
*Interrelationships of the Elasmobranchs with a Key to the
Order Galea*

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Article II.—INTERRELATIONSHIPS OF THE ELASMOBRANCHS WITH A KEY TO THE ORDER GALEA

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INTRODUCTION

The elasmobranch fishes have been the subject of many investigations in the past and numerous accurate and comprehensive works on them have already been published. The reason for reopening the question of their interrelationships is that owing to the great variability within the group, and to the consequent failure of certain external variations to correspond with internal ones, there have been considerable discrepancies in the different classifications formerly in use. This work has been undertaken with the intent to distinguish between physiological and phylogenetic characters, and to determine their relative value in classification. It is designed also to provide a swift and practical survey of the group for teachers and students by presenting in diagrammatic and comparative form the findings on which the conclusions have been based and by attempting to disentangle the confusion that has arisen in the recent attempts to reclassify the group from the older standard works. The confusion mentioned above has been due in part to the lack of uniformity in terminology and in the ranking of groups.

The three recent works used for comparison are those of Garman in 1913, of Goodrich in 1909, and of Tate Regan in 1908. The outline Classification of teleostomous fishes by William K. Gregory (1907) has been used as a guide for the grades assigned to groups, since this work presents a logical sequence where additional subdivisions are necessary. By adopting the series names "Superclass," "Class," and "Subclass," the confusion arising from the use of "Grades," "Groups," "Divisions," and "Tribes," is avoided.

Consistent endings have been applied to all groups and the following series adopted: for class, "ia," subclass, "i," superorder, "eae," order, "ea," suborder, "ida," superfamily, "oidea," and family, "idae." Subfamilies if used would have the ending "inae."

This work was originally undertaken at the suggestion of Dr. William K. Gregory, Curator of Ichthyology at The American Museum of Natural History in New York City, and several years have been spent in accumulating data from the literature and from available specimens. In order to examine certain rare and fresh material not available in New York, several months were spent during the winter of 1930-1931, while the writer was on a sabbatical leave of absence, studying the sharks of Japan and Java. Tokyo was chosen as a center for the work because of its peculiarly favorable location; the warm waters from the south meeting the colder waters from the north just off its shores, thus providing an environment favorable to a large variety of

species. A part of the time was spent at the Marine Biological Laboratory at Misaki, where some of the larger sharks could be examined at first hand. While there some rare specimens also were obtained from the old laboratory collector, Kuma Aoki.

The limited time at the author's disposal prevented the study of the Australian and Mediterranean types, but a group of South American sharks were placed at her disposal by Dr. T. Marini of Buenos Aires during his visit to the museum in New York as a Guggenheim Fellow in 1932.

The author wishes to express at this time her sincere appreciation to the following scientists and institutions:

Dr. William K. Gregory, Mr. John T. Nichols, Dr. E. W. Gudger, and Miss Helen Wilmann of the Department of Ichthyology, and Mr. R. Denison, at The American Museum of Natural History, who have given their cordial cooperation in the preparation of this work at all times, and who have placed invaluable material and research facilities at her command;

Dr. Naohide Yatsu, Dr. Megumi Eri, and Dr. Shigeho Tanaka, who made her stay in Tokyo and Misaki a pleasant and profitable one, and who provided access to much valuable material and research facilities at the Imperial University in Tokyo and at the Marine Biological Laboratory at Misaki in 1930;

Dr. H. C. Delsman and his associates who were in charge at the Laboratorium voor het Onderzoek der Zee, in Batavia, Java, in 1931, for material and research facilities at the laboratory;

Dr. T. Marini of Buenos Aires for the loan of his South American collection in 1932.

Below are listed the specimens which have been examined and dissected by the author. The greater part of the time was devoted to the Order Galea, and every attempt to obtain species from this order was made. Very little time was devoted to the rays since their relationships have not been under debate.

Where direct examination has been impossible comparisons have been drawn from the literature and many figures have been redrawn from other authors in order that complete comparisons might be made. For the convenience of students, also, outline figures have been included to illustrate every family of importance. Those of the Galea which could be drawn directly from the specimens are shaded, since the identification of species in this group often depends upon the arrangement of stripes and spots.

LIST OF SPECIMENS EXAMINED

CHISMOPNEAE

Callorhynchus callorhynchus.—Adult male specimen, preserved; Mar del Plata; collection of T. Marini.

SQUALEA

Squalus acanthias.—Adult male and female specimens, preserved; collection of American Museum of Natural History and of T. Marini.

Squalus fernandinus.—Young female specimen, preserved; Buenos Aires; collection of T. Marini.

Squalus mitsukurii.—Adult male specimen, fresh; Tokyo market.

Etmopterus lucifer.—Male and female specimens, preserved; Japan; collection of Imperial University.

Pristiophorus japonicus.—Male specimen, preserved; Japan; collection of American Museum of Natural History.

PLATOSOMEAE

Rhinobatus granulatus.—Young female specimen, fresh; Batavia market.

Pristis cuspidatus.—Young female specimen, fresh; Batavia market.

Raja; *Manta*; *Torpedo*.

HETERODONTEA

Heterodontus japonicus.—Adult female and young male specimens, fresh; Japan; Misaki.

HEXANCHEA

Heptanchias perlo.—Young male specimen, preserved; Japan; collection of Imperial University.

Notorhynchus pectorosus.—Young male and adult female specimens, preserved; Buenos Aires; collection of T. Marini.

Chlamydoselachus anguineus.—Adult female specimen, preserved, viscera removed; Kuma Aoki; Misaki, Japan.

GALEA

Orectoloboidea

Chiloscyllium indicum.—Male and female specimens, fresh; Batavia market.

Chiloscyllium griseus.—Male specimen, preserved; Batavia; collection of Batavia Laboratory.

Chiloscyllium plagiosum.—Young male specimen, preserved; Batavia; collection of Batavia Laboratory.

Stegostoma tigrinum.—Young female specimen, preserved; Batavia; collection of Batavia Laboratory.

Rhineodon typus.—Some parts of male specimen; Florida, 1928; collection of American Museum. Skull and visceral arches and heart from 30-foot specimen taken Long Island, N. Y., 1935; collection of American Museum.

Odontaspoidea

Carcharias taurus.—Young female specimen, preserved; Buenos Aires; collection of T. Marini.

Scapanorhynchus mitsukurii.—Female specimen, preserved; Japan; collection of American Museum of Natural History. Also a stuffed specimen in Kyoto, Japan.

Isuroidea

Cetorhinus maximus.—Skeletal parts of female specimen, including gill rakers; collection of American Museum.

Catuloidea

Catulus retifer.—Young male specimen, preserved; New York; collection of American Museum.

Catulus torazame (Garman), *Halaelurus torazame* (Tanaka).—Adult male and female specimens, preserved; Japan; collection of Imperial University.

Halaelurus burgeri.—Adult male and female specimens, preserved; Japan; collection of Imperial University.

Halaelurus bivius (Garman), *Scyliorhinus chilensis* (Smitt, 1898).—Adult male specimen, preserved; Buenos Aires; collection of T. Marini.

Calliscyllium venustum (Tanaka), *Triakis venusta* (Garman).—Adult male and female specimens, preserved; Japan; collection of Imperial University.

Parmaturus xaniurus.—Adult male specimen, preserved; New York; collection of American Museum.

Pristiurus eastmani.—Young female specimen, preserved; Batavia; collection of Batavia Laboratory.

Atelomycterus marmoratus (*Scyllium marmoratum*).—Adult male specimen, preserved; Batavia; collection of Batavia Laboratory.

Carcharinoidea

Triakidae

Triakis scyllium.—Adult and young male and female specimens, fresh; Japan; Tokyo market.

Galeorhinidae

Galeorhinus mustelus.—Adult male specimen, preserved; Buenos Aires; collection of T. Marini.

Galeorhinus fasciatus.—Young male specimen, preserved; Buenos Aires; collection of T. Marini.

Galeorhinus manazo Garman (*Cynias manazo* Tanaka).—Adult female specimen, preserved; Japan; collection of Imperial University. Also male specimen, fresh; Japan; Tokyo market.

Carcharinidae

Eugaleus galeus Garman (*Galeus canis* Rondelet).—Female specimen, preserved; Mar del Plata; collection of T. Marini.

Galeus glauca Garman (*Prionace glauca* Jordan).—Young female specimen, preserved; Japan; collection of Imperial University. Adult male specimen, viscera removed; Japan; Misaki market.

Carcharinus commersonii.—Adult male specimen, preserved; New York; collection of American Museum.

Carcharinus milberti.—Adult male specimen, preserved; New York; collection of American Museum.

Carcharinus acronotus.—Young female specimen, preserved; New York; collection of American Museum.

Carcharinus porosus.—Young female specimen, preserved; New York; collection of American Museum.

Carcharinus milberti japonicus.—Adult male specimen, viscera removed, fresh; Japan; Misaki market.

Carcharinus limbatus.—Female specimen, fresh; Batavia market.

Carcharinus sorrah.—Young female specimen, fresh; Batavia market.

Carcharinus dussumieri.—Young female specimen, preserved; Batavia; collection of Batavia Laboratory.

Carcharinus spallanzani.—Young female specimen, preserved; Batavia; collection of Batavia Laboratory.

Carcharinus borneensis.—Young male specimen, preserved; Batavia; collection of Batavia Laboratory.

Physodon mülleri.—Young female specimen, preserved; Batavia; collection of Laboratory.

Scoliodon wahlbeehmi.—Young female specimen, fresh; Batavia market.

Sphyrna zygaena.—Adult male specimen, viscera removed; Japan; Misaki market. Young male and female specimens, fresh; Batavia market.

Sphyrna blochii.—Young female specimen, fresh; Batavia market.

Sphyrna tudes.—Young male specimen, preserved; collection of American Museum.

