).

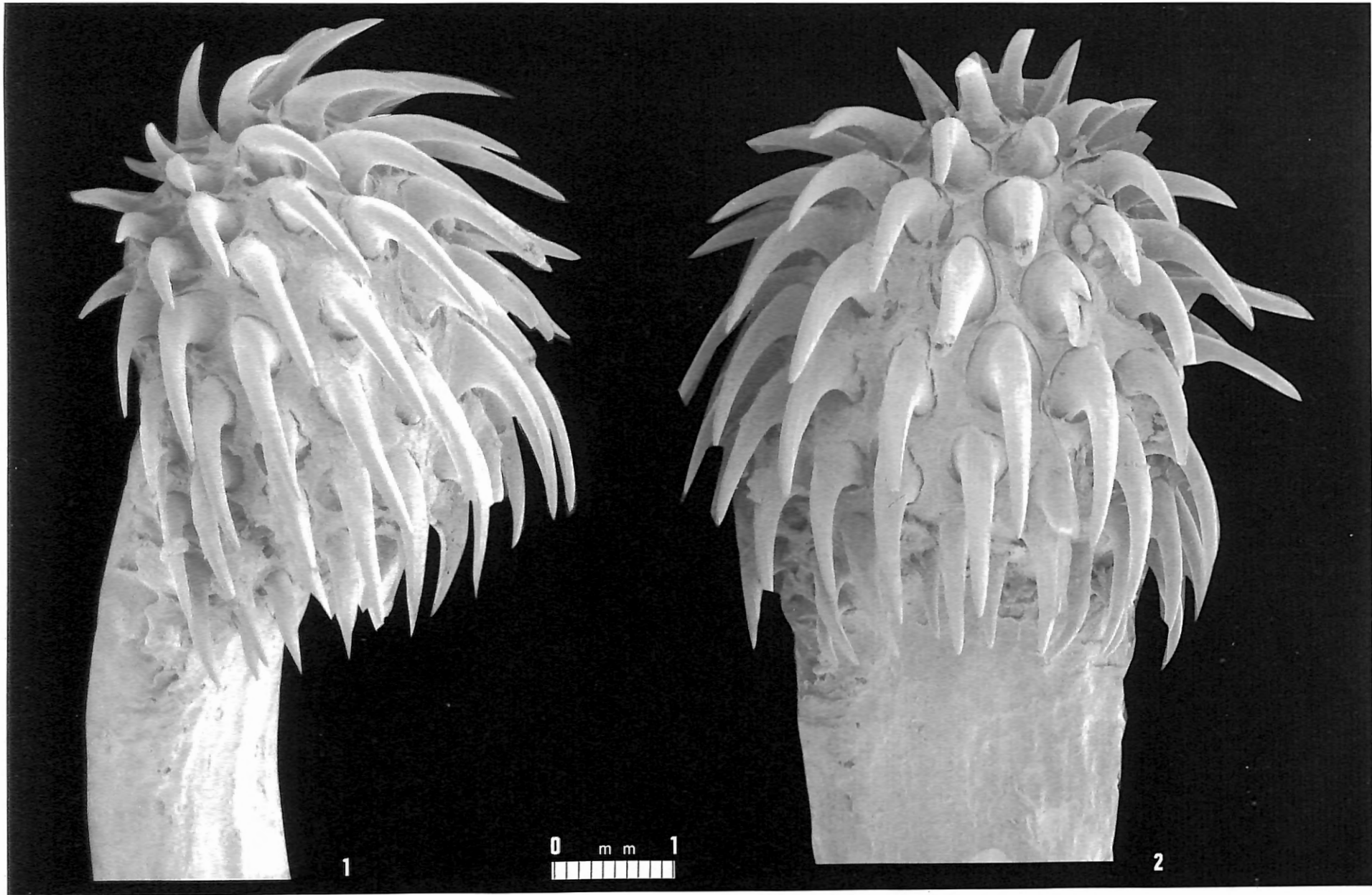


Plate 11. *Hydrolagus mirabilis* (COLLETT, 1904). Male circa 75 cm t.l., no precise locality data, «North East Atlantic». Right lateral (fig.1) and front (fig.2) views of the frontal *tenaculum* head.

