BULLETIN DE L'INSTITUT ROYAL DES SCIENCES NATURELLES DE BELGIQUE, BIOLOGIE, 73: 5-26, 2003
BULLETIN VAN HET KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPPEN, BIOLOGIE, 73: 5-26, 2003

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

Editor: M. STEHMANN

Part A: Selachii. Addendum to 1: Order Hexanchiformes - Family Hexanchidae, 2: Order Carcharhiniformes, 2a: Family Triakidae, 2b: Family Scyliorhinidae, 2c: Family Carcharhinidae, Hemigaleidae, Leptochariidae, Sphyrnidae, Proscylliidae and Pseudotriakidae , 3: Order Squaliformes: Family Echinorhinidae , Oxynotidae and Squalidae. Tooth vascularization and phylogenetic interpretation.

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

59640

Abstract

In the early issues of this series, tooth vascularization was not incorporated in the descriptions. This addendum provides the illustrations and descriptions of the tooth vascularization of the taxa in Part A: No.1 Hexanchidae, No.2a Triakidae, No.2b Scyliorhinidae, No.2c Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae and Carcharhinidae and No.3 Squalidae of this series. Moreover, tooth vascularization in combination with morphology and fossil records is validated for interpretation of phylogenetic interrelationships, and a hypothetical systematic review is given for the taxa concerned.

Key-words: Elasmobranchii – Selachii – Hexanchiformes – Carcharhiniformes – Squaliformes – tooth vascularization – phylogenetic hypothesis.

Résumé

Dans les premiers fascicules de cette série, la vascularisation dentaire ne fut pas associée à la description de la morphologie dentaire. Cet addendum fournit description et illustration de la vascularisation dentaire des taxa concernant les fascicules suivants de la Partie A : N°.1Hexanchidae, N°.2a Triakidae, N°.2b Scyliorhinidae, N°2c. Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae and Carcharhinidae, and N°.3 Squalidae. En outre, la vascularisation dentaire en combinaison avec la morphologie et les données paléontologiques est proposée comme élément interprétatif potentiel des lignées phylogénétiques. Un examen systématique des taxa concernés basé sur les présentes observations histologiques permet d'avancer certaines hypothèses.

Mots-clés: Elasmobranchii – Selachii – Hexanchiformes – Squaliformes – vascularisation dentaire – hypothèses phylogenetiques .

Kurzfassung

Die innere Gefäss- und Nervenstruktur (Vaskularisierung) war in den anfänglichen Ausgaben dieser Serie nicht Bestandteil der Zahnbeschreibungen. Diese Ergänzungsausgabe bringt die Abbildungen und Beschreibungen zur inneren Zahn-Versorgungsstruktur der Taxa in Teil A: Nr.1 Hexanchidae, Nr.2a Triakidae, Nr.2b Scyliorhinidae, Nr.2c Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae und Carcharhinidae und Nr.3 Squalidae dieser Serie. Ferner wird dokumentiert, dass die Vaskularisierung der Zähne, in Kombination mit Zahnmorphologie und fossiele Funde, von Bedeutung ist für die Interpretation phylogenetischer Verwandtschaftsbeziehungen. Hierzu wird eine hypothetische Übersicht zur entsprechenden Systematik der betroffenen Taxa präsentiert.

Schlüsselwörter: Elasmobranchii – Selachii – Hexanchiformes – Carcharhiniformes – Squaliformes – Zahnvaskularisierung – phylogenetische Hypothesen.

Addendum to Part A: No.1 Hexanchidae, No.2a Triakidae, No.2b Scyliorhinidae, No.2c Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae and Carcharhinidae, and No.3 Squaliformes.

General introduction

In the early issues on sharks of this series of Part A, No.1 Hexanchidae, No.2a Triakidae, No.2b Scyliorhinidae, No.2c Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae and Carcharhinidae and No.3 Squalidae, tooth vascularization was not incorporated in the descriptions. This addendum provides with their tooth vascularization with a

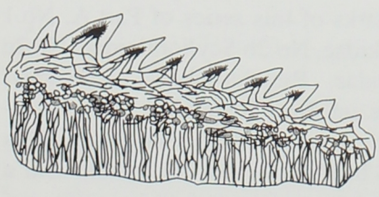
schematic drawing and a description of the tooth vascularization of the species concerned, as far as material was available for this research. Additionally, the Sphyrnidae are included as also carcharhiniform taxa. Material was available of the following taxa: Hexanchidae: *Heptranchias*, *Hexanchus* and *Notorhynchus*, Triakidae: *Furgaleus*, *Galeorhinus*, *Hemitriakis*, *Hypogaleus*, *Iago*, *Mustelus*, *Scylliogaleus*, *Triakis*, Scyliorhinidae: *Apristurus*, *Asymbolus*, *Atelomycterus*, *Cephaloscyllium*, *Cephalurus*, *Galeus*, *Halaelurus*, *Haploblepharus*, *Holohalaelurus*, *Parmaturus*, *Pentanchus*, *Poroderma*, *Schroederichthys* and *Scyliorhinus*, Carcharhinidae: *Carcharhinus*, *Galeocerdo*, *Glyphis*, *Lamiopsis*, *Loxodon*, *Nasolamia*, *Negaprion*, *Prionace*, *Rhizoprionodon*, *Scoliodon* and *Triaenodon*, Hemigaleidae : *Chaenogaleus*, *Hemigaleus*, *Hemipristis* and *Paragaleus*, Leptocharidae: *Leptocharias*, Sphyrnidae: *Eusphyra* and *Sphyrna*, Proscylliidae: *Proscyllium*, *Eridacnis* and *Ctenacis*, Pseudotriakidae: *Pseudotriakis*, Family Echinorhinidae: *Echinorhinus*, Oxynotidae: *Oxynotus* and Squalidae: *Centrophorus*, *Centroscyllium*, *Centroscymnus*, *Dalatias*, *Deania*, *Etmopterus*, *Isistius*, *Scymnodon*, *Somniosus*, *Squaliolus* and *Squalus*.
Tooth vascularization is used here for an interpretation of phylogenetic interrelationships and a hypothetical systematic review is given for the taxa concerned to be taken in account in future systematic research.
The vascularization canals have been made visible by soaking in anise oil a thin section of the tooth thus becoming translucent.
For the terminology used here see HOVESTADT & HOVESTADT-EULER (1993).

Part A: No.1 Hexanchidae

This family is subdivided into the genera *Heptranchias*, *Hexanchus* and *Notorhynchus*.

Genus *Heptranchias* RAFINESQUE, 1810
Heptranchias perlo (BONNATERRE, 1788)

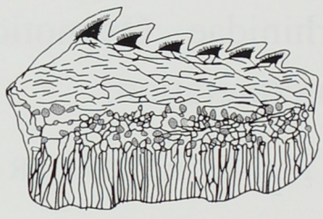
The entire midsection of the tooth shows a band of relatively large osteons, from which vertical, more or less parallel canals pierce the lower root part and end at the inner face of the root as an opening to the vascular system outside.
Above the midsection, the osteons become narrow to form a reticulated system of more or less horizontal canals. This system is connected to remains of separate triangular-shaped pulp cavities in each mesial cusplet of the crown. These cavities are more or less filled with osteodentine. From these cavities numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusplets.



Textfigure 1: *Heptranchias*

Genus *Hexanchus* RAFINESQUE, 1810
Hexanchus griseus (BONNATERRE, 1788)

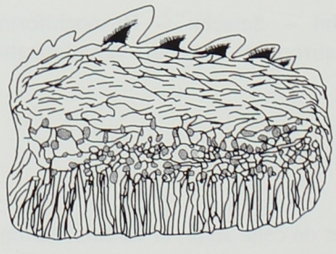
The entire midsection of the tooth shows a band of relatively large osteons, from which vertical, more or less parallel canals pierce the lower root part and end at the inner face of the root as an opening to the vascular system outside.
Above the midsection, the osteons become narrow to form a reticulated system of more or less horizontal canals. This system is connected to separate triangular-shaped pulp cavities in each mesial cusplet of the crown. From these cavities, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusplets.



Textfigure 2: *Hexanchus*

Genus *Notorhynchus* AYRES, 1855
Notorhynchus cepedianus (PERON, 1807)

The entire midsection of the tooth shows a band of relatively large osteons, from which vertical, more or less parallel canals pierce the lower root part and end at the inner face of the root as an opening to the vascular system outside.
Above the midsection, the osteons become narrow to form a reticulated system of more or less horizontal canals. This system is connected to separate triangularl-shaped pulp cavities in each mesial cusplet of the crown. From these cavities numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusplets.



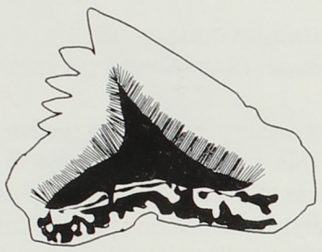
Textfigure 3: *Notorhynchus*

Part A: No.2a Triakidae

This family comprises the genera *Furgaleus*, *Galeorhinus*, *Gogolia*, *Hemitriakis*, *Hypogaleus*, *Iago*, *Mustelus*, *Rhinotriacis*, *Scylliogaleus* and *Triakis*.
The following species were selected to represent the tooth vascularization of these genera: *Furgaleus macki*, *Galeorhinus galeus*, *Hemitriakis japanica*, *Hypogaleus hyugaensis*, *Iago omanensis*, *Mustelus mustelus*, *Rhinotriacis henlei*, *Scylliogaleus quecketti* and *Triakis semifasciata*. Material of *Gogolia* was not available for histological examination.