TERMINOLOGY

Tables I to IV

Any attempt to follow priority rules throughout a classification results in conflict with general usage and in the discarding of certain names of more appropriate derivation. In general, however, the law avoids a great deal of confusion and is followed in the present classification. Priority, by general agreement does not go farther back than 1758, yet the name Chondropterygii (Greek *chondros*, cartilage, and *pteryx*, wing or fin) was applied to the cartilaginous fishes by Linnaeus as early as 1735. The group then included elasmobranchs, lampreys, and sturgeons, and had been recognized by Aristotle and Pliny.¹ In 1686 Willughby separated the Cartilaginei plani (with ventral gills) from the Cartilaginei longi (with lateral gills), and in 1806 Duméril divided the cartilaginous fishes into the Trematopnés (Gr. *trēma*, hole, and *pnēō*, to breathe) and the Chismopnés (from Gr. "*chismē*" = *schisma*, a cleft). This division was made according to the presence or absence of an opercular covering over the gills. The lampreys he placed in a family under the Trematopnés, using the terms Plagiostomes (Gr. *plagios*, oblique, and *stoma*, mouth) and Cyclostomes (Gr. *kyklos*, circle).

In 1817 Cuvier used the term "Sélachiens" (Gr. *selachos*) to include sharks, rays, and chimaeras; and in 1832 Bonaparte introduced the subclass Elasmobranchii (Gr. *elamos*, metal plate, and Gr. *branchia*, gills). These terms are still in familiar use in the literature but have been dropped as group headings. Bonaparte was the first to separate the Cyclostomes from the group, dividing it into the Selacha and Holocephala (Gr. *holos*, whole, and *kephalē*, head).

At about the same time Agassiz from his study of fossil fishes reunited all groups under the Placoidei (Gr. *plax*, plate) for the placoid scales, but the elasmobranch grouping had become too well recognized for this division to stand.

The first systematic account of the elasmobranchs was made by Müller and Henle in 1837. They divided the Elasmobranchii directly into families without subdivisions. In 1846 Johannes Müller returned to Bonaparte's terminology, dividing the subclass Selachii into the

¹ Woodward, A. Smith, 1889.

Plagiostomi and Holocephali. Sir Richard Owen in 1860 made three subdivisions: the Squalidae, Raiidae, and Cestraciontidae, using family names previously established, and in 1865 Duméril introduced the terms Pleurotrèmes (Gr. *pleura*, side, and *trēma*, hole) and Hypotrèmes (*hypo*, under) to distinguish between the lateral and ventral gill openings.

There followed a period of intense internal examination of the elasmobranchs and each investigator attempted to divide the group according to some single skeletal structure. Hasse in 1882 divided the Elasmobranchii according to vertebral structure into the Diplospondyli (Gr. *diploos*, double, and *sphondylos*, vertebra) or Palaeospondyli (Gr. *palaios*, ancient) for the notidanids; dividing the rest into the Cyclospondyli (Gr. *kyklos*, circle) for the Squalea; the Tectospondyli (L. *tectum*, roof, cover) for the rays and *Pristiophorus*; and the Asterospondyli (Gr. *astēr*, star) for the Galea and Port Jacksons.

This was the first recognition of the fundamental differences between the subdivisions of the elasmobranchs, and, although Hasse's names have fallen into disuse and his definitions of the asterospondylic and tectospondylic types do not hold, this distinction is, in general, useful.

In 1883 Gill made a division on the character of the jaw articulation: (1) Opisarhtri (Gr. *opisthe*, behind; *arthron*, joint) for the notidanids, with a postorbital articulation between the pterygoquadrate and the cranium; (2) Prosarhtri (Gr. *pro*, before) for the Port Jacksons, with an antorbital articulation; and (3) the Anarthri, with no orbital articulation, including all the modern sharks.

W. A. Haswell in 1884 divided the elasmobranchs into the Palaeoselachii (Gr. *palaios*, ancient) and Neoselachii (Gr. *neos*, young), and this also was done on the basis of endoskeletal characters. In the same year Cope introduced the Ichthyotomi (Gr. *ichthys*, fish, and *tomos*, a slice) to separate certain fossil sharks from the modern groups.

At the present time it is the subdivisions which are the main subject of dispute, and also the family relationships. Several of the recent groupings are shown schematically in Tables II-IV. The proposed classification is shown for comparison in Table I. It differs from that of Tate Regan, 1908 (Table II) chiefly in the separation of the Port Jacksons from the Squalea, making a fourth parallel order, Heterodontea. Tate Regan recognized the fundamental differences between the Galea and the Squalea but called the groups Galeoidei and Squaloidei. Squalea is from the Latin *squalus*, dogfish, Greek *skulax*,

a young dog, and Galea from *galeos*, shark or *galē*, spotted cat. The familiar names dogfishes and cat sharks come from these terms. Although when raised to ordinal rank they have lost their primary significance, they are nevertheless convenient and easy to remember.

The classification of Goodrich, 1909 (Table III), is shown mainly to demonstrate his group headings, Divisions, Tribes, etc., which are confusing and difficult to remember. Garman, 1913 (Table IV), breaks the Antacea into eight family groups, thus denying the fundamental differences between the orders. Garman's is the latest exhaustive work and he has followed the law of priority in general for his terminology, although in some instances he overlooks it without explanation, while in other cases he uses it to the confusion of familiar names. I have adopted his terms in the present work, therefore, except where they add to the general confusion or disagree with my findings.

The terminology of the genera and species presents more difficulties than that of the main headings. The Port Jacksons have for many years been known by the name *Cestracion*. Garman adopts this name for the hammerhead sharks on the ground of priority, but fails to make use of priority with the Port Jacksons. These sharks were named *Heterodontus* by Blainville in 1816, *Cestracion* by Cuvier in 1817, and *Centracion* by Gray in 1831. Garman adopts the latter name, justifying his choice on the suitability of its derivation from the Greek *kentron*, a spur or spine. He maintains that Cuvier's use of *Cestracion* was either a misspelling or an error, since *kestra* means a hammer. He does not, however, explain why he lays aside Blainville's name *Heterodontus*, which has an equally suitable derivation from the Greek *heteros*, different and *odous*, tooth, applying to the two types of teeth in that shark. I have adopted *Heterodontus*, therefore, in the present work; and in order to avoid the confusion arising from the use of the name *Cestracion* for a widely separated group, the hammerheads, I have eliminated it from the latter as well. Its priority claim from Klein, 1742, may be disregarded because "priority" is commonly dated from 1758. For the hammerheads I have adopted the next name to be applied, therefore, that of *Sphyrna* Rafinesque, 1810.

I have retained the name *Catulus* as used by Garman for the large genus *Scyllium*, which has been subdivided in the recent literature to such an extent as to make its use misleading. *Catulus* was introduced by Valmont in 1768, *Scyliorhinus* by Blainville in 1816, and *Scyllium* by Cuvier in 1817. As used in the literature the latter name includes some of the orectolobids as well as the catulids.

I have retained the names *Carcharias* and *Carcharinus* as used by Garman, the former for the odontaspids, and the latter for the large genus of requiem sharks named *Carcharinus* by Blainville in 1816. The name *Carcharias* was applied to the sand sharks in 1810 by Rafinesque, so that Cuvier's use of the name was incorrect. In the proposed classification I am using *Carcharias* for the sand sharks even though the name *Odontaspis* Agassiz, 1853, has had wide popular usage. I have retained the latter name for the superfamily (Odontaspoidea) in order to identify the group with the names to be found in the literature.

I have completely revised the order Galea to include two major suborders with superfamilies. The division has been made on the basis of vertebral structure combined with other consistent characters. The analysis of genera and species will be found at the end of the paper. The key to families is based on structures which I have examined. The details of the genera and species have been taken in many cases from Garman's work, since access to all species was impossible.