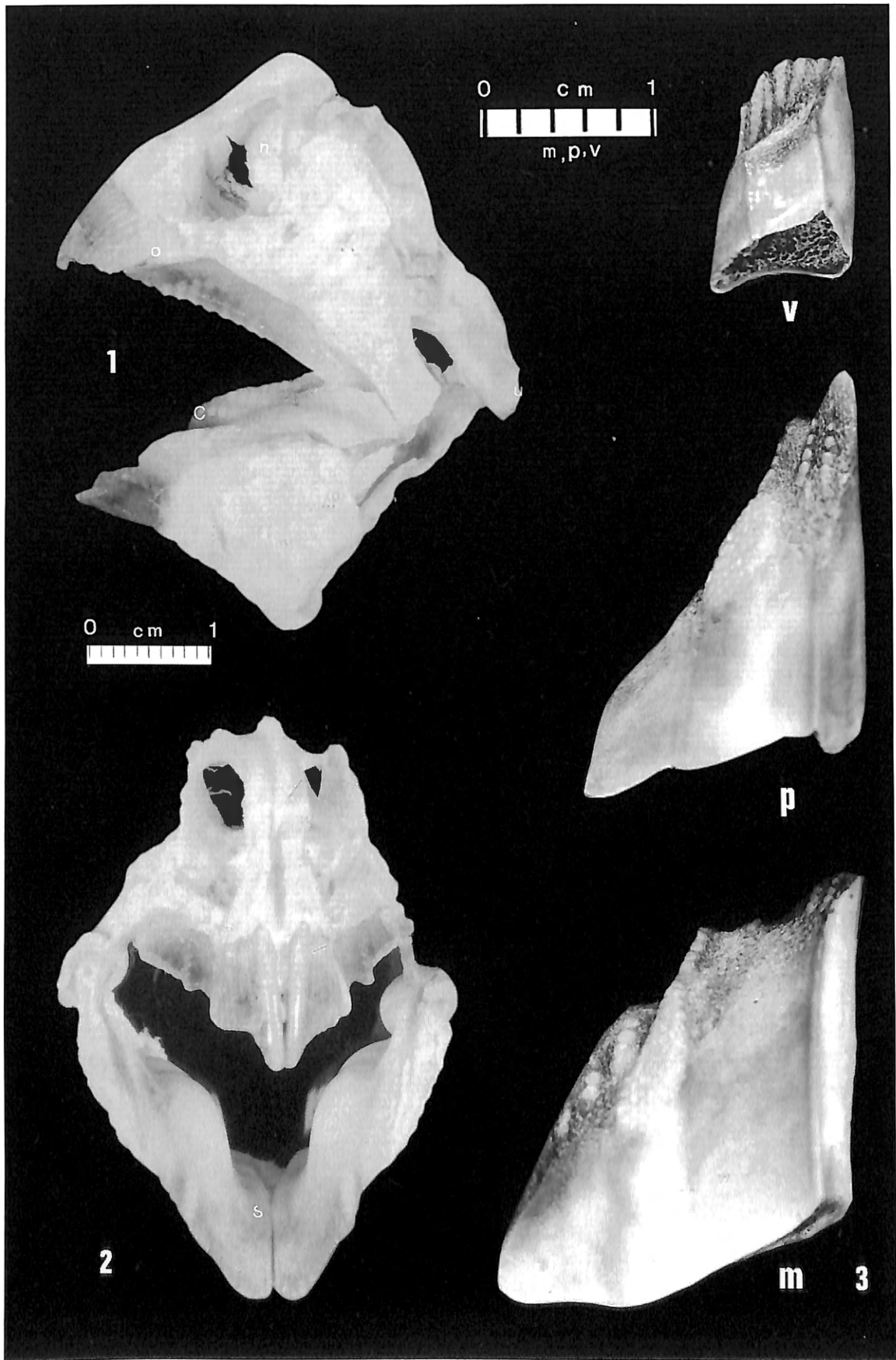


Plate 12. *Hariotta raleighana* GOODE & BEAN, 1895. Male circa 80 cm t.l., no precise locality data, «North East Atlantic». Left lateral (fig.1) and facial views (fig.2) of part of the skull. Lingual views of right vomerine (v) and palatine (p) dental plates and lingual view of the left mandibular (m) dental plate. Specimen ANSP 177811, «off New Zealand».