Genus *Furgaleus* WHITLEY, 1951
Furgaleus macki (WHITLEY, 1943)

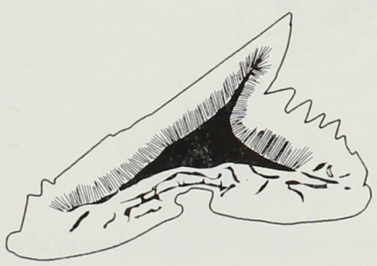
The root shows a coarse, reticulated system of relatively large osteons. This system is connected to a relatively large, more or less triangularl-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the mesial cusplets.



Textfigure 4:
Furgaleus

Genus *Galeorhinus* BLAINVILLE, 1816
Galeorhinus galeus (LINNAEUS, 1758)

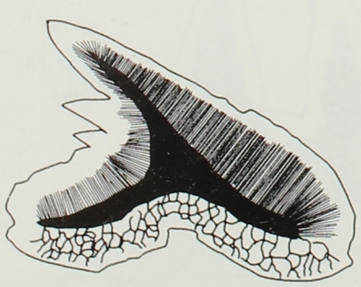
The root shows a coarse, reticulated system of relatively narrow osteons. This system is connected to a relatively large, more or less triangularl-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the mesial cusplets.



Textfigure 5:
Galeorhinus

Genus *Hemitriakis* HERRE, 1923
Hemitriakis japanica (MULLER & HENLE, 1839)

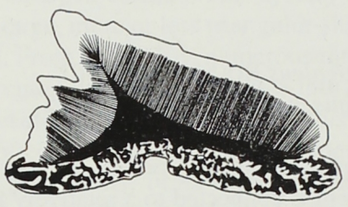
The root shows a fine, reticulated system of relatively narrow osteons. This system is connected to a relatively large, more or less triangularl-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the mesial cusplets.



Textfigure 6:
Hemitriakis

Genus *Hypogaleus* SMITH, 1957
Hypogaleus hyugaensis (MIYOSI, 1939)

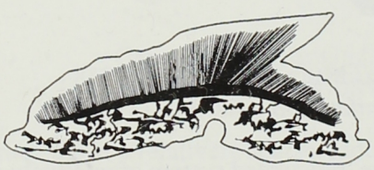
The root shows a fine, reticulated system of relatively narrow osteons that become courser toward the mesial and distal margins. The system is connected to a relatively large, more or less triangular- shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the mesial cusplets.



Textfigure 7:
Hypogaleus

Genus *Iago* COMPAGNO & SPRINGER, 1971
Iago omanensis (NORMAN, 1939)

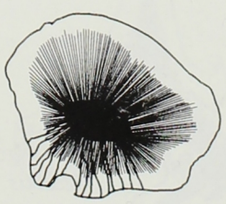
The root shows a fine, reticulated system of relatively narrow osteons. This system is connected to a relatively large, low pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 8:
Iago

Genus *Mustelus* LINCK, 1790
Mustelus mustelus (LINNAEUS, 1758)

The root shows a fine, reticulated system of relatively narrow osteons. This system is connected to a relatively large, more or less circular pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the crown.



Textfigure 9:
Mustelus

Genus *Rhinotriacis* GILL, 1863
Rhinotriacis henlei GILL, 1863

The root shows a coarse reticulated system of relatively large osteons. This system is connected to a relatively small, more or less irregularly shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar

dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp cusp.

Textfigure 10:
Rhinotriacis

Genus *Scylliogaleus* BOULENGER, 1902
Scylliogaleus quecketti BOULENGER, 1902

The root shows a coarse, reticulated system of relatively large osteons. This system is connected to a relatively large, more or less low pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.

Textfigure 11:
Scylliogaleus

Genus *Triakis* MULLER & HENLE, 1838
Triakis semifasciata (GIRARD, 1854)

The root shows a coarse, reticulated system of relatively narrow osteons. This system is connected to a relatively narrow, more or less low pulp cavity, with a narrow, but elongated central canal toward the apex of the principal cusp of the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Another narrow but elongated protrusion is directed toward each lateral cusplet at the mesial and distal margins of the pulp cavity. From these protrusions, tiny parallel canaliculi radiate into each cusplet.

Textfigure 12:
Triakis

Part A: No.2b Scyliorhinidae

This family comprises the genera *Apristurus*, *Asymbolus*, *Atelomycterus*, *Aulohalaelurus*, *Cephalurus*, *Cephaloscyllium*, *Galeus*, *Halaelurus*, *Haploblepharus*, *Holohalaelurus*, *Parmaturus*, *Pentanchus*, *Poroderma*, *Schroederichthys* and *Scyliorhinus*. The teeth of the following species represent these genera respectively: *Apristurus laurussoni*, *Asymbolus vincenti*, *Atelomycterus marmoratus*, *Cephalurus cephalus*, *Cephaloscyllium isabellum*, *Galeus melastomus*, *Halaelurus canescens*, *Haploblepharus edwardsii*, *Holohalaelurus regani*, *Parmaturus pilosus*, *Pentanchus profundicolus*, *Poroderma pantherinum*, *Schroederichthys maculatus* and *Scyliorhinus canicula*. Material of *Aulohalaelurus* was not available for histological examination.

Genus *Apristurus* GARMAN, 1913
Apristurus laurussoni (SAEMUNSSON, 1922)

The root shows a relatively coarse, reticulated system of relatively narrow osteons. This system is connected to a relatively narrow, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Another narrow, moderately elongated canal is directed toward each lateral cusplet at the mesial and distal margins of the pulp cavity. From these canals, tiny parallel canaliculi radiate into each cusplet.

Textfigure 13:
Apristurus

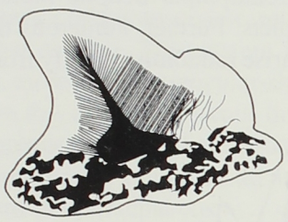
Genus *Asymbolus* WHITLEY, 1939
Asymbolus vincenti (ZEITZ, 1908)

The root shows a relatively coarse, reticulated system of relatively narrow osteons. This system is connected to a relatively short, more or less triangular-shaped pulp cavity with the ower lateral angles extended. A central elongated canal runs from the pulp cavity toward the apex of the crown. From the cavity and the central canal, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the mesial cusplets.

Textfigure 14:
Asymbolus

Genus *Atelomycterus* GARMAN, 1913
Atelomycterus marmoratus (BENNETT, 1830)

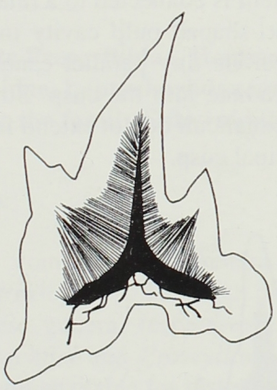
The root shows a relatively fine, reticulated system of relatively large osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 15:
Atelomycterus

Genus *Cephalurus* BIGELOW & SCHROEDER, 1941
Cephalurus cephalus (GILBERT, 1892)

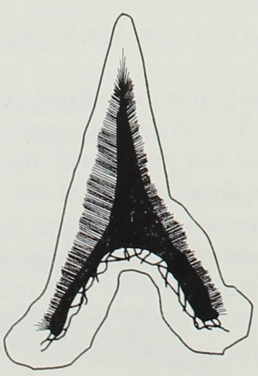
The root shows a relatively coarse, reticulated system of relatively narrow osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 16:
Cephalurus

Genus *Cephaloscyllium* GILL, 1862
Cephaloscyllium isabellum (BONNATERRE, 1788)

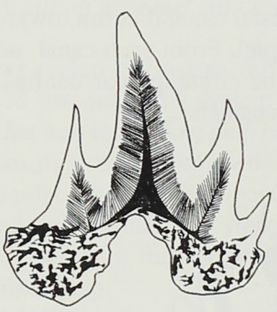
The root shows a relatively coarse, reticulated system of relatively narrow osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 17:
Cephaloscyllium

Genus *Galeus* RAFINESQUE, 1810
Galeus melastomus RAFINESQUE, 1810

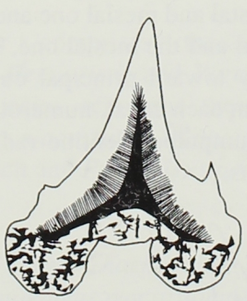
The root shows a relatively fine, reticulated system of relatively enlarged osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into principal cusp and cusplet. Another narrow but elongated canal runs from this the pulp cavity toward apex of each lateral cusplet at the mesial and distal margins of the pulp cavity. From these protrusions, tiny parallel canaliculi radiate into principal cusp and cusplet.



Textfigure 18:
Galeus

Genus *Halaelurus* GILL, 1862
Halaelurus canescens (GUNTHER, 1878)

The root shows a relatively coarse, reticulated system of relatively narrow osteons. This system is connected to a relatively large, more or less triangular-shaped pulp in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 19:
Halaelurus

Genus *Haploblepharus* GARMAN, 1913
Haploblepharus edwardsii (VOIGT, 1832)

The root shows a relatively fine, reticulated system of relatively enlarged osteons. This system is connected to a relatively large, more or less low pulp cavity that possesses one central, a distal and mesial canal that run toward the apex of

principal cusp and cusplet. From each canal, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the principal cusp and cusplets.

Textfigure 20:
Haploblepharus

Genus *Holohalaelurus* FOWLER, 1934
Holohalaelurus regani (GILCHRIST, 1922)

The root shows a relatively fine, reticulated system of relatively enlarged osteons. This system is connected to a relatively large, more or less low pulp cavity that possesses one central, a distal and mesial canal that run toward the apex of principal cusp and cusplet. From each canal, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the principal cusp and cusplets.