TABLE I.—CHART SHOWING THE PROPOSED CLASSIFICATION Modern Groups Only

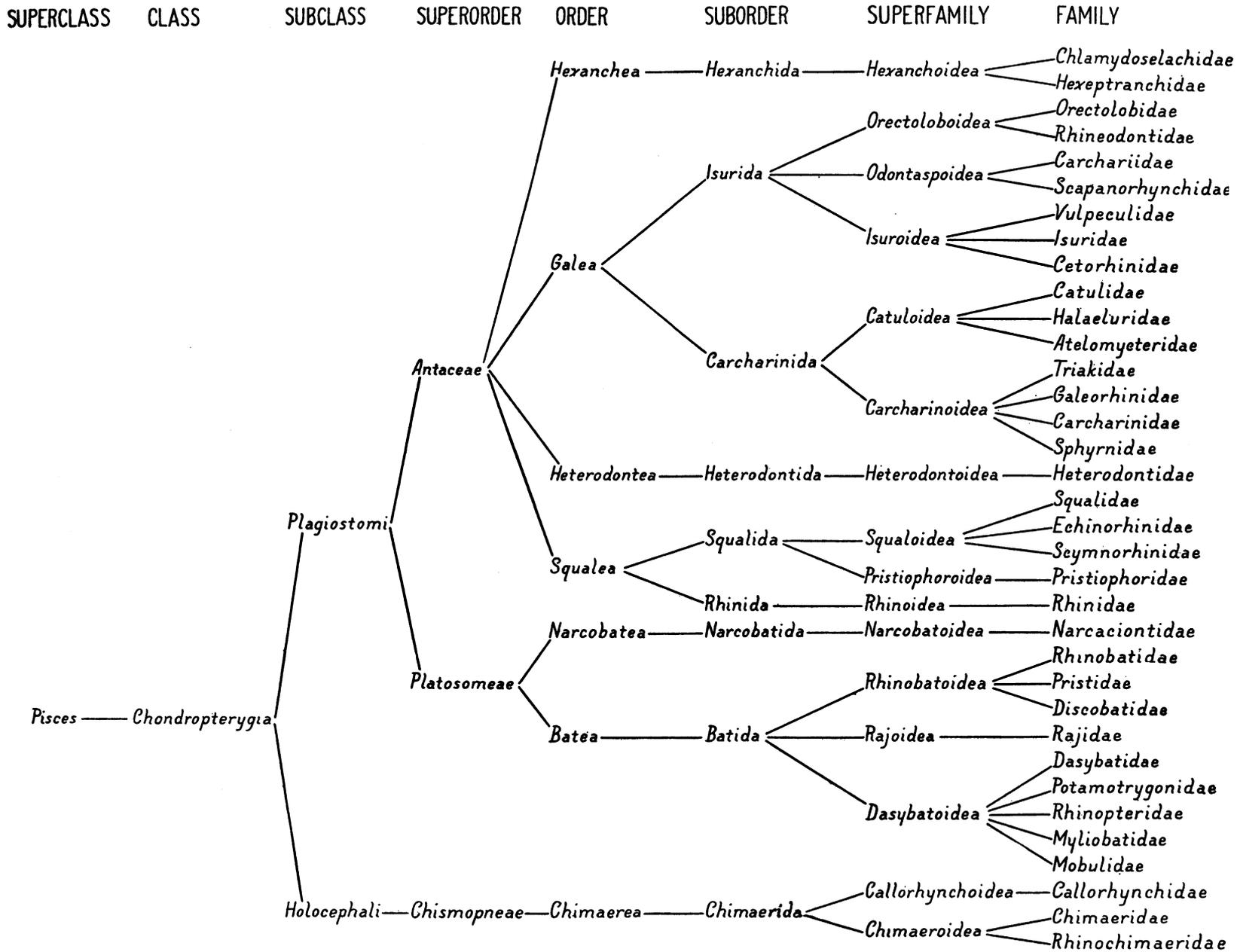


TABLE II.—CHART SHOWING THE CLASSIFICATION OF TATE REGAN, 1906

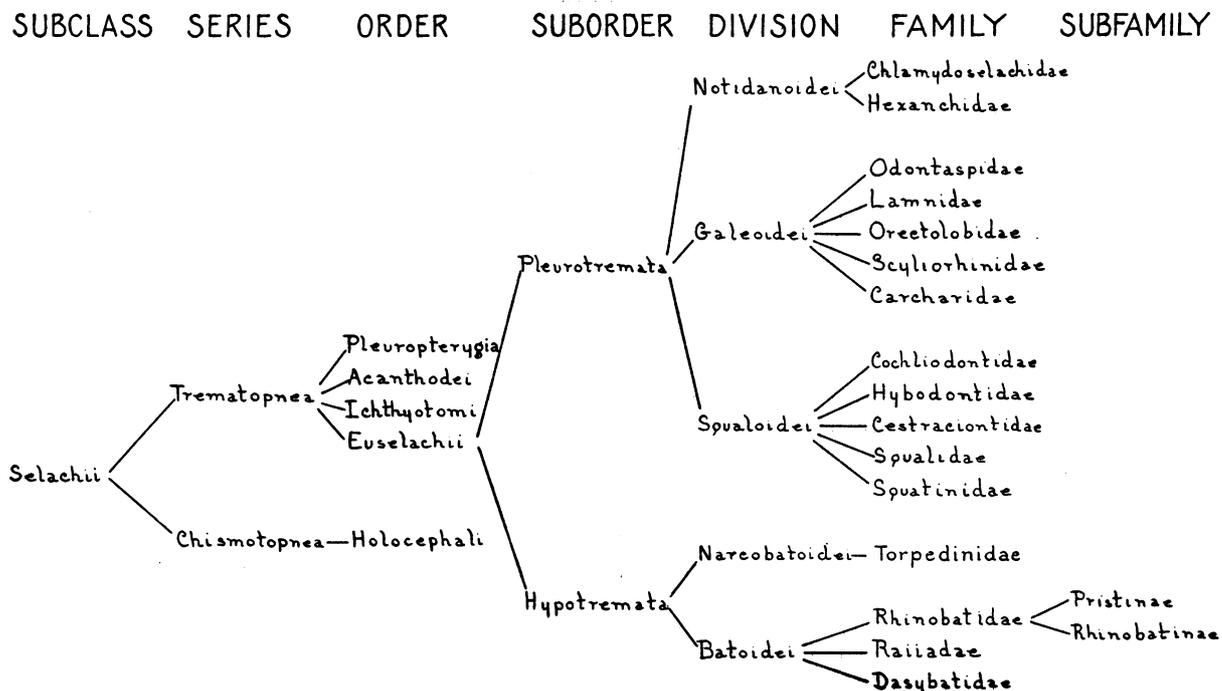


TABLE III.—CHART SHOWING THE CLASSIFICATION OF GOODRICH, 1909
The Final Subdivisions into Families Have Been Omitted

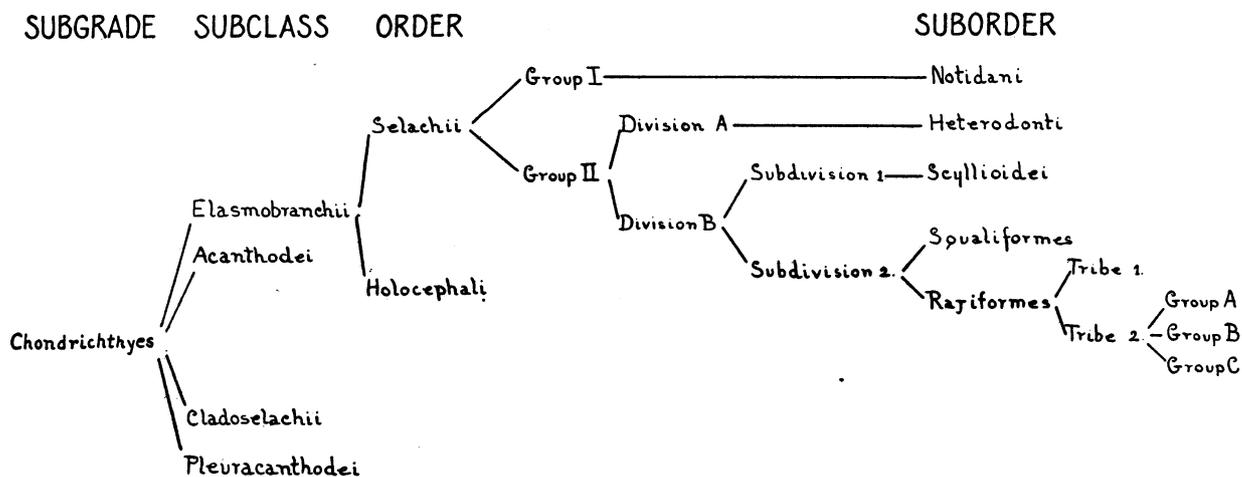
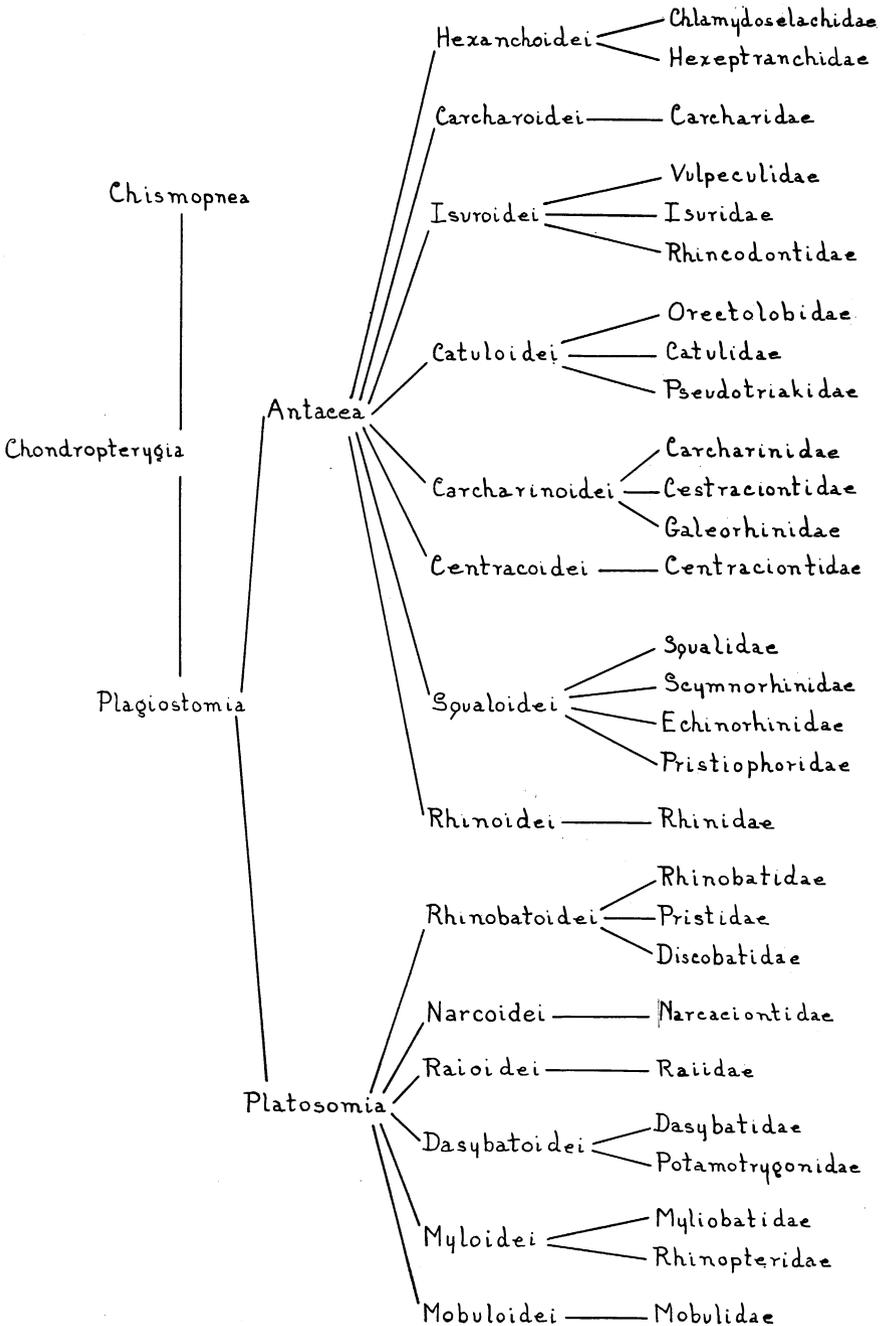


TABLE IV.—CHART SHOWING THE CLASSIFICATION OF GARMAN, 1913
 CLASS ORDER SUBORDER GROUP FAMILY



OUTLINE CLASSIFICATION OF THE ELASMOBRANCHS

Table I; Figures 1 to 62

Superclass Agnatha

Superclass Pisces

Class Chondropterygia (elasmobranch fishes)