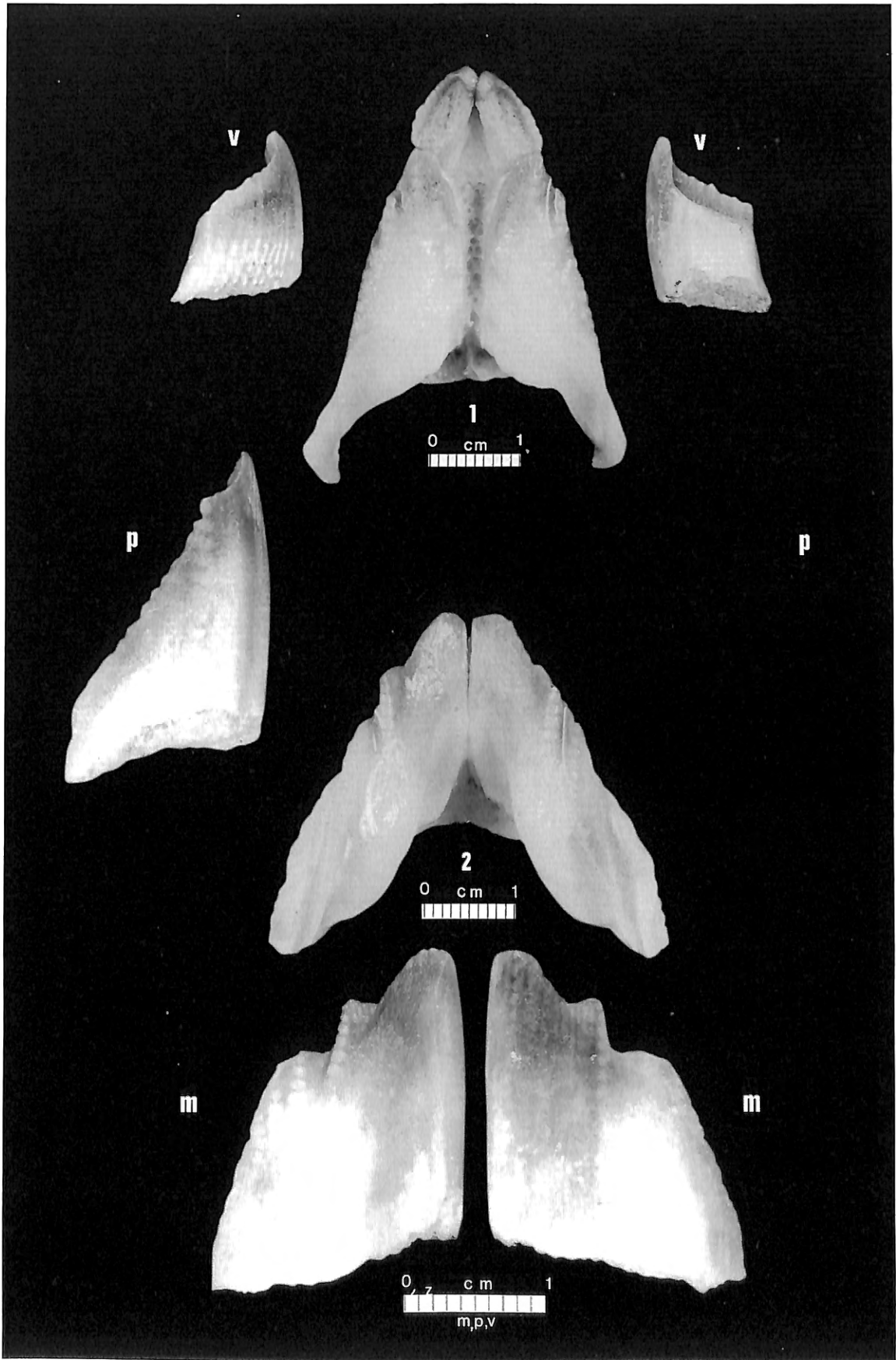


Plate 13. *Hariotta raleighana* GOODE & BEAN, 1895. Female circa 90 cm t.l., no precise locality data, "North East Atlantic".
 Inner view of upper (fig.1) and lower jaws (fig.2). Lingual (functional) and labial views of the three left dental plates (**v**, **p**, **m**).