Textfigure 21:
Holohalaelurus

Genus *Parmaturus* GARMAN, 1906
Parmaturus pilosus GARMAN, 1906

The root shows a relatively fine, reticulated system of relatively enlarged osteons. This system is connected to a relatively large, more or less low pulp cavity that possesses five canals: a central one, a distal and mesial one and one each in between the central, distal and the mesial one. These canals run from the pulp cavity toward principal cusp and each cusplet, respectively. From each canal, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the principal cusp and cusplets.

Textfigure 22:
Parmaturus

Genus *Pentanchus* SMITH & RADCLIFFE, 1912
Pentanchus profundicolus SMITH & RADCLIFFE, 1912

The root shows a relatively fine, reticulated system of relatively enlarged osteons. This system is connected to a relatively large, more or less low pulp cavity that possesses five canals: a central one, a distal and mesial one and one each in between the central, distal and the mesial one. These canals run from the pulp cavity toward principal cusp and each cusplet, respectively. From each canal, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the principal cusp and cusplets. Further, numerous tiny, irregularly shaped canaliculi arise randomly directly from the pulp.

Textfigure 23:
Pentanchus

Genus *Poroderma* SMITH, 1837
Poroderma pantherinum (SMITH, 1838)

The root shows a coarse, reticulated system of relatively large osteons. This system is connected to a relatively large, more or less triangularl-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.

Textfigure 24:
Poroderma

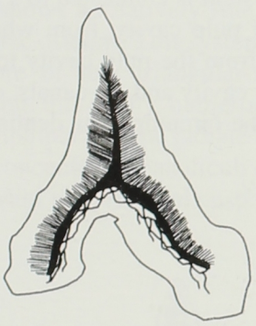
Genus *Schroederichthys* SPRINGER, 1966
Schroederichthys maculata SPRINGER, 1966

The root shows a relatively fine, reticulated system of relatively enlarged osteons. This system is connected to a relatively large, more or less low pulp cavity that possesses a central canal, as well as a distal and mesial one, These canals run from the pulp cavity toward principal cusp and each cusplet, respectively. From each canal, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the principal cusp and cusplets. Further, numerous tiny, irregularly shaped canaliculi arise randomly directly from the pulp.

Textfigure 25:
Schroederichthys

Genus *Scyliorhinus* BLAINVILLE, 1816
Scyliorhinus canicula (LINNAEUS, 1758)

The root shows a relatively coarse, reticulated system of relatively narrow osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 26:
Scyliorhinus

Part A: No.2c Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae and Carcharhinidae. Additionally, the family Sphyrnidae is included.

Proscylliidae

This family comprises the genera *Ctenacis*, *Eridacnis*, *Gollum* and *Proscyllium*. The teeth of the following species represent these genera, respectively: *Ctenacis fehlmanni*, *Eridacnis radcliffei* and *Proscyllium habereri*. Material of *Gollum* was not available for histological examination.

Genus *Ctenacis* COMPAGNO, 1973)
Ctenacis fehlmanni (SPRINGER, 1968)

The root shows a relatively fine, reticulated system of relatively enlarged osteons. This system is connected to a relatively large, more or less low pulp cavity possesses canals running toward the apex of each cusplet. From each canal, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusplets.

Textfigure 27:
Ctenacis

Genus *Eridacnis* SMITH, 1913
Eridacnis radcliffei SMITH, 1913

The root shows a relatively coarse, reticulated system of relatively enlarged osteons. This system is connected to a relatively large, low pulp cavity at the root-crown junction. From this cavity, narrow enlarged canals run toward the apex of each cusplet. Numerous tiny parallel canaliculi of the circumpulpar dentine radiate from these canals and the pulp cavity into the crown.

Textfigure 28:
Eridacnis

Genus *Proscyllium* HILGENDORFF, 1904
Proscyllium habereri HILGENDORFF, 1904

The root shows a relatively coarse, reticulated system of relatively enlarged osteons. This system produces a relatively large osteon that serves as a low pulp cavity at the root-crown junction. From this cavity numerous tiny semi-parallel, irregular canaliculi of the circumpulpar dentine radiate into the cusp. A central larger canal runs from the cavity toward the principal cusp radiating further irregular canaliculi radiate into the principal cusp.

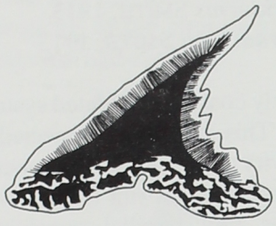
Textfigure 29:
Proscyllium

Hemigaleidae

This family comprises the genera *Chaenogaleus*, *Hemigaleus*, *Hemipristis* and *Paragaleus*. The teeth of the following species represent these genera, respectively: *Chaenogaleus macrostoma*, *Hemigaleus microstoma*, *Hemipristis elongata* and *Paragaleus pectoralis*.

Genus *Chaenogaleus* GILL, 1862
Chaenogaleus macrostoma (BLEEKER, 1852)

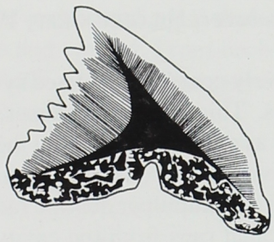
The root shows a relatively fine, reticulated system of relatively coarse osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 30:
Chaenogaleus

Genus *Hemigaleus* BLEEKER, 1852
Hemigaleus microstoma BLEEKER, 1852

The root shows a relatively fine, reticulated system of relatively coarse osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity that is present in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 31:
Hemigaleus

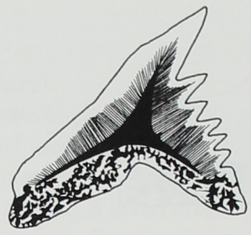
Genus *Hemipristis* AGASSIZ, 1843
Hemipristis elongata (KLUNZINGER, 1871)

The root shows a relatively fine, reticulated system of relatively fine, enlarged osteons. From this system, a narrow, enlarged central canal runs toward the apex of the crown. From this canal, an irregularly reticulated system of narrow osteons radiates randomly into the crown. Besides a small band of rudimentary circumpulpar dentine at the crown margins, the crown is filled with osteodentine.

Textfigure 32:
Hemipristis

Genus *Paragaleus* BUDKER, 1935
Paragaleus pectoralis (GARMAN, 1906)

The root shows a relatively fine, reticulated system of relatively coarse osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 33:
Paragaleus

Pseudotriakidae

This family is represented by the single genus *Pseudotriakis*, which is monotypic with *Pseudotriakis microdon*.

Genus *Pseudotriakis* CAPELLO, 1868
Pseudotriakis microdon CAPELLO, 1868

The root shows a relatively coarse, reticulated system of relatively large osteons. This system is connected to a relatively small, more or less circular pulp cavity, from which about three elongated canals run from the pulp cavity toward the apex of the crown. From the cavity and the canals, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp.

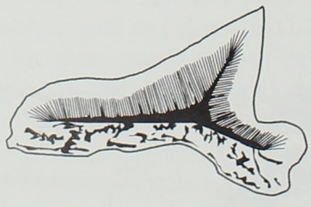
Textfigure 34:
Pseudotriakis

Leptochariidae

This family is represented by the single genus *Leptocharias*, which is monotypic with *Leptocharias smithii*.

Genus *Leptocharias* SMITH, 1838
Leptocharias smithii (Muller & HENLE, 1839)

The root shows a relatively coarse, reticulated system of relatively fine osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



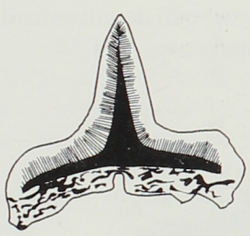
Textfigure 35:
Leptocharias

Carcharhinidae

This family Carcharhinidae comprises the genera *Carcharhinus*, *Galeocerdo*, *Glyphis*, *Isogomphodon*, *Lamiopsis*, *Loxodon*, *Nasolamia*, *Negaprion*, *Prionace*, *Rhizoprionodon*, *Scoliodon* and *Triaenodon*.
The teeth of the following species represent these genera respectively: *Carcharhinus melanopterus*, *Galeocerdo cuvier*, *Glyphis gangeticus*, *Lamiopsis temmincki*, *Loxodon macrorhinus*, *Nasolamia velox*, *Negaprion brevirostris*, *Prionace glauca*, *Rhizoprionodon acutus*, *Scoliodon laticaudus* and *Triaenodon obesus*.
Material of *Isogomphodon* was not available for examination.

Genus *Carcharhinus* BLAINVILLE, 1816
Carcharhinus melanopterus (QUOY & GAIMARD, 1824)

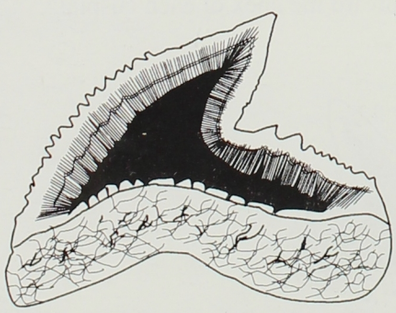
The root shows a relatively fine, reticulated system of relatively coarse osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 36:
Carcharhinus

Genus *Galeocerdo* MULLER & HENLE, 1837
Galeocerdo cuvier (PERON & LE SUEUR, 1822)

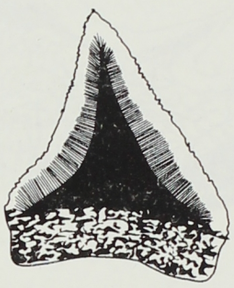
The root shows a relatively fine, reticulated system of fine osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 37:
Galeocerdo

Genus *Glyphis* AGASSIZ, 1843
Glyphis gangeticus (MULLER & HENLE, 1839)

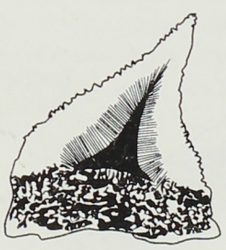
The root shows a relatively fine, reticulated system of more or less coarse osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity that is present in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 38:
Glyphis

Genus *Lamiopsis* GILL, 1862
Lamiopsis temmincki (MULLER & HENLE, 1839)

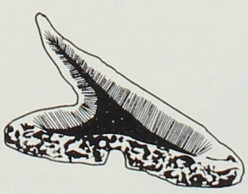
The root shows a relatively fine, reticulated system of more or less coarse osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity that is present in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 39:
Lamiopsis

Genus *Loxodon* MULLER & HENLE, 1838
*Loxodon macrorhinus*MULLER & HENLE, 1839

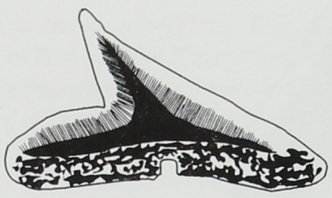
The root shows a relatively fine, reticulated system of more or less coarse osteons. This system is connected to a relatively large, more or less triangularl-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp cusp.