Subclass Stegoselachi (armored sharks)

Superorder Stegoselacheae

Family Macropetalichthyidae (Devonian) (Fig. 3)

Family Cratoselachidae (Carboniferous)

Subclass Rhenanidini

Superorder Rhenanidineae

Order Rhenanidinida

Family Gemündinidae (Devonian)

Subclass Pleuropterygii

Superorder Pleuropterygeae

Order Cladodea

Family Cladoselachidae (Devonian, Carboniferous)
(Fig. 4)

Family Symmoriidae (Devonian, Carboniferous)

Family Ctenacanthidae (Devonian-Permian)

Subclass Ichthyotomi

Superorder Pleuracanthaeae

Order Pleuracantha

Family Pleuracanthidae (Permian) (Fig. 5)

Subclass Plagiostomi (sharks and rays)

Superorder Antaceae (sharks)

Order Hexanchea

Suborder Hexanchida

Superfamily Hexanchoidea

Family Chlamydoselachidae (Fig. 12)

Family Hexepranchidae (Fig. 13)

Order Galea

Suborder Isurida

Superfamily Orectoloboidea

Family Orectolobidae (Figs. 15-17)

Family Rhineodontidae (Fig. 18)

Superfamily Odontaspoidea

Family Carchariidae (Fig. 19)

Family Scapanorhynchidae (Fig. 20)

Superfamily Isuroidea

Family Vulpeculidae (Fig. 22)

Family Isuridae (Fig. 21)

Family Cetorhinidae (Fig. 23)

- Suborder Carcharinida
 - Superfamily Catuloidea
 - Family Catulidae (Figs. 24-28)
 - Family Halaeluridae (Figs. 29-31)
 - Family Atelomycteridae (Fig. 32)
 - Superfamily Carcharinoidea
 - Family Triakidae (Fig. 33)
 - Family Galeorhinidae (Fig. 34)
 - Family Carcharinidae (Figs. 35-38)
 - Family Sphyrnidae (Figs. 39-41)
- Order Heterodontea
 - Suborder Heterodontida
 - Superfamily Heterodontoidea
 - Family Heterodontidae (Fig. 42)
 - Suborder Hybodontida
 - Superfamily Hybodontoidea
 - Family Hybodontidae (Triassic, Jurassic) (Fig. 6)
 - Suborder Edestida
 - Superfamily Edestoidea
 - Family Edestidae (Carboniferous, Permian) (Pl. XVI, *e-g*)
- Order Squalea
 - Suborder Squalida
 - Superfamily Squaloidea
 - Family Squalidae (Figs. 43-45)
 - Family Echinorhinidae (Fig. 46)
 - Family Scymnorhinidae (Fig. 47)
 - Superfamily Pristiophoroidea
 - Family Pristiophoridae (Fig. 48)
 - Suborder Rhinida
 - Superfamily Rhinoidea
 - Family Rhinidae (Fig. 49)
- Superorder Platosomeae (rays)
- Order Narcobatea
 - Suborder Narcobatida
 - Superfamily Narcobatoidea
 - Family Narcaciantidae (Fig. 53)
- Order Batea
 - Suborder Batida
 - Superfamily Rhinobatoidea

Family Rhinobatidae (Fig. 50)

Family Pristidae (Fig. 51)

Family Discobatidae

Superfamily Rajoidea

Family Rajidae (Fig. 52)

Superfamily Dasybatoidea

Family Dasybatidae (Fig. 54)

Family Potamotrygonidae (Figs. 55, 56)

Family Myliobatidae (Fig. 57)

Family Rhinopteridae (Fig. 58)

Family Mobulidae (Fig. 59)

Subclass Bradyodonti

Superorder Bradyodonteae

Order Bradyodonteae

Suborder Bradyodontida

Family Petalodontidae (Devonian, Carboniferous, Permian)

Family Cochliodontidae (Devonian, Carboniferous, Permian)

Family Psammodontidae (Carboniferous)

Family Copodontidae (Carboniferous)

Subclass Ptyctodonti

Superorder Ptyctodonteae

Suborder Ptyctodontida

Family Ptyctodontidae (Devonian, Mississippian)

Subclass Holocephali

Superorder Chismopneae

Order Chimaerea

Suborder Chimaerida

Superfamily Callorhynchoidea

Family Callorhynchidae (Fig. 61)

Superfamily Chimaeroidea

Family Chimaeridae (Fig. 60)

Family Rhinochimaeridae (Fig. 62)

Order Squalorajea

Suborder Squalorajida

Superfamily Squalorajoidea

Family Squalorajidae (Jurassic)

Family Myriacanthidae (Jurassic, Cretaceous)

Class Acanthodia

Class Osteopterygia

Figures 1-7 illustrate fossil forms of interest in the development of the modern elasmobranchs. All redrawn.

Figures 8-62 illustrate the family divisions of the proposed classification. The outline figures have been redrawn from various authorities; the shaded figures have been drawn from the specimens.

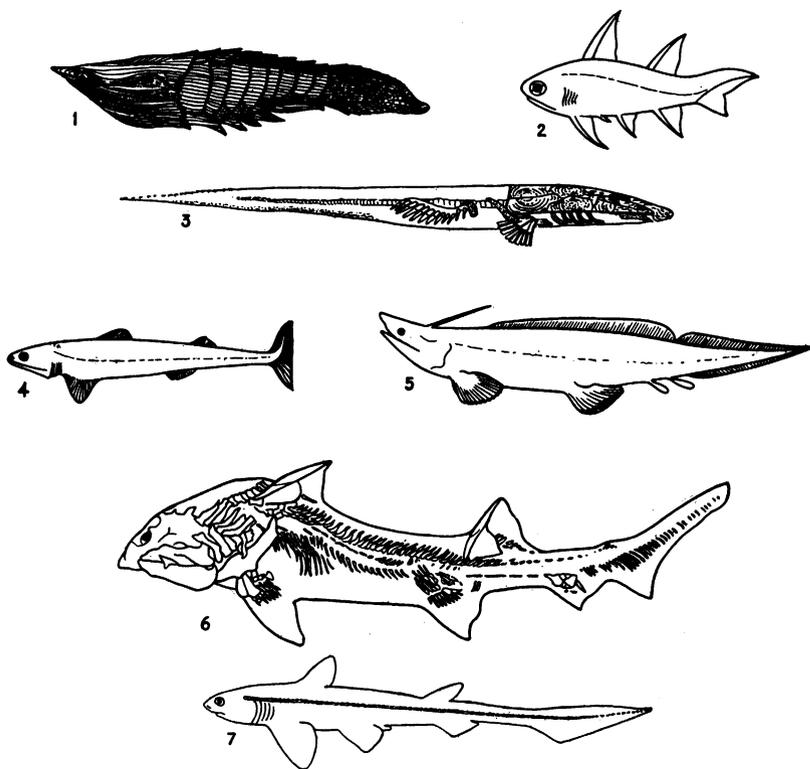


Fig. 1. Superclass Agnatha: *Anglaspis heintzi*, after Kiaer, 1932. Upper Silurian.

Fig. 2. Class Acanthodia: *Diplacanthus striatus*, after Traquair. Devonian.

Fig. 3. Superclass Pisces, Class Chondropterygia, Subclass Stegocephali: *Macropetalichthys prumiensis*, after Broili, 1933. Lower Devonian.

Fig. 4. Class Chondropterygia, Subclass Pleuropterygii: *Cladoselache*, after Dean, 1909. Upper Devonian.

Fig. 5. Subclass Ichthyotomi: *Pleuracanthus*. Permian.

Fig. 6. Subclass Plagiostomi, Superorder Antaceae, Order Heterodontea, Family Hybodontidae: *Hybodus hauffianus* E. Fraas, after Koken. Upper Lias.

Fig. 7. Family Hybodontidae: *Palaeospinax priscus*, after Dean, 1919. Lias.

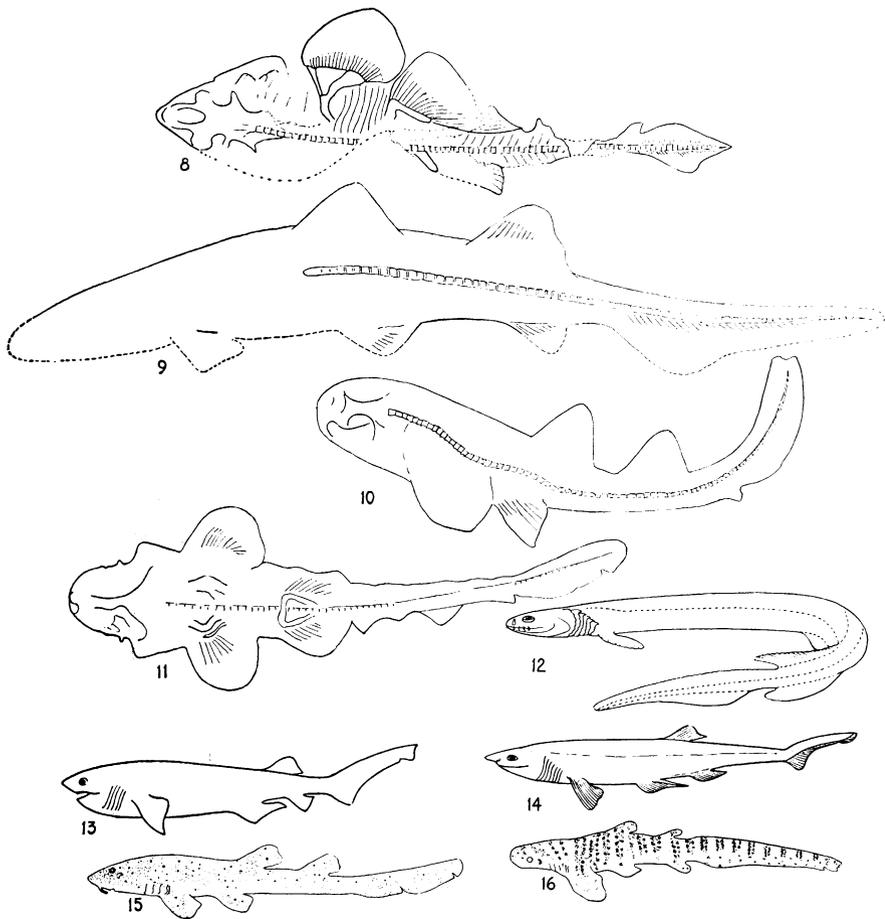


Fig. 8. Order Squalea, Family Protospinacidae: *Protospinax annectans*, after Smith Woodward, 1918. Upper Jurassic.