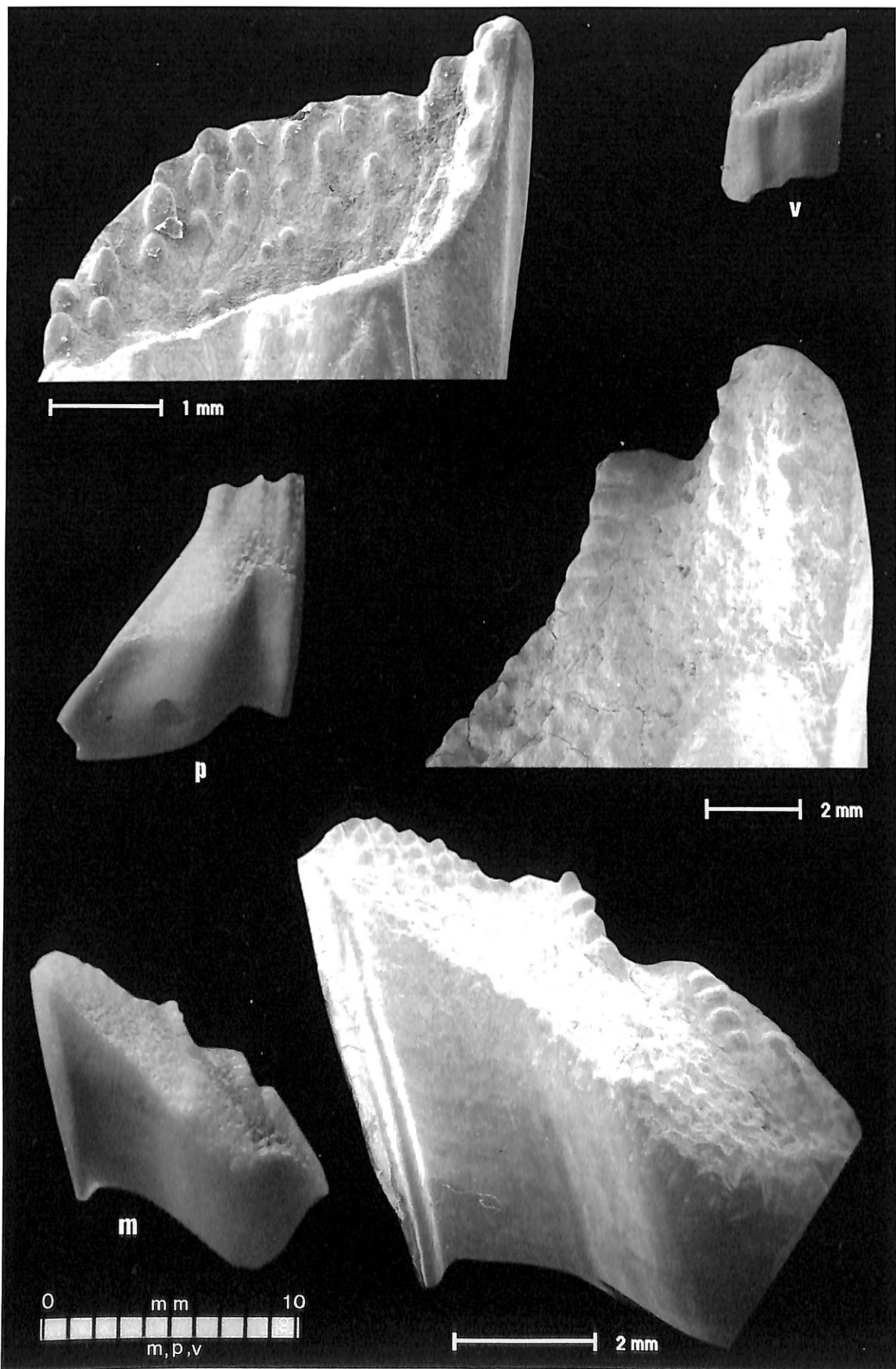


Plate 14. *Neohariotta punila* DIDIER & STEHMANN, 1996. Paratype, off Socotra Island. ANSP 172538, Stat. 2565, cr. 17 R/V *Vityaz*, 1000-1120 m depth. Lingual or functional face of the three dental plates, macrophotos and SEM magnification illustrations.