Textfigure 40:
Loxodon

Genus *Nasolamia* COMPAGNO & GARRICK, 1983
Nasolamia velox (GILBERT, 1898)

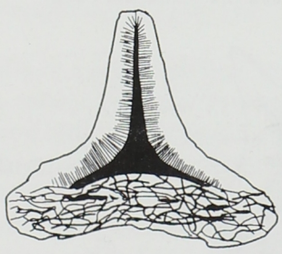
The root shows a relatively fine, reticulated system of more or less coarse osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 41:
Nasolamia

Genus *Negaprion* WHITLEY, 1940
Negaprion brevirostris (POEY, 1868)

The root shows a relatively fine, reticulated system of fine osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 42:
Negaprion

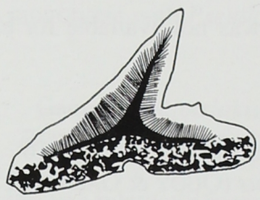
Genus *Prionace* CANTOR, 1843
Prionace glauca (LINNAEUS, 1758)

The root shows a relatively fine, reticulated system of more or less coarse osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.

Textfigure 43:
Prionace

Genus *Rhizoprionodon* WHITLEY, 1929
Rhizoprionodon acutus (RUPPEL, 1837)

The root shows a relatively fine, reticulated system of more or less coarse osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 44:
Rhizoprionodon

Genus *Scoliodon* MULLER & HENLE, 1837
Scoliodon laticaudus MULLER & HENLE, 1838

The root shows a relatively fine, reticulated system of more or less coarse osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.

Textfigure 45:
Scoliodon

Genus *Triaenodon* MULLER & HENLE, 1837
Triaenodon obesus (RUPPEL, 1837)

The root shows a relatively fine, reticulated system of more or less coarse osteons. This system is connected to a relatively large, more or less triangular-shaped pulp in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Near the mesial and distal margins of the pulp cavity, a narrow canal runs from the pulp cavity toward the apex of each cusplet.

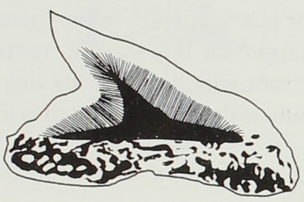
Textfigure 46:
Triaenodon

Sphyrnidae

This family comprises the genera *Eusphyra* and *Sphyrna* and the teeth of the following species represent these genera respectively: *Eusphyra blochii* and *Sphyrna zygaena*.

Genus *Eusphyra* GILL, 1862
Eusphyra blochii (CUVIER, 1837)

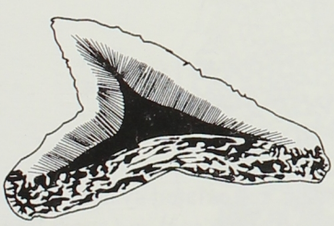
The root shows a relatively fine, reticulated system of coarse osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 47:
Eusphyra

Genus *Sphyrna* RAFINESQUE, 1810
Sphyrna zygaena (LINNAEUS, 1758)

The root shows a relatively fine, reticulated system of coarse osteons. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.



Textfigure 48:
Sphyrna

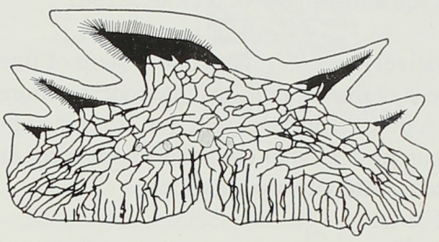
Part A: No.3 Squaliformes. Families: Echinorhinidae, Oxynotidae and Squalidae.

Echinorhinidae

This family consists of one single genus *Echinorhinus*. The teeth of the following species represent this genus: *Echinorhinus brucus*.

Genus *Echinorhinus* BLAINVILLE, 1816
Echinorhinus brucus (BONNATERRE, 1788)

The entire midsection of the tooth shows a band of relatively large osteons, from which vertical, more or less parallel canals pierce the lower root part and end at the inner face of the root as an opening to the vascular system outside.
From the midsection upward, the osteons become narrow, to form a reticulated canals system. This system is connected to separate triangular-shaped pulp cavities in principal cusp and each mesial cusplet of the crown. From these cavities, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusplets.



Textfigure 49:
Echinorhinus

Oxynotidae

The family Oxynotidae consists of one single genus *Oxynotus*. The teeth of the following species represent this genus: *Oxynotus centrina*.

Genus *Oxynotus* RAFINESQUE, 1810
Oxynotus centrina (LINNAEUS, 1758)

The root shows a relatively coarse system of osteons that is connected to a large, irregularly shaped central pulp cavity, from which coarse osteons radiate toward the margins of the root. From the upper part of this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp.

Textfigure 50:
Oxynotus

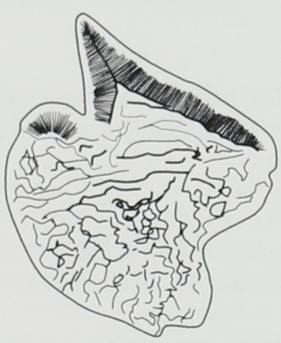
Squalidae

The family Squalidae comprises the genera *Centrophorus*, *Centroscyllium*, *Centroscymnus*, *Cirrhigaleus*, *Dalatias*, *Deania*, *Etmopterus*, *Euprotomicroides*, *Euprotomicrus*, *Heteroscymnoides*, *Isistius*, *Mollisquama*, *Scymnodalatias*, *Scymnodon*, *Somniosus*, *Squaliolus*, *Squalus* and *Trigonognatus*.
The teeth of the following species represent these genera, respectively: *Centrophorus squamosus*, *Centroscyllium fabricii*, *Centroscymnus crepidater*, *Dalatias licha*, *Deania*

calceus, *Etmopterus princeps*, *Isistius brasiliensis*, *Scymnodon ringens*, *Somniosus microcephalus*, *Squaliolus laticaudus* and *Squalus acanthias*.
Material of *Cirrhigaleus*, *Euprotomicroides*, *Euprotomicrus*, *Heteroscymnoides*, *Mollisquama*, *Scymnodalatias* and *Trigonognatus* was not available for histological examination.

Genus *Centrophorus* MULLER & HENLE, 1837
Centrophorus squamosus (BONNATERRE, 1788)

The root shows a relatively coarse, reticulated system of fine osteons, of which those of the upper part of the root run more or less horizontally. A pulp cavity is absent, but from the upper osteons, numerous tiny parallel canaliculi appearing as circumpulpar dentine radiate into the cusp.



Textfigure 51:
Centrophorus

Genus *Centroscyllium* MULLER & HENLE, 1841
Centroscyllium fabricii (REINHARDT, 1825)

The root shows a relatively coarse, reticulated system of fine osteons that become coarser toward the mesial and distal margins. This system is connected to a relatively large, more or less triangular-shaped pulp cavity in the crown. From this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp.

Textfigure 52:
Centroscyllium

Genus *Centroscymnus* BOCAGE & CAPELLO, 1864
Centroscymnus crepidater BOCAGE & CAPELLO, 1864

The root shows a relatively coarse system of osteons that is connected to a large, irregularly shaped central pulp cavity, from which coarse osteons radiate toward the margins of the root. From the upper part of this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp.

Textfigure 53:
Centroscymnus

Genus *Dalatias* RAFINESQUE, 1810
Dalatias licha (BONNATERRE, 1788)

The root shows a relatively coarse, reticulated system of osteons that are coarser in the lower part and mid-section. They are oriented more or less vertically in the lower part of the root. At the upper margins of this system, remains of a pulp cavity are present, from which numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp.

Textfigure 54:
Dalatias

Genus *Deania* JORDAN & SNYDER, 1902
Deania calceus (LOWE, 1839)

The root shows a relatively coarse, reticulated system of fine osteons in the lower and upper part of the root and some large ones in the mid-section. Those of the upper part tend to be more or less horizontally directed. A pulp cavity is absent, but from the upper osteons, numerous tiny parallel canaliculi that appear as circumpulpar dentine radiate into the cusp.

Textfigure 55:
Deania

Genus *Etmopterus* RAFINESQUE, 1810
Etmopterus princeps COLLETT, 1904

The root shows a relatively coarse system of osteons that is connected to a large upper central pulp cavity, from which fine and coarse osteons more or less radiate toward the margins of the root. From the upper part of this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp.