Fig. 9. Order Galea, Family Catulidae: *Palaeoscyllium formosum*, after Wagner, 1861. Upper Jurassic.

Fig. 10. Family Orectolobidae: *Crossorhinops minus* White, 1936.¹ (*Palaeoscyllium minus* Smith Woodward 1889). Upper Jurassic.

Fig. 11. Family Orectolobidae: *Crossorhinus jurassicus*, after Smith Woodward, 1918.

Fig. 12. Family Chlamydoselachidae: *Chlamydoselachus anguineus*.

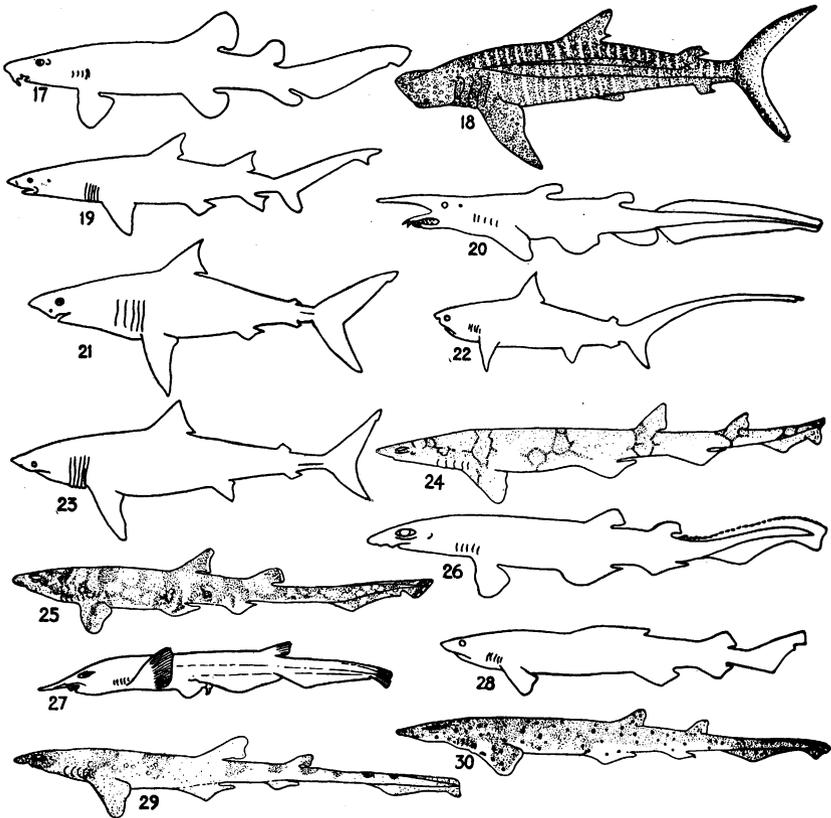
Fig. 13. Family Hexepranchidae: *Hexanchus corinus*.

Fig. 14. Family Hexepranchidae: *Hepranchias perlo*.

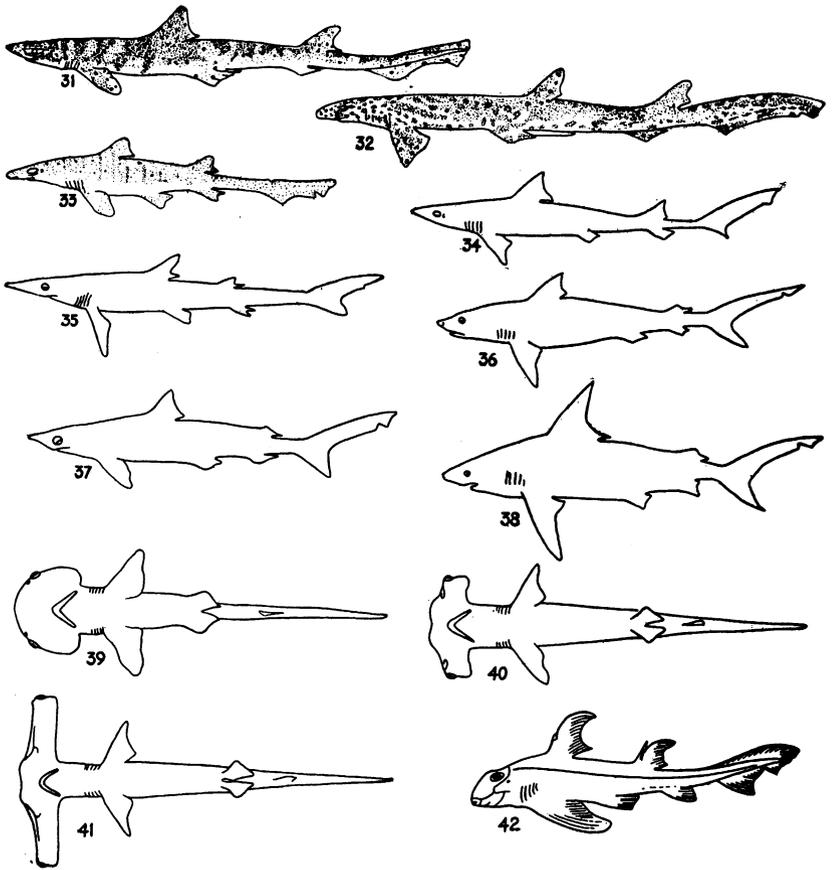
Fig. 15. Family Orectolobidae: *Chiloscyllium indicum*.

Fig. 16. Family Orectolobidae: *Stegostoma tigrinum*.

¹ 1936, Novitates, No. 837, pp. 14, 15, April 3.



- Fig. 17. Family Orectolobidae: *Ginglymostoma cirratum*.
 Fig. 18. Family Rhineodontidae: *Rhineodon typus*.
 Fig. 19. Family Carchariidae: *Carcharias taurus*.
 Fig. 20. Family Scapanorhynchidae: *Scapanorhynchus owstoni*.
 Fig. 21. Family Isuridae: *Isurus punctatus*.
 Fig. 22. Family Vulpeculidae: *Vulpecula marina*.
 Fig. 23. Family Cetorhinidae: *Cetorhinus maximus*.
 Fig. 24. Family Catulidae: *Catulus retifer*.
 Fig. 25. Family Catulidae: *Catulus torazame*.
 Fig. 26. Family Catulidae: *Parmaturus xaniurus*.
 Fig. 27. Family Catulidae: *Pentanchus profundicolus*.
 Fig. 28. Family Catulidae: *Pseudotriakis microdon*.
 Fig. 29. Family Halaeluridae: *Halaelurus burgeri*.
 Fig. 30. Family Halaeluridae: *Halaelurus bivius*.



- Fig. 31. Family Halaeluridae: *Calliscyllium venustum*.
 Fig. 32. Family Atelomycteridae: *Atelomycterus marmoratus*.
 Fig. 33. Family Triakidae: *Triakis scyllium*.
 Fig. 34. Family Galeorhinidae: *Galeorhinus canis*.
 Fig. 35. Family Carcharinidae: *Galeus glaucus*.
 Fig. 36. Family Carcharinidae: *Galeocerdo tigrinum*.
 Fig. 37. Family Carcharinidae: *Scoliodon wahlbeehmi*.
 Fig. 38. Family Carcharinidae: *Carcharinus milberti*.
 Fig. 39. Family Sphyrnidae: *Sphyrna tudes*.
 Fig. 40. Family Sphyrnidae: *Sphyrna zygaena*.
 Fig. 41. Family Sphyrnidae: *Sphyrna blochii*.
 Fig. 42. Order Heterodontea, Family Heterodontidae: *Heterodontus philippi*