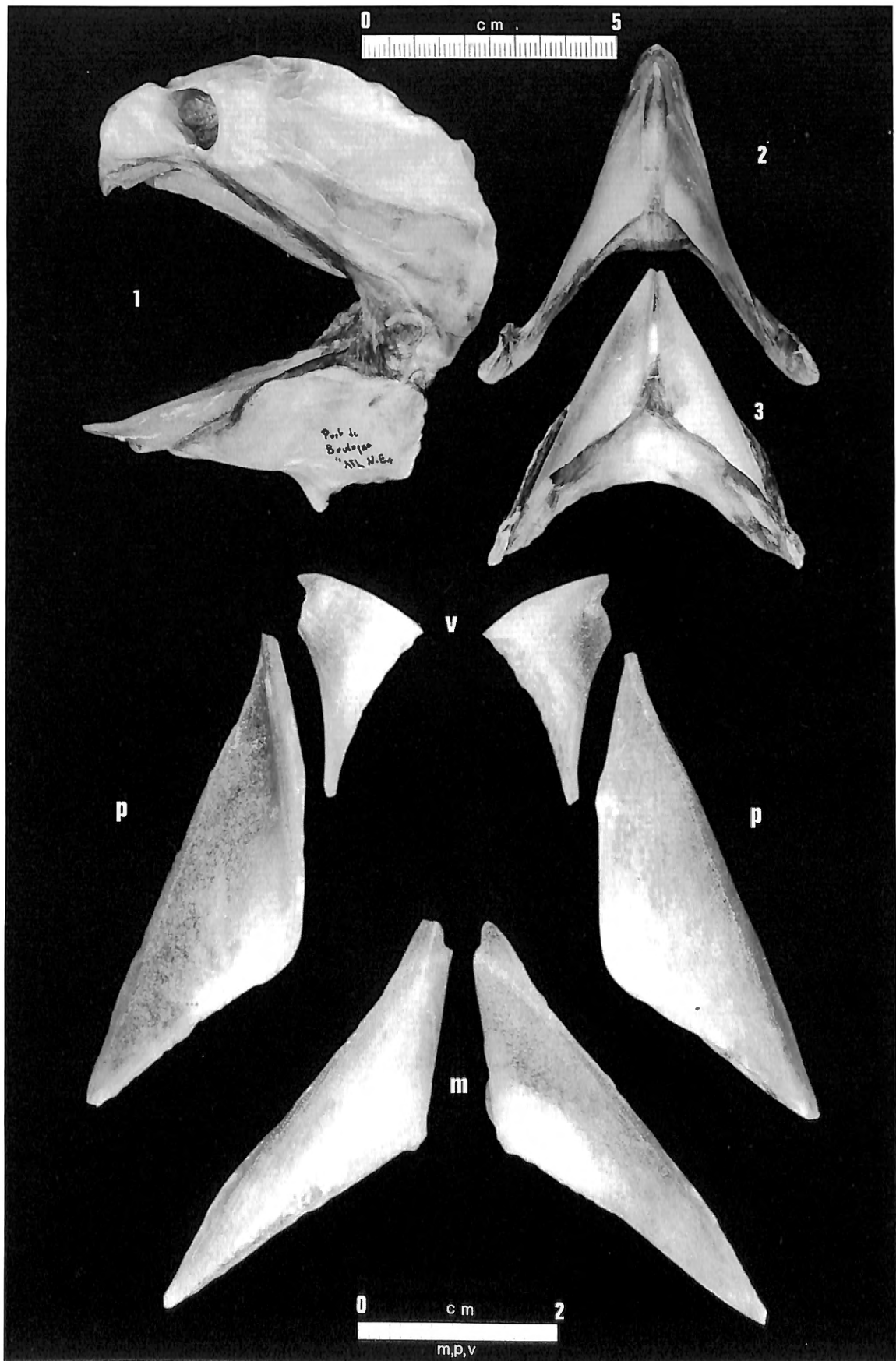


Plate 15. *Rhinochimaera atlantica* HOLT & BYRNE, 1909. Female circa 130 cm t.l., South Lousy Bank, North East Atlantic. Left lateral view of the skull (fig.1). Lingual or functional and labial views of the three dental plates of a female specimen circa 120 cm t.l. (Boulogne Fishharbour).