Textfigure 56:
Etmopterus

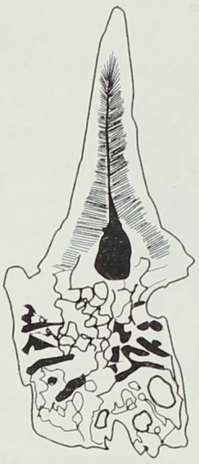
Genus *Isistius* GILL, 1864
Isistius brasiliensis (QUOY & GAIMARD, 1824)

The root shows a relatively fine, reticulated system of osteons, that are coarser in the mid-section. They become more or less vertically oriented in the lower part of the root. At the upper margins of this system, remains of a pulp cavity are present, from which numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp.

Textfigure 57:
Isistius

Genus *Scymnodon* BOCAGE & CAPELLO, 1864
Scymnodon ringens BOCAGE & CAPELLO, 1864

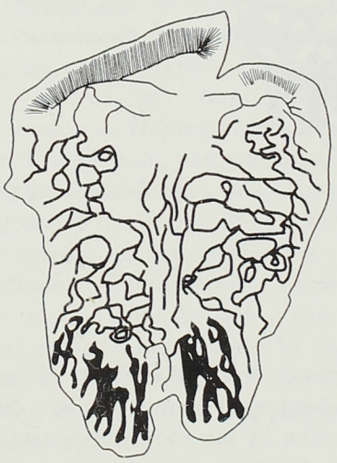
The root shows a relatively coarse system of osteons, that is connected to a central pulp cavity, from which fine osteons radiate toward the margins of the root. The osteons in the mid-section of the root are coarser. From the upper part of the pulp cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp.



Textfigure 58:
Scymnodon

Genus *Somniosus* LE SUEUR, 1818
Somniosus microcephalus (BLOCH & SCHNEIDER, 1801)

The root shows a relatively coarse, reticulated system of fine osteons, of which those of the upper part of the root run more or less horizontally. The osteons become coarser toward the lower part of the root and are vertically directed. A pulp cavity is absent, but from the upper osteons, numerous tiny parallel canaliculi that appear as circumpulpar dentine radiate into the cusp.



Textfigure 59:
Somniosus

Genus *Squaliolus* SMITH & RADCLIFFE, 1912
Squaliolus laticaudus SMITH & RADCLIFFE; 1912

The root shows a large, irregularly shaped central pulp cavity, from which coarse osteons radiate, toward the margins of the root. From the upper part of this cavity, numerous tiny parallel canaliculi of the circumpulpar dentine radiate into the cusp. Strings of particularly concentrated canaliculi do not extend from the pulp cavity toward the principal cusp cusp.

Textfigure 60:
Squaliolus

Genus *Squalus* LINNAEUS, 1758
Squalus acanthias LINNAEUS, 1758

The root shows a relatively coarse, reticulated system of very coarse osteons, of which those of the upper part of the root run more or less horizontally. A pulp cavity is absent, but from the upper osteons, numerous tiny parallel canaliculi that appear as circumpulpar dentine radiate into the cusp.

Textfigure 61:
Squalus

Differential diagnosis

HEXANCHIDAE

The vascularization systems of *Heptranchias*, *Hexanchus* and *Notorhynchus* are identical. The more or less circular apertures in the mid-section of the root, the vertically directed canals in the lower part, the horizontally directed ones of the upper part and the small pulp cavities, from which circumpulpar dentine radiates into the cusplets, are typical for this family.

TRIAKIDAE

The vascularization system varies within the Triakidae. All genera possess osteodentine in the root, but have taken different developments in detail. *Galeorhinus*, *Mustelus* and *Triakis* have a coarse reticulated system of fine osteons. *Hemitriakis* has a fine reticulated system of fine osteons. *Furgaleus*, *Rhinotriacis* and *Scylliogaleus* have a coarse, reticulated system of coarse, osteons and *Hypogaleus* and *Iago* have a fine, reticulated system of coarse osteons.
Further, all genera possess a pulp cavity with circumpulpar dentine in the crown. However, the development of the pulp cavity varies. *Galeorhinus*, *Furgaleus*, *Hemitriakis* and *Hypogaleus* have a more or less triangular-shaped pulp cavity, whereas that of *Mustelus* and *Rhinotriacis* is more or less circular, and that of *Scylliogaleus* and *Iago* is compressed low.

SCYLIORHINIDAE

The vascularization system varies within the Scyliorhinidae. All genera possess osteodentine in the root, but have taken different developments in detail. *Apristurus*, *Asymbolus*, *Cephaloscyllium*, *Cephalurus* and *Scyliorhinus* have a coarse, reticulated system of fine osteons. *Atelomycterus* and *Poroderma* have a coarse, reticulated system of coarse osteons, and *Galeus*, *Halaelurus*, *Haploblepharus*, *Holohalaelurus*, *Parmaturus*, *Pentanchus* and *Schroederichthys* have a fine, reticulated system of coarse osteons.
Further, all genera possess a pulp cavity with circumpulpar dentine in the crown. However, the development of the pulp cavity varies. *Atelomycterus*, *Cephaloscyllium*, *Cephalurus*, *Galeus*, *Halaelurus* and *Poroderma* have a more or less triangular-shaped pulp cavity, whereas that of *Apristurus*, *Asymbolus*, *Halaelurus*, *Haploblepharus*, *Holohalaelurus*, *Parmaturus*, *Pentanchus*, *Schroederichthys* and *Scyliorhinus* is reduced to a low strip with one or more vertical canals, depending on the development of cusplets. From these canals, circumpulpar dentine radiates into the crown. *Pentanchus* and *Schroederichthys* have additional canals between the principal ones that lack circumpulpar dentine.

PROSCYLLIIDAE

The vascularization system varies within the Proscylliidae. All genera possess osteodentine in the root, with a fine, reticulated system of coarse osteons. Further, all genera possess a low pulp cavity with relatively irregularly shaped circumpulpar dentine in the crown. However, the development of the pulp cavity varies. In *Proscyllium* the circumpulpar dentine, radiates directly from the low pulp cavity, whereas in *Ctenacis* and *Eridacnis* several vertical canals are present, depending on the development of cusplets.

HEMIGALEIDAE

The vascularization system varies within the Hemigaleidae. Except *Hemipristis*, all genera possess osteodentine in the root, with a fine, reticulated system of coarse osteons and a more or less triangular-shaped pulp cavity with circumpulpar dentine radiating into the crown. However, *Hemipristis* has a fine, reticulated system of fine osteons in the root, with a main canal in the crown, partly surrounded by pulpar dentine like canaliculi, as well as a reticulated system of canaliculi.

PSEUDOTRIAKIDAE

Pseudotriakis has a vascularization system of a fine, reticulated system of relatively coarse osteons in the root. Circumpulpar dentine radiates into the crown from a semicircularly shaped pulp cavity.

LEPTOCHARIIDAE

Leptocharias has a vascularization system of a coarse, reticulated system of relatively fine osteons in the root. Circumpulpar dentine radiates into the crown from a more or less triangularly shaped pulp cavity.

CARCHARHINIDAE

The vascularization system varies only little within the Carcharhinidae. All genera possess osteodentine in the root, but have taken different developments in detail. *Carcharhinus*, *Galeocerdo* and *Negaprion* have a fine reticulated system of fine osteons. *Glyphis*, *Lamiopsis*, *Loxodon*, *Nasolamia*, *Prionace*, *Rhizoprionodon*, *Scoliodon* and *Triaenodon* have a fine, reticulated system of coarse osteons. Further, all genera possess a pulp cavity with circumpulpar dentine in the crown. However, *Triaenodon* additionally has vertical canals near the cusplets.

SPHYRNIDAE

Eusphyra and *Sphyrna* share the same vascularization consisting of a fine, reticulated system of relatively coarse osteons in the root. Circumpulpar dentine radiates into the crown from a more or less triangularly shaped pulp cavity.

SQUALIDAE

The vascularization system varies within the Squalidae. All genera possess osteodentine in the root, but have taken different developments in detail. *Centrophorus* and *Somniosus* have a coarse, reticulated system of fine osteons that are a little coarser in the lower part of the root in *Somniosus*. *Centroscymnus*, *Squaliolus* and *Squalus* have a coarse, reticulated system of coarse osteons, whereas *Centroscyllium*, *Deania*, *Etmopterus* and have a coarse, reticulated system of mixed coarse and fine osteons. *Dalatias* and *Isistius* have a fine, reticulated system of coarse osteons.
Further, some genera possess a pulp cavity with circumpulpar dentine in the crown. However, the development of the pulp cavity varies. *Centroscyllium*, *Centroscymnus*, *Etmopterus* and *Squaliolus* have pulp cavity, which is more or less triangular-shaped in *Centroscyllium* only, and is irregularly shaped in *Centroscymnus*, *Etmopterus* and *Squaliolus*. Other genera lack a pulp cavity and their crown is filled with osteodentine. Orthodentine radiates from the upper osteons into the crown near the margins in *Centrophorus*, *Dalatias*, *Deania*, *Isistius*, *Somniosus* and *Squalus*.

ECHINORHINIDAE

Echinorhinus has a vascularization system with more or less circular apertures in the mid-section of the root, vertically directed canals in the lower part, horizontally directed ones in the upper part and small pulp cavities, from which circumpulpar dentine radiates into the cusplets.

OXYNOTIDAE

Oxynotus has a vascularization of a coarse reticulated system of coarse osteons in the root. Circumpulpar dentine radiates into the crown from an irregularly shaped pulp cavity.

Conclusions

GENERAL

Besides the tooth morphology and the vascularization systems described and illustrated by HERMAN, HOVESTADT-EULER & HOVESTADT (1988,1989, 1990) and the vascularization systems, also the fossil records of the different extant genera are significant to group the taxa into various developmental lineages (extinct taxa are not included, as they are beyond the scope of this study). This is described and illustrated below in four hypothetical phylogenetic diagrams, depicting the eventual origin of these genera. The paleoichthyological information is based on CAPPETTA (1987).