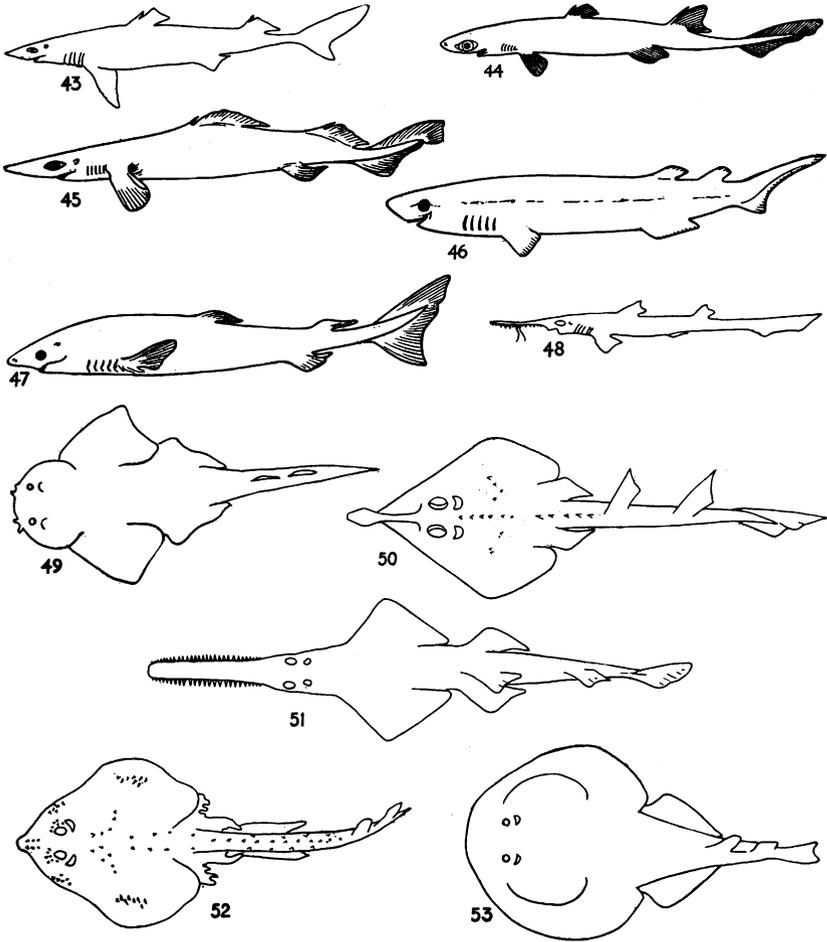
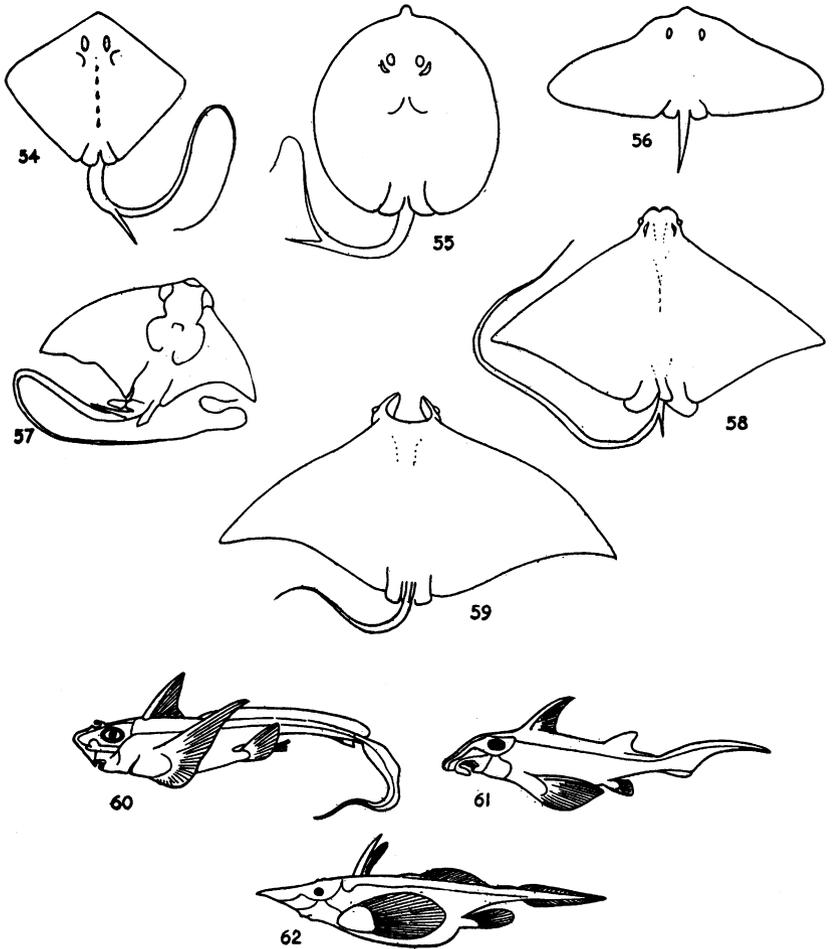


Fig. 43. Order Squalea, Family Squalidae: *Squalus acanthias*.
 Fig. 44. Family Squalidae: *Etmopterus lucifer*.
 Fig. 45. Family Squalidae: *Acanthias hystricosum*.
 Fig. 46. Family Echinorhinidae: *Echinorhinus brucus*.
 Fig. 47. Family Scymnorhinidae: *Somniosus microcephalus*.
 Fig. 48. Family Pristiophoridae: *Pristiophorus japonicus*.
 Fig. 49. Family Rhinidae: *Rhina californica*.
 Fig. 50. Order Batea, Family Rhinobatidae: *Rhinobatus granulatus*.
 Fig. 51. Family Pristidae: *Pristis clavata*.
 Fig. 52. Family Rajidae: *Raja erinacea*.
 Fig. 53. Order Narcobatea, Family Narciontidae: *Narcine brasiliensis*.



- Fig. 54. Order Batea, Family Dasybatidae: *Dasybatus longus*.
 Fig. 55. Family Potamotrygonidae: *Potamotrygon laticeps*.
 Fig. 56. Family Potamotrygonidae: *Pteroplatea japonica*.
 Fig. 57. Family Myliobatidae: *Myliobatis californicus*.
 Fig. 58. Family Rhinopteridae: *Rhinoptera quadriloba*.
 Fig. 59. Family Mobulidae: *Mobula hypostoma*.
 Fig. 60. Subclass Holocephali, Family Chimaeridae: *Chimaera monstrosa*.
 Fig. 61. Family Callorhynchidae: *Callorhynchus callorhynchus*.
 Fig. 62. Family Rhinochimaeridae: *Harriotta raleighana*.

ANTIQUITY OF THE ELASMOBRANCHS

Tables V, VI

Modern elasmobranchs are a survival of a Paleozoic race, relatively unsuccessful as fishes but of interest because they were the oldest of the jawed vertebrates. Their possible relationships with their predecessors the Agnatha may be briefly considered. These Agnatha were an armored race of jawless vertebrates appearing sporadically in the early Silurian formations, becoming abundant in the late Silurian and Devonian, and becoming extinct at the close of the Devonian. Great progress in the knowledge of this group has been made in the last decade or so due to the discoveries of the Danish, Norwegian, and Swedish expeditions to Spitzbergen, East Greenland, and adjacent regions. The superb material thus revealed has enabled Stensiö to give accurate descriptions of the chambers containing the central nervous system and of the tubes transmitting the nerves and blood vessels of the head. The labors of Stensiö and Kiaer have resulted in many far reaching conclusions concerning the relationships of these early forms.

Two groups of Agnatha are important phylogenetically: the Osteostraci, which lead to the modern cyclostomes, and the Heterostraci, some of which may lead to the elasmobranchs. The head and thorax in the Heterostraci are characteristically encased in an armor composed of five pieces: a dorsal shield, a ventral shield, two lateral plates, and a rostral plate. In the Osteostraci the dorsal shield bends over the sides to form a carapace. The abdominal region is covered with separate overlapping plates or with minute denticles. The axis of the tail may be straight or turned downward.

The material of the shields on microscopic examination shows four layers of tissue: a basal layer, which in the Osteostraci contains true bone cells, a cancellated layer, a reticular layer, and an external layer of dentine. The canals of the lateral line system pass through the reticular layer and open by pores on the outside. On the ventral surface of the dorsal shield impressions of the internal structures are often found, showing the course of the lateral line system, the nasal openings, and the gills. Some endoskeletal elements have been found.

In the Osteostraci there are numerous gills, from nine to fifteen, several of which lie anterior to the region of the spiracle in fishes. Each has a separate opening on the ventral surface just back of the pineal impression, and the two very small orbits lie close together behind it. Stensiö has worked out the anatomy of the cephalaspids in detail, and finds that all the cavities and canals are lined with bone cells. The

brain case, head shield, and gill cavities all suggest the modern *Petro-myzon*, as do also the single dorsal nasal opening and the two semi-circular canals in the ear. Thus the cyclostomes today are a degenerate race but are, no doubt, a survival of this ancient group.

The Heterostraci are less specialized and more primitive than the Osteostraci although not an earlier development since both groups date from the Upper Silurian. The Heterostraci are mostly small, fusiform to depressed grovellers without paired appendages (Fig. 1). The gills are only six or seven in number and there is a single opening for them on each side. The mouth is a slit on the ventral surface and the hypophysial opening seems to be within the mouth cavity. In certain cases the presence of two nasal sacs is suggested by paired swellings in the endoskeletal cast. The armor has no bone cells and the shield varies from five plates in *Poraspis* to minute denticles in *Thelodus*.

Smith Woodward (1915) suggested that the plates were formed by the fusion of denticles and that the shape of the plates was determined by the arrangement of the soft parts underneath. Kiaer (1932) suggests that the single piece is primitive and that the separate plates are due to the breaking up of the shield. He has shown in his plates many gradations from fine parallel lines all over the primary five plates to many small whorls. The intermediate stages look like finger prints. They extend all over the shields even where no muscles are present underneath. This suggests that the breaking up of the plates has been due to a change in the rates of development of the different regions, and indicates a genetic drift rather than the influence of muscles. For a series showing the possible course of this process, see the section on Dermal Denticles.

Three groups of jawed vertebrates appeared in the early Devonian, all possible derivatives of the earliest Heterostraci. The Arthrodiros were a grovelling group with the whole body encased in a bony armor. Stensiö has suggested a possible connection with the Holocephali. Otherwise they show no relation to higher forms but a contemporary related group is found in the Antiarchi. These were even more depressed and were almost completely encased in armor. Both groups became extinct in the upper Devonian. The Acanthodians (Fig. 2) were fusiform, fish-like types in which the armor was composed of small quadrangular plates, larger on the head and covered with a substance like ganoine which is suggestive of the higher fishes. The paired and unpaired fins were fishlike and all bore spines. In some species accessory paired fins appeared. The spines had a remnant of the tubercular armor

on their front margins and each of the five pairs of gills had a separate opercular covering. These have sometimes been classed as sharks but the discrepancies are too great for any close relationship. There is very little axial endoskeleton and at most vestigial endoskeletal supports for the fins. They probably represent an unsuccessful attempt at open water life for, like many of the Paleozoic specializations, they became extinct in the Permian.

The elasmobranchs first appeared in the early Devonian. Possibly the most primitive known is the small marine *Macropetalichthys prumiensis* E. Kayser (Fig. 3). This, as described by Broili, 1933, was an armored "shark," retaining a dorsal shield composed of several bony plates but having an endoskeleton well preserved and distinctly on the elasmobranch plan. The body is depressed anteriorly but not extremely so. It dwindles to a point at the tail with no unpaired fins, but the paired fins are large and have complete endoskeletal supports. For a description of this fin, see the section on Fin Skeletons. Its appearance at this early period suggests that the elasmobranchs had their origin in the Silurian, although no forms have been found, and that the paired fins of fishes had a much earlier origin than has been supposed. In the Agnatha, where the lateral appendages are present they are in about the position of the normal pectoral fins. If these outgrowths were stimulated by the muscular movements, the form may have been determined by the bony armor, and the elasmobranch fins, stimulated in a similar way but with freer movement, may have taken a different form.