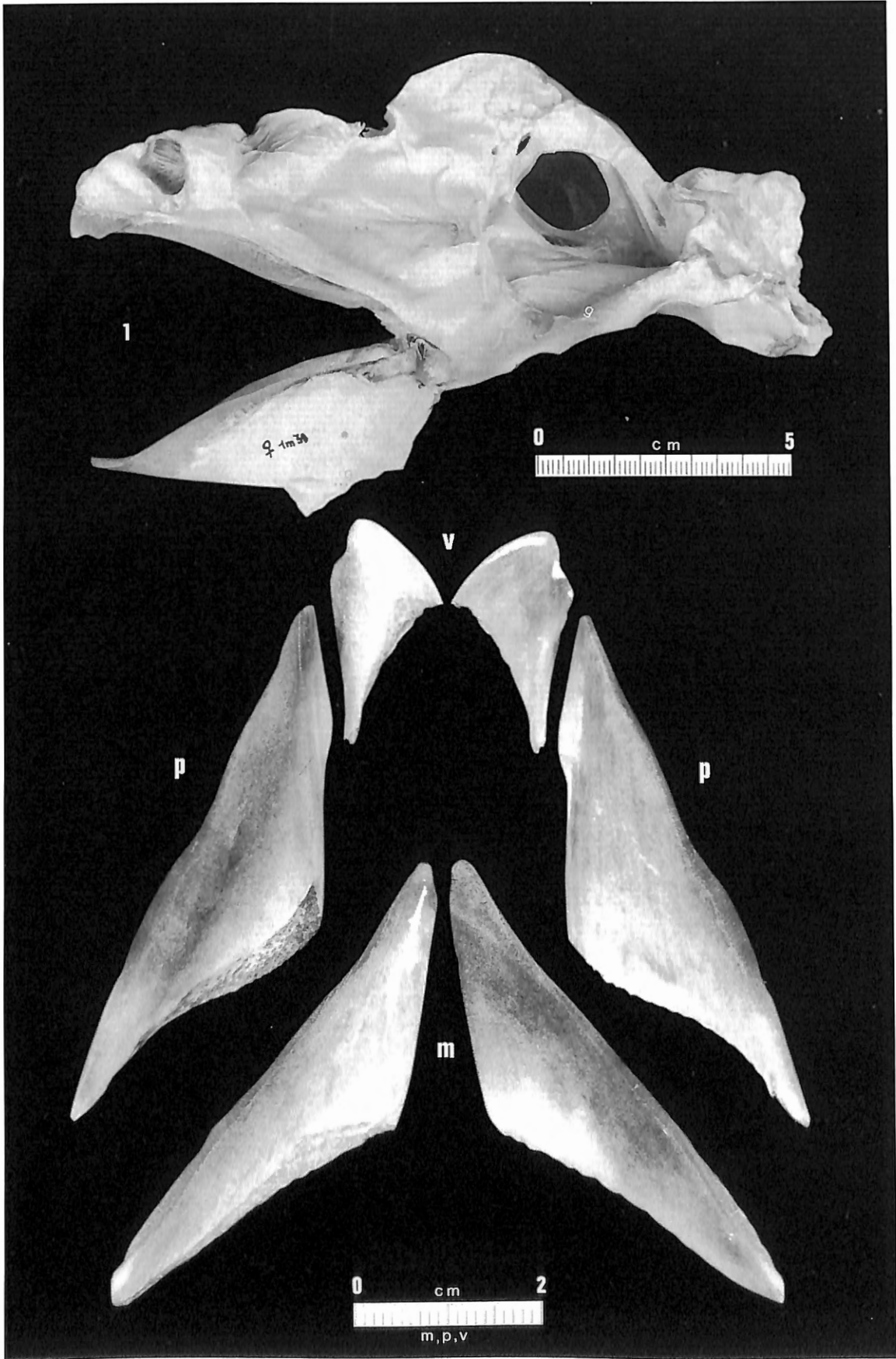


Plate 16. *Rhinochimaera atlantica* HOLT & BYRNE, 1909. Male circa 110 cm t.l., no precise data of locality, «North East Atlantic». Left lateral view of the jaws (fig.1). Male circa 105 cm t.l., Hatton Bank. North East Atlantic. Lingual or functional and labial views of the three dental plates (v, p, m).