HEXANCHIDAE AND SQUALIFORMES

The genera of the Hexanchidae share an identical vascularization system. The archaic hexanchiform line dates back to the Devonian, and the concept of its tooth morphology, as well as the vascularization system is still tha same as in the extant successors *Heptranchias*, *Hexanchus* and *Notorhynchus*. In *Heptranchias*, the separate pulp cavities in the small cusplets are partly filled with osteodentine.
Among the Squaliformes, several variations were observed, that appear to represent different developments. *Echinorhinus* possesses a vascularization system equal to the Hexanchidae. *Centrophorus*, *Dalatias*, *Deania*, *Isistius*, *Somniosus* and *Squalus* lack a true pulp cavity, but share parts of an orthodont system by the orthodentine in their crowns. In *Centroscyllium*, *Centroscymnus*, *Etmopterus*, *Oxynotus*, and *Squaliolus*, the pulp cavity is made up by enlarged osteons.
Considering this, besides sharing a flattened root and a typical dignathic heterodonty (broad and flat teeth in the lower, and narrow, thicker teeth in the upper jaw), the Hexanchidae and Squaliformes share many morphological features, as well as a more or less similar tooth vascularization system. Based on these similarities, a close relationship of both families is assumed. However, within the Squalidae there exist another significant difference, manifested in monognathic and dignathic heterodonty (HERMAN, HOVESTADT-EULER & HOVESTADT, 1989), which divides this family into two developmental lines.
The vascularization system, tooth morphology and the paleoichthyological information of the Hexanchiformes and Squaliformes are integrated into one hypothetical phylogenetic diagram below (diagram 1).
Based on an assumed close relationship between Hexanchiformes and Squaliformes, *Hexanchus* and *Echinorhinus* might have separated from the archaic hexanchiform

lineage in the early Cretaceous, as they conserve the dignathic heterodont dentition and its changing to monognathic heterodont development, respectively. In the Eocene, *Notorhynchus* and *Heptranchias* branched from the *Hexanchus*-line by possessing a higher root and a different crown structure, respectively. In the late Cretaceous, *Squalus* (also monognathic heterodont) branched from the *Echinorhinus*-line by developing a coarser vascularization system and changes of tooth morphology by less and irregularly directed mesial and distal cusplets. Information about the vascularization system is lacking of *Cirrhigaleus*, *Trigonognatus* and *Aculeola*. *Cirrhigaleus* is by its tooth morphology related to *Squalus* (HERMAN, HOVESTADT-EULER & HOVESTADT, 1989), and *Trigonognatus*, *Aculeola* and *Centroscyllium* are tentatively related here to *Squalus* by their monognathic heterodonty.

Centrophorus with dignathic heterodont dentition also branched in the late Cretaceous from the *Hexanchus*-line by attaining narrower teeth and cusplets reduced to a blade in lower teeth.

Two main branches separated from the *Centrophorus*-line: One in the middle Cretaceous with *Etmopterus*, *Centroscymnus* and *Oxynotus* having larger, cave-like osteons in the vascularization system, and a second one in the late Cretaceous with *Somniosus*, *Dalatias* and *Isistius* with more elongated roots and slightly larger osteons in the vascularization system.

From the *Etmopterus*-line, *Squaliolus* branched in the Thanetian by having an extremely large cave-like osteon in the vascularization system, and the origin of *Euprotomicrus* and *Heteroscymnoides* may be assumed here too? *Scymnodon* separated from the *Isistius*-line in the Eocene possessing an enlarged osteon in the vascularization system, and later the origin of *Scymnodalatias*, *Mollisquama* and *Euprotomicroides* may be assumed here. *Deania* branched from the *Somniosus*-line by having a shorter root and developing larger osteons in the vascularization system.

CARCHARHINIDAE, SPHYRNIDAE, LEPTOCHARIIDAE, HEMIGALEIDAE

The genera of the Carcharhinidae, Sphyrnidae, Leptocharidae, Hemigaleidae and the Triakidae more or less share a similar vascularization system by having an osteodont root part and an orthodont crown part. Further, their tooth morphological features are described and illustrated by HERMAN, HOVESTADT-EULER & HOVESTADT (1988, 1990), and much of their paleoichthyological information is summarized by CAPPETTA (1987).

The genus *Galeocerdo* is reported from the Lower Eocene and early triakids are reported from late cretaceous deposits and are considered here to form two separate phylogenetic lineages. Triakidae, therefore, are separately described below. However, *Furgaleus* is the only triakid genus that presents dignathic heterodonty, and from the odontological point of view is thus not triakid-like. The general tooth morphology of this genus rather shows similarity with the Hemigaleidae, with lower teeth having a cusplet-like serrated distal cutting edge.

The teeth of the genera of the hemigaleid genera possess a similar vascularization system as *Carcharhinus*, and also is their dentition dignathic heterodont. From this point of view, it is suggested here, that by being possibly related *Carcharhinus* and the genera *Hemigaleus*, *Paragaleus* and *Chaenogaleus* branched more or less parallel from the *Galeocerdo*-lineage in the Eocene. *Carcharhinus* and the hemigaleid genera are however distinguished, in that the latter ones developed upper teeth with more oblique and serrated distal cutting edges. The tooth morphology of *Prionace* is more similar to the Hemigaleidae, than to the Carcharhinidae in that *Prionace* has upper teeth with a cusplet-like serrated distal cutting edge. *Furgaleus* and *Prionace* are each separated from the hemigaleid-lineage by having a coarser reticulated system of also coarser osteons and an enlarged pulp cavity, respectively. *Hemipristis* branched from *Prionace*. *Prionace* and *Hemipristis* seem to follow a parallel development, in which *Prionace* attains a larger pulp cavity, and the pulp cavity of *Hemipristis* becomes filled which osteodentine (COMPAGNO, 1988). Due to a very similar vascularization system of the three hemigaleid genera, the predecessor of *Furgaleus* and *Prionace* cannot be determined. This is indicated by a single line in diagram 2.

According to the tooth morphological features it is concluded here, that the *Carcharhinus*-lineage creates derived developments in *Lamiopsis*, *Nasolamia* and *Glyphis*. They appeared probably on this lineage in the Pliocene, but this cannot be confirmed by fossil records yet.

Rhizoprionodon and *Scoliodon* with monognathic heterodont dentition also might have branched from the *Galeocerdo*-lineage in the Eocene by the loss of mesial serration and distal cusplets changing to become a blade. All younger developments of carcharhinid taxa with monognathic heterodont dentition, namely the *Sphyrna*, *Eusphyra*, *Negaprion*, *Isogomphodon*, *Triaenodon*, *Loxodon* and *Leptocharias* are assumed to have derived from these two genera.

Sphyrna separated in the Miocene by attaining broader cusps, and *Eusphyra* might have branched from the latter lineage in the Pliocene, but this is not confirmed by fossil records.

Negaprion separated in the Pliocene by attaining upright principal cusps, and probably *Isogomphodon* with also upright cusps derived from the latter lineage.

Leptocharias, *Loxodon* and *Triaenodon* probably derived from the *Rhizoprionodon-Scoliodon*-lineage by attaining in the late Pliocene more specialized tooth morphological features, but this cannot be confirmed by fossil records.

TRIAKIDAE

The triakid phylogenetic line originates from the late Cretaceous and subdivides into three separate lineages in the Eocene (diagram 3). The *Mustelus*-lineage is defined by attaining a low and thick crown, and *Rhinotriacis* and *Scylliogaleus* derived from the latter by development of a coarse, reticulated system with fine and coarse osteons of a mixed size and a coarse, reticulated system of coarse osteons in the root, respectively. Probably this separation occurred in the late Pliocene, but fossil records are lacking to confirm this.

The *Galeorhinus*-lineage separated by attaining an inclined

cusp and a cusplet-like serrated distal cutting edge. Its vascularization system has a coarse, reticulated system of fine osteons in the root. Although not confirmed by fossil records, *Hypogaleus*, *Hemitriakis* and *Gogolia* probably have separated from the *Galeorhinus*-lineage in the late Pliocene by attaining a finer, reticulated system of fine osteons in the root. Material for examination of the vascularization system was lacking, but *Gogolia* is tentatively related to *Hypogaleus* and *Hemitriakis* due to its similar tooth morphology.
The *Triakis*-lineage differs from the other lineages by developing cusplets and an extraordinary vascularization system with a strongly constricted pulp cavity, reduced to a low base and a central canal with lateral canals directed toward each cusplet. *Iago* is presumed to branch from this lineage in the late Pliocene, but this cannot be confirmed by fossil records.