Smith Woodward (1915) suggested that the fusiform shape with the anterior dorsal fin was primitive, and believed that open sea life preceded the grovelling life in any group. In the modern sharks, however, the slightly depressed groups retain more of the archaic characters than do the fusiform groups and, looking back through the geological record, we can see that the grovellers must always have preceded the swimmers if only because of the abundance of invertebrate life on the bottom and near the shores. The first vertebrates must necessarily have depended upon the invertebrates for food, and Romer suggests that the bony armor was first acquired as a protection against the large and voracious eurypterids, which were among the scorpion-like invertebrates that flourished during the same period.

A great many types of aquatic life, both invertebrate and vertebrate, became extinct at the close of the Paleozoic, and only a few of the grovelling fishes were able to persist through what must have been a

period of famine in the greatly depleted seas. Therefore I look upon the grovelling types and littoral types as more primitive than the pelagic types in any group except where the bottom-living habit has become so exaggerated as to constitute an extreme specialization, as in the rays. Broili (1930) described a very similar specialization from the Upper Devonian, *Gemündina stürtzi* Traquair, a curiously flattened fish with expanded pectorals and a terminal mouth. The dorsal shield has lost the central plates, the lateral plates are fenestrated, and the endoskeleton is plainly on the elasmobranch plan.

In the late Devonian are found the first true elasmobranchs (Fig. 4) in which the dermal armor has become reduced to the covering of minute denticles, and the dorsal fin spines. The spines are often greatly ornamented with dentine ridges and with rows of tubercles. Tooth development determined the success of the group and more can be learned of the history of the elasmobranchs from tooth structure than from any other single character. This is largely true because often the teeth were the only things preserved in the geological strata, and because the teeth reflect closely the feeding habits of the animals. For a discussion of tooth development, see the section on Teeth (p. 65).

The teeth of the Paleozoic sharks were all broad-based and firmly attached to the jaw. The modern teeth have two roots and are easily extruded. The transition occurred through the group of hybodonts that lived during the Triassic. As the seas became restocked with small teleostomous fishes elasmobranch development began to flourish again, and during the Jurassic the really great elasmobranch radiation took place. Only the Holocephali and the Hexanchea of the groups existing today can be traced back to an earlier date than the Jurassic, so that they must owe their origin to forms more ancient than the hybodonts. The Holocephali are mollusk eaters and can be traced back to a Paleozoic group of mollusk eaters, the Bradyodonti. The link lies in the predominance of the tubular dentine structure in the crushing teeth. This is a vasodentine substance called palaeodentine by Jaekel (1901). No connecting forms have been found in the Triassic strata but, since they were all grovellers at that time, their persistence may be surmised. The Hexanchea (Pl. XVII) have highly specialized teeth, but they are cuspidate instead of crushing and must owe their origin to the multicuspitate teeth of the *Cladodus* type (Plate XII, *m*, *n*), which was common from the Upper Devonian to the Permian.

All of the other modern groups can be traced directly to the Jurassic, when the greatest elasmobranch radiation of all time took place. The

modern Heterodontea were established at this time in such forms as *Ganodus* and *Heterodontus* (Fig. 42). They differ from *Hybodus* (Fig. 6) largely in the less massive jaw articulation, and are direct descendants of the main hybodont stock. All the other modern types can be traced to the hybodonts through a more modernized type found in the Liassic strata, *Palaeospinax priscus* (Fig. 7). It retains the heterodont dentition with very sharply cuspidate teeth in front, and has the same enamelled dorsal fin spines, but is less overemphasized in the head region and has the general form of the more freely swimming littoral types.

An important group of very small sharks has been described from the Lithographic Stone of Bavaria, an Upper Jurassic formation. These include *Protospinax annectans* (Fig. 8) Smith Woodward (1919), *Crossorhinus jurassicus* (Fig. 11) Smith Woodward (1919), *Palaeoscyllium formosum* (Fig. 9) Wagner (1861), and another type closely resembling *Crossorhinus*, which Smith Woodward has named *Palaeoscyllium minus*. It is difficult to reconcile Smith Woodward's figure with Wagner's *Palaeoscyllium formosum*. The general shape and size suggest *Crossorhinus*, as do the small size and position of the anal fin. The position of the head of the specimen probably conceals any dermal modifications such as the dermal lappets of *Crossorhinus*. I have named¹ this genus *Crossorhinops minus* (Fig. 10), therefore, in order to distinguish between the ancestors of the Orectoloboidea and of the Catuloidea.

Other Jurassic types which have been described from time to time include *Rhina* (*Squatina*) (Fig. 49), *Rhinobatus* (Fig. 50), and *Pristiurus*. The groups established by the Jurassic sharks are the Squalea from *Protospinax*, the Platosomeae from *Rhinobatus* through *Rhina*, thus showing that the rays, while derived from the squaloid line, branched off before the modern squaloids had become established, the Orectoloboidea from *Crossorhinops* and *Crossorhinus*, and the Catuloidea from *Palaeoscyllium* and *Pristiurus*.

The resemblance between the two small orectolobids and *Protospinax annectans* is striking, so that the derivation of this group of the Galea from the squaloid line is most probable. *Palaeoscyllium formosum*, however, shows more general resemblance to *Palaeospinax* and was probably derived directly from the hybodont stock but at a later time than *Protospinax*.

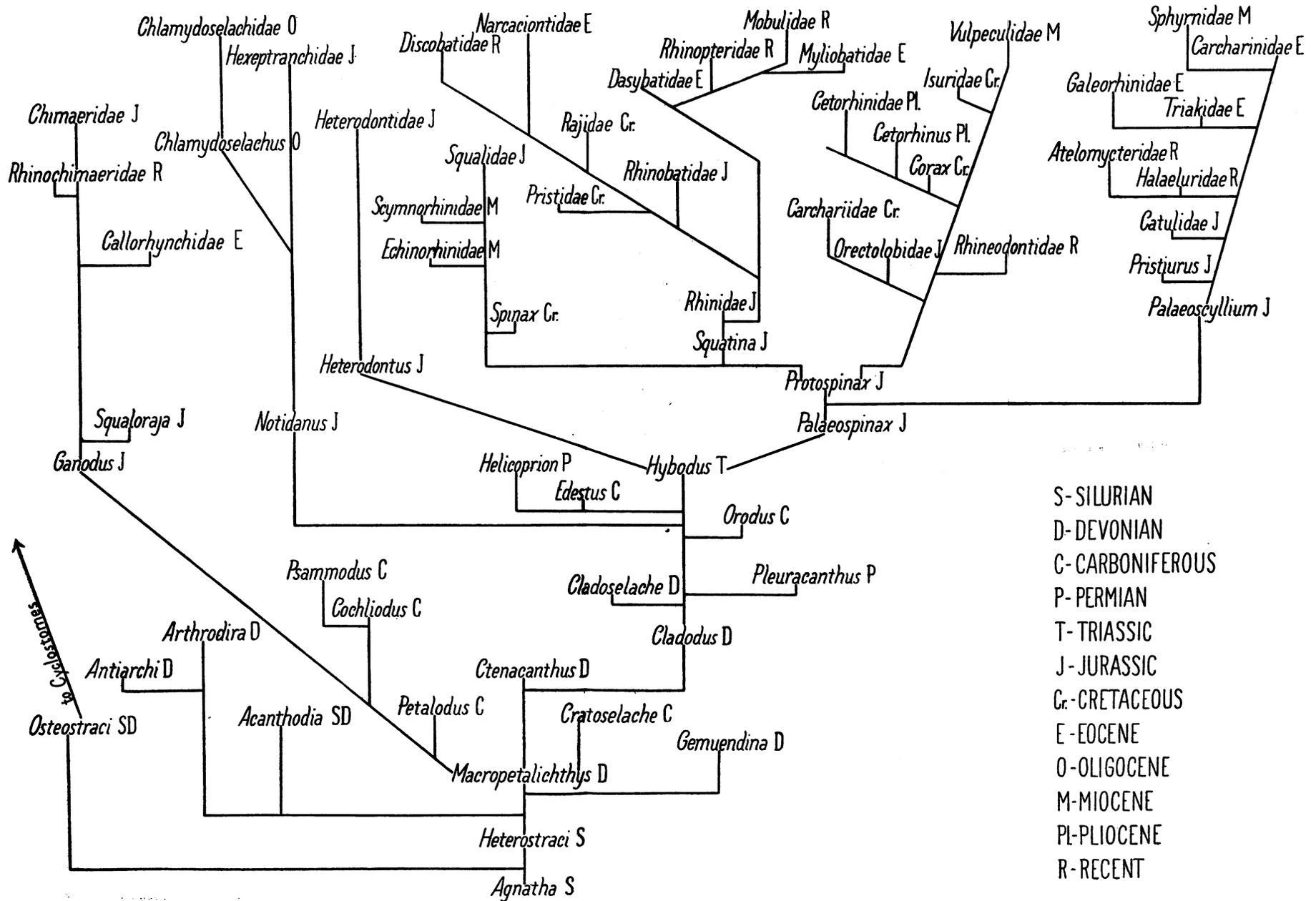
The known Jurassic types were all either bottom-living or littoral.

¹ Novitates, No. 837, pp. 14, 15. April 3, 1936.

It was not until the Cretaceous that the pelagic forms began to develop, and from that time on fossil shark teeth are found in great abundance. The multicuspidate teeth of the orectolobids and catulids are numerous and indicate that the Jurassic teeth were probably of that type. The Odontaspoidea and the Isuroidea with their large unicuspid teeth (Pl. XII) also began to appear. These are the pelagic groups derived from the Orectoloboidea and form the suborder Isurida of the Galea. The pelagic forms of the other suborder, Carcharinida, do not put in their appearance until the Eocene, when they attained great size, and the specialized Sphyrnidae are not abundant until the Miocene.

The geological history is shown in Table V, and the phylogenetic relationships in Table VI. It can be seen from this outline that in all groups the grovelling or littoral forms have preceded the pelagic, and it will be seen from the following sections that the earlier groups retain a greater variability while those more recently established have become more stable as to their phylogenetic characters. The physiological characters vary greatly in all groups.