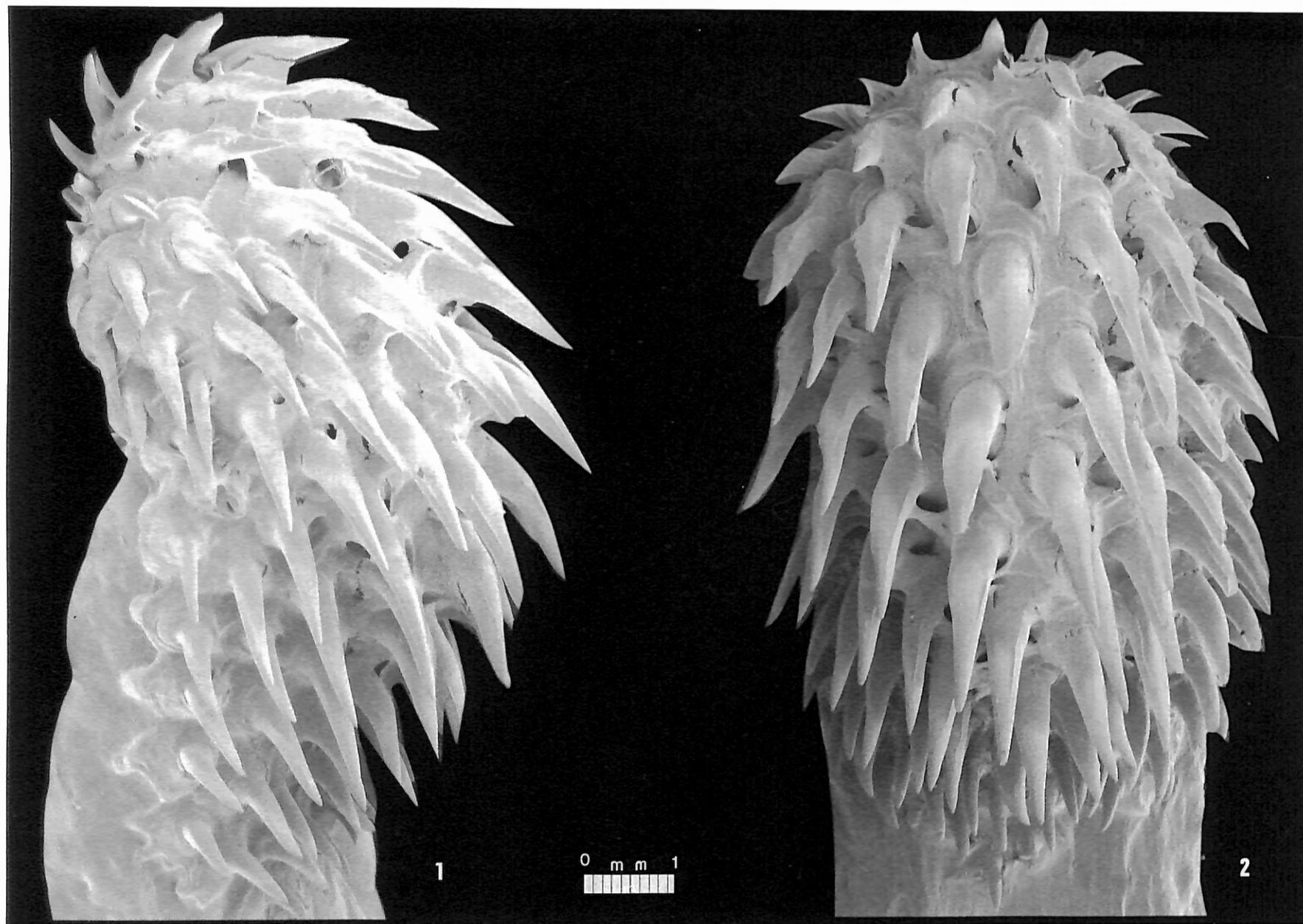


Plate 17. *Rhinochimaera atlantica* HOLT & BYRNE, 1909. Male circa 105 cm t.l., Hatton Bank North East Atlantic. Right lateral (fig.1) and front (fig.2) views of the frontal *tenaculum* head.

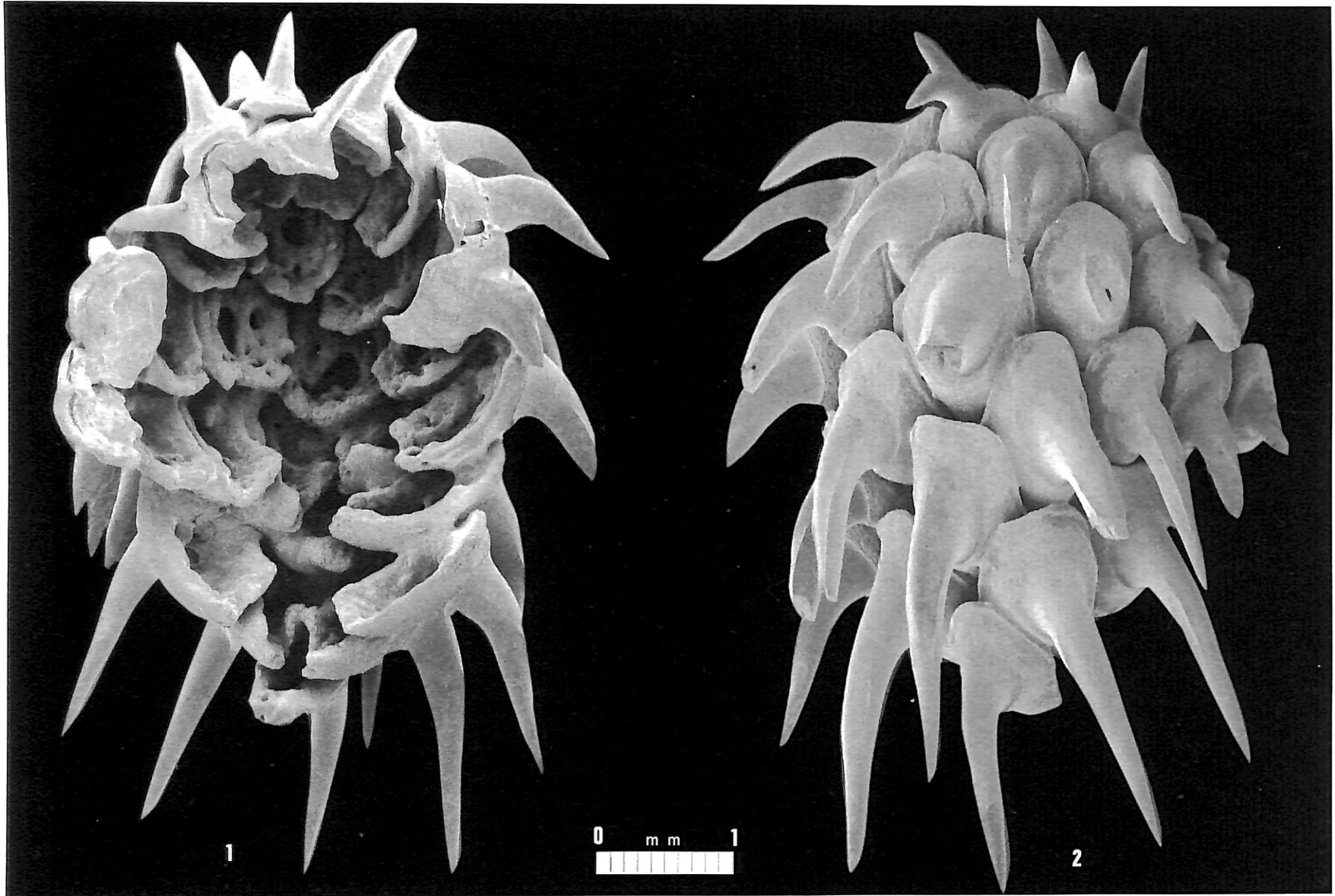


Plate 18. *Rhinochimaera atlantica* HOLT & BYRNE, 1909. Male circa 105 cm t.l., Hatton Bank North East Atlantic. Inner (fig.1) and outer (fig.2) views of the frontal *tenaculum* head after removing both cartilage and fleshy attachment with single bacterial help.