SCYLIORHINIDAE, PROSCYLLIIDAE AND PSEUDOTRIAKIDAE

Although Scyliorhinidae, Proscylliidae and Pseudotriakidae share a similar vascularization system, with osteodentine in the root and orthodentine in the crown, and many tooth morphology features, existing variations indicate three significantly different developments. The tooth morphology of each genus of these three genera was described and illustrated by HERMAN, HOVESTADT-EULER & HOVESTADT (1989 and 1990). Due to the relatively minor intergeneric differences in tooth morphology and having mainly teeth available as fossil representatives, the fossil species of the Scyliorhinidae, Proscylliidae and Pseudotriakidae are generally lumped under the genus "*Scyliorhinus*" and need to be revised in the future. Therefore, paleoichthyological information is not usable here. Lacking this information, the interrelationships between the genera is here only based on the development of vascularization system and external tooth morphology only. This information has been used for constructing the hypothetical phylogenetic diagram 4 below.
The Scyliorhinidae can be subdivided by three developments of their vascularization system: *Cephaloscyllium* has a coarse reticulated system of fine osteons and a large pulp cavity; *Galeus* has a fine reticulated system of coarser osteons and a constricted pulp cavity with lateral canals directed toward the cusplets; *Halaelurus* has a fine reticulated system of coarse osteons and a constricted pulp cavity without lateral canals.
Cephalurus and *Scyliorhinus* derive from the *Cephaloscyllium*-line because of their more constricted pulp cavities, but still presenting a coarse reticulated system of fine osteons. *Cephalurus* shows stronger developed circumpulpar dentine toward the cusplets than *Scyliorhinus*, and therefore, it is suggested here that *Asymbolus* and *Apristurus* might have derived from *Cephalurus* by having attained a reduced small circular and lateral canals directed toward the cusplets, respectively. *Pseudotriakis* derived from *Asymbolus* with a similar small circular cavity but having coarser osteons.
Haploblepharus derived from the *Galeus*-line with a pulp cavity reduced to a low base with one central and two lateral canals directed toward principal cusp and cusplets. This development continues in *Holohalaelurus*, but the canals diminish in size, and the circumpulpar dentine becomes finer to hardly visible. From the *Holohalaelurus*-line, *Parmaturus* separates by having two lateral canals at each side of the central one. This multiplying of lateral canals continues in *Ctenacis*, *Eridacnis*, *Pentanchus* and *Schroederichthys*. Although the vascularization system of *Gollum* was not examined, its tooth morphology with multicusped lateral teeth suggests its having derived from *Parmaturus* as well.
In *Proscyllium*, the pulp cavity is restricted to a fine central canal only, and more irregularly shaped canaliculi of the circumpulpar dentine. Possessing also a reticulated system with coarser osteons, *Proscyllium* is considered here as having derived from *Haploblepharus* as a second branch.
Poroderma and *Atelomycterus* separate from the *Halaelurus*-line by attaining very coarse osteons.

Acknowledgements

The authors thank Dr.D.Nolf, Institut Royal des Sciences naturelles de Belgique, Brussels, M.McGrouther, Australian Museum, Sydney, and J. Johnson, Queensland Museum, Brisbane, for permission to examine specimens at their disposal. We also would like to thank Mr.J.-P.Herber, Luxemburg for making teeth of *Glyphis gangeticus* available for examination.

Bibliography

CAPPETTA, H. 1987. Handbook of Paleoichthyology. Ed. SCHULZE, H.- P. *Gustav Fischer Verlag, Stuttgart*: 1-193.

COMPAGNO, L.J.V. 1988. Sharks of the Order Carcharhiniformes. *Princeton University Press. New Jersey*: 1-486.

HERMAN, J., HOVESTADT-EULER, M., HOVESTADT, D. 1987. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living suprageneric taxa of Chondrichthyan fishes. Part A Selachii No. 1: Order Hexanchiformes - Family: Hexanchidae. Commissural teeth. Ed. Stehmann, M. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie*, 57: 41-42.

HERMAN, J., HOVESTADT-EULER, M., HOVESTADT, D. 1988. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living suprageneric taxa of Chondrichthyan fishes. Part A Selachii No. 2a: Order Carcharhiniformes - Family: Triakidae. Ed. Stehmann, M. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie*, 58: 99-126.

HERMAN, J., HOVESTADT-EULER, M., HOVESTADT, D. 1989. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living suprageneric taxa of Chondrichthyan fishes. Part A Selachii No. 3: Order Squaliformes - Families: Echinorhinidae, Oxynotidae and Squalidae. Ed. Stehmann, M. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie*, 59: 101-157.

HERMAN, J., HOVESTADT-EULER, M., HOVESTADT, D. 1990. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living suprageneric taxa of Chondrichthyan fishes. Part A Selachii No. 2b: Order Carcharhiniformes - Family: Scyliorhinidae. Ed. Stehmann, M. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie*, 60: 181-230.

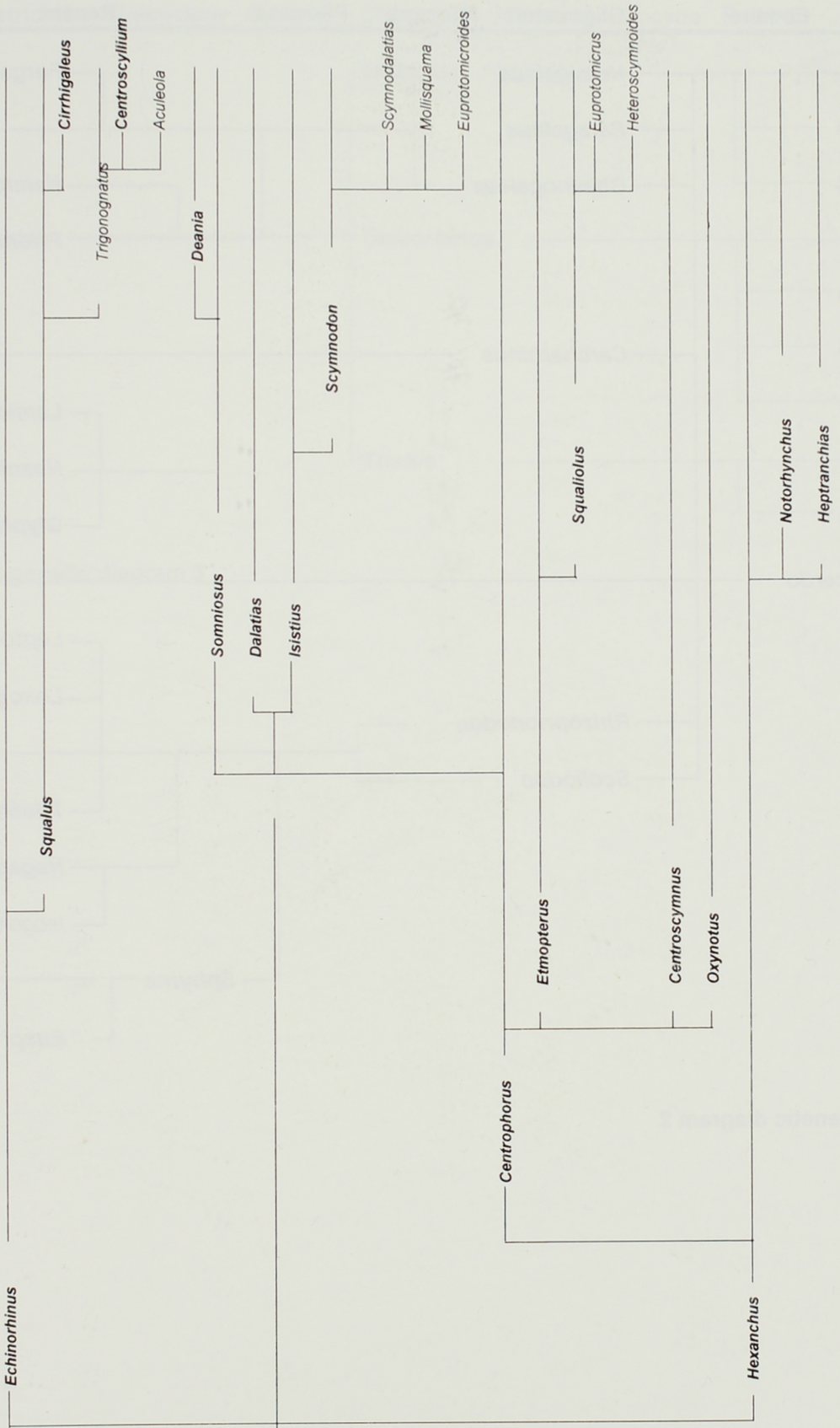
HERMAN, J., HOVESTADT-EULER, M., HOVESTADT, D. 1991. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living suprageneric taxa of Chondrichthyan fishes. Part A Selachii No. 2c: Order Carcharhiniformes - Families: Proscyliidae, Hemigaleidae, Pseudotrikiadae, Leptocharhiidae and Carcharhinidae. Ed. Stehmann, M. *Bulletin de l'Institut Royal des Sciences naturelles de Belgique, Biologie*, 61: 73-120.

HERMAN, J., HOVESTADT-EULER, M. 1993. The vascularization system in teeth of Selachii. In : Elasmobranches et Stratigraphie eds. Herman,J; and Van Waes, H *Belgian Geological Survey Professional Paper1993/6*, 264: 241 - 249..