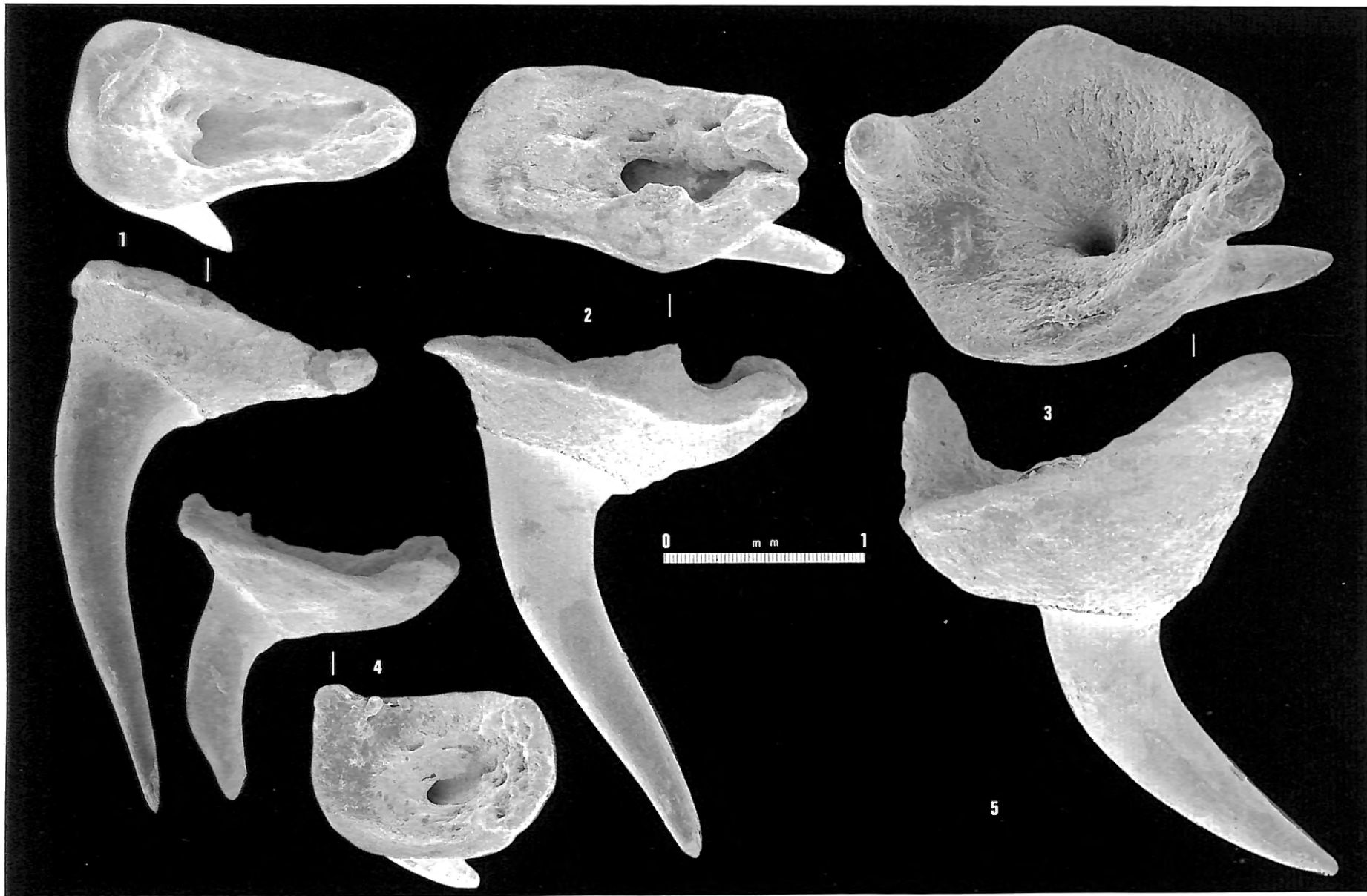


Plate 19. *Rhinochimaera atlantica* HOLT & BYRNE, 1909. Male circa 105 cm t.l., Hatton Bank North East Atlantic. Basal or radicular and lateral views of some of the tooth-like dermal denticles of the frontal *tenaculum* head.



Plate 20. Lateral view of the frontal *tenaculum* (fig.1), magnification x3; left lateral and front views of the *tenaculum* head (figs. 2a and 2b); lateral view of the first dorsal fin spine (fig.3), magnification X2.