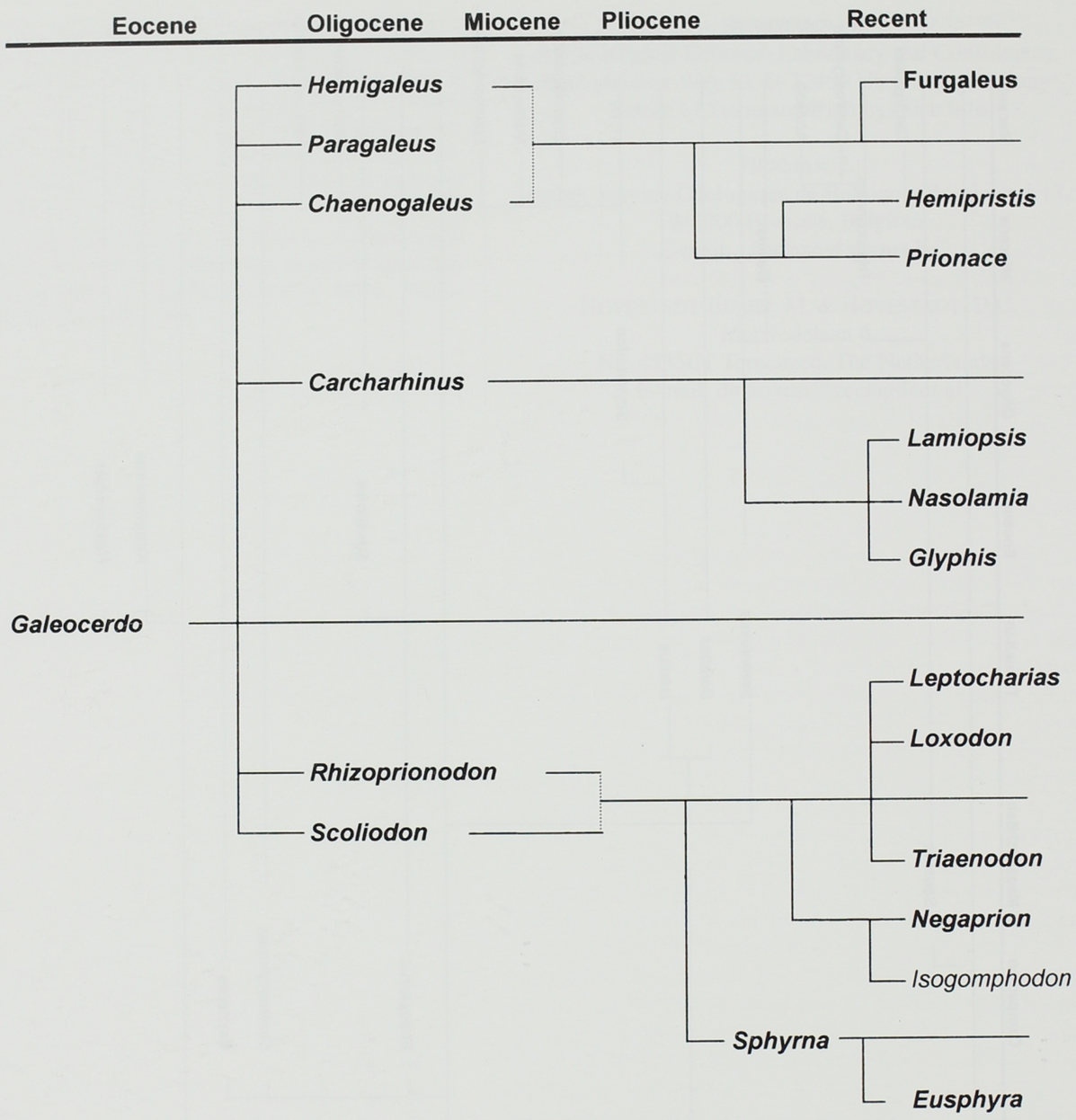
STEHMANN, M.
Ichthyological Research Laboratory and Consultancy,
Hildesheimer Weg 13, D-22459 Hamburg, Germany.
Email: M.Stehmann@ichthys-fish.info

HERMAN, J.
IRSNB, Service Géologique de Belgique. Rue Jenner 13,
B-1000 Brussels, Belgium.
E-mail: j.herman@skynet.be

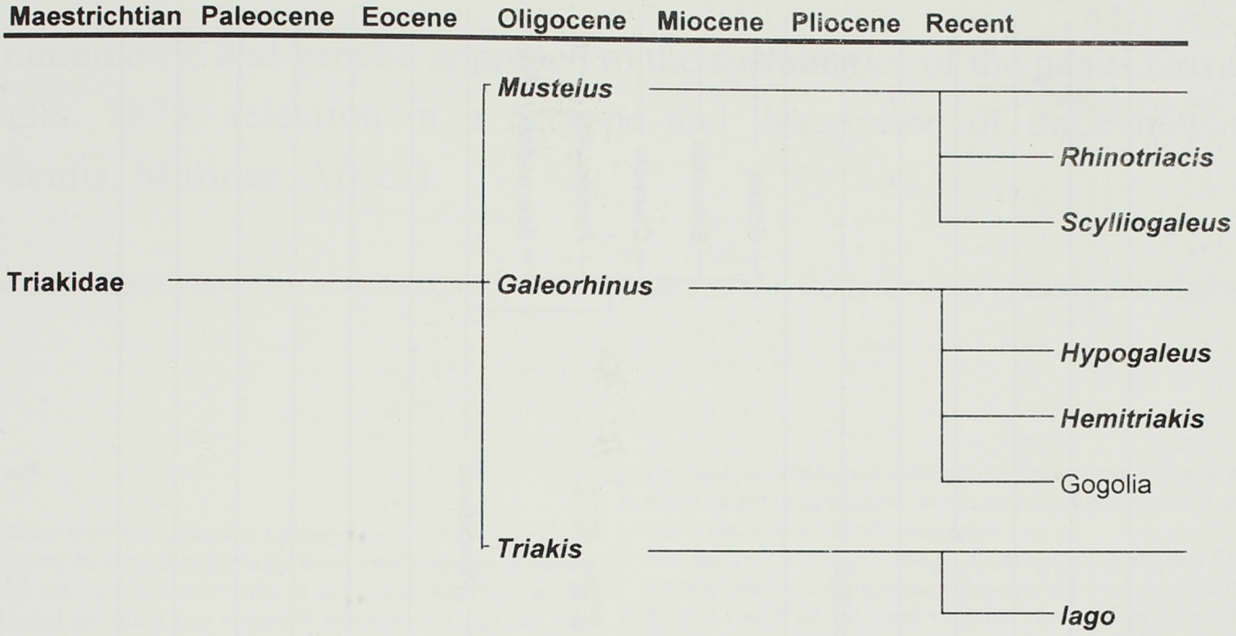
HOVESTADT-EULER, M. & HOVESTADT, D.C.
Merwedelaan 6,
NL-4535ET Terneuzen, The Netherlands.
E-mail: dmhovest@zeelandnet.nl



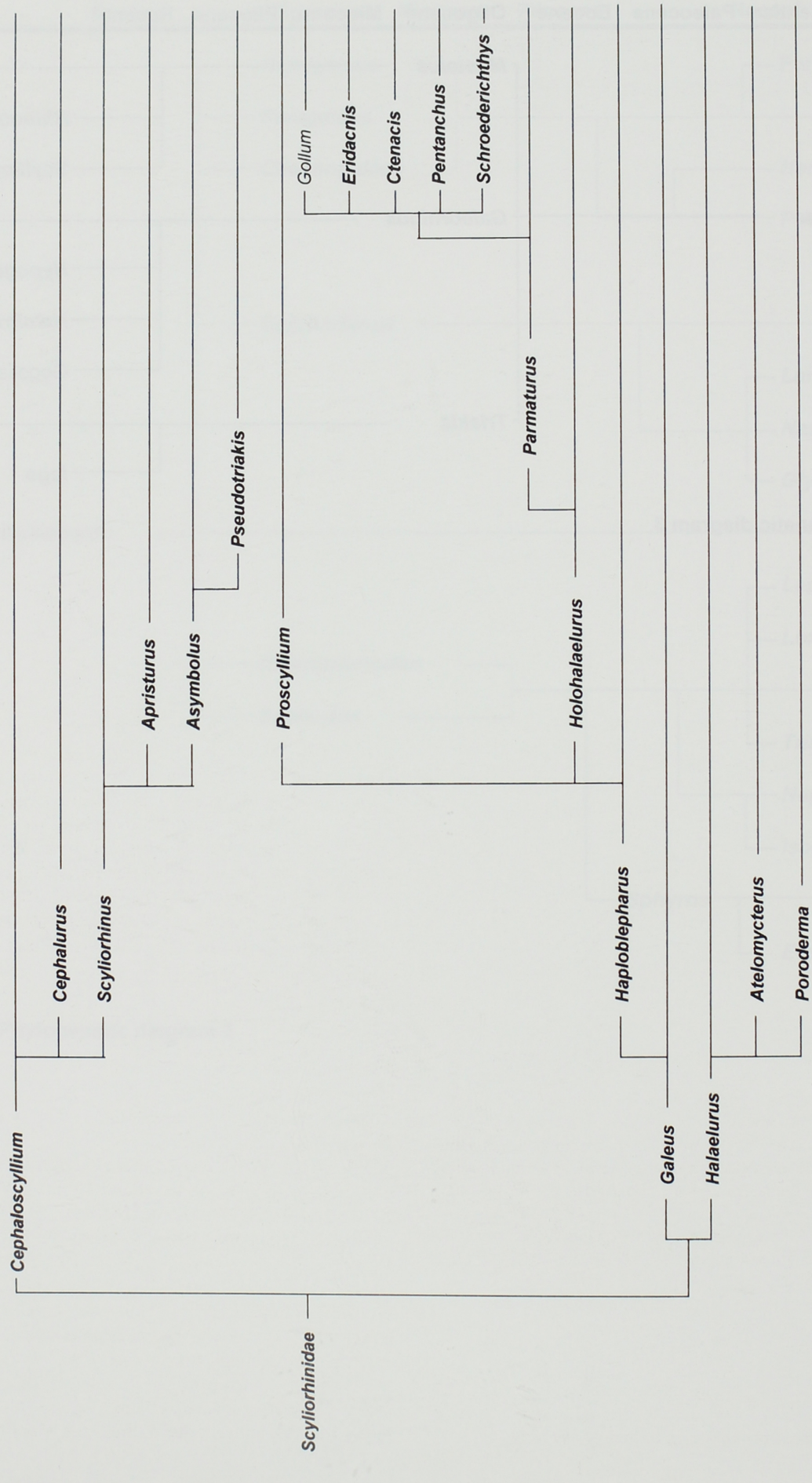
Phylogenetic diagram 1



Phylogenetic diagram 2



Phylogenetic diagram 3



Phylogenetic diagram 4