TABLE VI.—CHART SHOWING THE PHYLOGENETIC RELATIONSHIPS OF THE ELASMOBRANCHS WITH THE PROBABLE STEM FORMS



CHARACTERS USED IN CLASSIFICATION

External characters have always been preferred in the classification of genera and species because of the need of a method of swift identification, and because in the first description of new species authors of the past have seldom made any internal descriptions. External characters are of only physiological importance, however, and many cases in doubt could probably be cleared up by the examination of the internal anatomy. Internal characters for distinguishing between the larger groups have been used by many of the earlier observers, as outlined in the section on Terminology, page 31, but each author relied upon a single character for the division into groups.

Müller and Henle made the first exhaustive account of the elasmobranchs in 1837. They used external characters entirely, and for this reason divided the elasmobranchs immediately into families, basing the distinction upon the position of the dorsal fins. Hasse in 1879 subdivided them on the basis of vertebral structure, and Gill in 1893 on the attachment of the palatoquadrate to the skull. Huber, 1901, suggested the stem joints of the myxopterygia (the basipterygia) as distinguishing characters, and Tate Regan, 1908, used the rostral cartilages and pectoral fin skeletons. Garman, 1913, relied almost entirely on external characters, using teeth, nasoral grooves and valves, and the position of the last two gill openings, among many of the varying characters. Tate Regan also made use of the myxopterygia as distinguishing between orders and between family groups. Leigh Sharpe, 1920-1926, suggested the clasper siphons and clasper glands as not only distinguishing characters but as showing transitional tendencies as well. Garman made an extensive study of the heart valves but beyond suggesting a possible reduction throughout the groups made no use of them systematically. The spiral valves have been examined extensively and have been divided into types by various authors but have never been used in a systematic classification.

In the studies on the specimens listed on page 28, I made a detailed examination of each of the structures mentioned above with the exception of the clasper glands and siphons, and, wherever possible, made comparisons with the literature. As a result I have found that the external characters are in general too variable for anything but identification of genera and species, except where the external character is determined by an internal skeletal structure, such as the position of the gill openings in the sharks and rays. The denticles and teeth, while varying within

families to a large extent, do show a consistent tendency to change in definite directions toward more specialized groups. The position of the dorsal fin has been strangely constant, but the constancy is not absolute, so that it has been a dangerous tool in making certain assignments. I consider all such variable characters to be of physiological rather than phylogenetic significance and believe that doubtful cases can be settled only by examination of the more deeply seated phylogenetic structures.

I find that Hasse's contention is fundamentally sound, but by indefinitely describing his tectospondylic type he has confused certain of the tectospondylic with the asterospondylic. In the corrected sense I have based my divisions upon the supposition that vertebral structure is the basic phylogenetic character upon which the development of the elasmobranchs has hinged, and that in the linking of groups of characters with the vertebral structure even aberrations in the vertebrae can be placed without question. I find also that the suggestions of Gill and Huber hold good without exception, and that the natural groups so established coincide with the vertebral groups. I find the rostral cartilages and pectoral fins to be of inestimable value in distinguishing certain superfamily groups, and to have some value as ordinal characters. The myxopterygia in their basic shape distinguish between orders but their use in distinguishing the lower groups is not sound, since they are subject to extreme variation in details even within a genus.

I find the spiral valves to have some value because of the linkage of certain types of valve with vertebral structure, and I find the heart valves useful in distinguishing superfamily groups and transitional forms.

As a result I conclude that certain groups of characters have been linked together in the evolution of the elasmobranchs, and that to be consistent in classification internal as well as external structure should be examined. Fundamental phylogenetic characters are more stable in development than the surface physiological characters and when doubtful species are found, like the whale shark, *Rhineodon typus*, which combines bottom-living adaptations at the head end with pelagic adaptations in the trunk and tail, only the phylogenetic characters are of substantial use. In this case also the peculiar modifications of the vertebral structure preclude definite decision. Only upon a group of characters, therefore, can an unquestionable taxonomic decision be made.

In distinguishing between phylogenetic and physiological characters I find that the basals of the pectoral fins are stable phylogenetic char-

acters, while the radials are physiological and subject to variation; the general type of rostrum is stable but in certain groups, such as the *Squalea*, the specific development undergoes extreme variation; the basic vertebral structure has been stable but variation has occurred in the radiating calcifications, which are the latest calcifications to develop. The type of spiral valve has been so stable as to have phylogenetic value although not ostensibly a phylogenetic structure. Variation is limited to the number of valves within the type. The same is true of the heart valves. Variations are so frequent that on first thought no type would seem to be stable, yet I find them to vary within any specific group within definite limits so that transition from group to group may be indicated. The basals of the myxopterygia and the fundamental shape of the axial cartilages have proved stable, but the opening and closing of the axial cartilages is subject to much variation.

For the convenience of the reader I have arranged the group characters in parallel columns on pages 97-103. Careful perusal of these tables will demonstrate the linkage of the basic phylogenetic characters and the unexpected linkage of such characters as the ring type of spiral valve with the radial asterospondylic vertebrae, and of the nictitating fold or membrane with the Maltese cross type of vertebra.

EXTERNAL CHARACTERS

Position of Fins

Figures 1 to 62

The position of the dorsal fins is correlated with the mode of locomotion. When both dorsals are behind the pelvic fins greater strength is provided to the posterior region. The shark is able to hold this part of the body steady while swishing the forward part from side to side in search of prey. Fish with this structure are characteristically small and the tail is typically longer than the body. They live near the bottom or fairly close to shore and are littoral types. They feed on schools of smaller fishes. The shape is correlated with a narrow mouth gape. Two large groups of sharks answer this description, the *Orectoiboidea* and the *Catuloidea*, and in all previous classifications these have been given parallel standing. On the basis of a fundamental difference in vertebral structure, however, I have divided these groups into separate suborders.

Both of these groups originated in the Jurassic when the great radiation in elasmobranch structure took place, and like all primitive groups they started in the shallow waters close to shore. I find that variation is more active in primitive than in specialized groups, and as a consequence these groups are highly variable. This is true in the position of the dorsal fins, and in *Calliscyllium venustum* (Fig. 31) and *Pseudotriakis microdon* (Fig. 28) the first dorsal has assumed the anterior position characteristic of the pelagic groups. In *Pseudotriakis*, however, this is accompanied by a general elongation of the unpaired fins and a thickening of the body; in *Calliscyllium* the body is slender but elongate, and while the species is found in fairly deep water in the Sagami Sea, Japan, there is no deepening of the anterior region characteristic of the pelagic forms.

Nevertheless, on fin structure either type might be classed with the higher group, the Carcharinoidea, and as a matter of fact in 1913 Garman listed *Calliscyllium* as a species of *Triakis* (Fig. 33). *Pseudotriakis* he placed in a separate family. On examination of their vertebral structure, however, *Pseudotriakis* is found to agree with all of the Catulidae in having the cyclospondylic type, and *Calliscyllium* has the intermediate type characteristic of the Halaeluridae. The latter family I have established on the vertebral structure.

When the first dorsal is in an anterior position the anterior region of the body is typically deepened and strengthened. The position is correlated with a narrower head, a large, triangular mouth with a wide gape, and strong, piercing teeth. The body is fusiform in shape and motion through the water is swift and effective. This type is found in the large pelagic sharks (Figs. 36-38). It is a type developed late geologically. The Isuroidea (Figs. 21, 22) attained this grade in the Cretaceous and the Carcharinoidea (Figs. 36-38) in the Eocene.

In the rays (Figs. 50-59) the dorsals are found far back on the tail and eventually disappear. This is correlated with extreme depression of the body where no strength for swimming is needed. Movement is controlled by the greatly expanded pectoral fins, which move in wide, flapping motions. This is an extreme specialization in the opposite direction but is probably not a retrogressive specialization from previously fusiform types. The rays originated in the Jurassic and their direction of development was determined at that time before the fusiform shape had been established. Their nearest antecedents were the Jurassic squaloids, probably the Rhinidae, just assuming a more depressed form from the small littoral types.

The position of the dorsal fin is a corollary of the method of locomotion and is only successful as a taxonomic character when the environment and habits do not vary within a group. In the more primitive groups which vary widely it is of little value.

Characters of the Head

Plates I to III

The shape of the head, the position of the mouth and nasal organs, and the size of the spiracle are all characters correlated with water depth. In the Orectoloboidea (Pl. I, *d, e, f*) the head is greatly depressed and the mouth nearly terminal. The nasal grooves reach the mouth, dividing the lip into lobes. These are known as nasoral grooves and the condition is suggestive of the embryonic stage before the lip is completely fused. It is found only in bottom-living forms and it is possible that the grooves have a sensory function, directing food to the mouth. They are frequently accompanied by dermal papillae on the skin about the mouth region.

This condition is found also in the Heterodontea (Pl. I, *g*) and in the Holocephali. The former are Jurassic types strongly resembling the Triassic hybodonts, and are grovelling forms with small mouth openings and lateral crushing teeth. The latter can be traced back to the Paleozoic and are the most archaic of all living elasmobranchs. They are mollusk eaters and have highly modified crushing teeth. Thus the presence of nasoral grooves is a primitive condition passed on from the early grovelling type.

In the Catuloidea (Pl. I, *a, b* and II, *a, b, c, d, e*), which are only slightly less primitive than the Orectoloboidea, the condition is less persistent. These are littoral types and are less adherent to the bottom. Also there is great variability within the group, so that while some have the nasoral grooves, others have the nasal valves at varying distances from the mouth. This is determined directly by the environment, some living in restricted and some in freer waters.

The spiracles (Pl. III) are large or medium in all the bottom-living or littoral types. They grow smaller and finally disappear in the deep sea swimmers. The eyes are lateral in position in all except the extreme bottom-living types. They are narrower and more elongate in the littoral, and large and round in the pelagic types.

The nictitating membrane (Pl. III) is a physiological character which I have found to correlate consistently with one type of vertebral

structure, the Maltese cross type. The only possible explanation of such a correlation must lie in the establishment of linkage groups as recognized by geneticists, and since more than one such group has been found to be consistent, this explanation is offered.

The membrane exists in a rudimentary state in the Catuloidea and is completed in the Carcharinoidea. Several transitional stages are found. *Triakis* (Pl. III, *h*), for example, retains the fold characteristic of the Catuloidea, although having the general body form and the vertebral structure of the Carcharinoidea. *Atelomycterus* (Fig. 32 and Pl. III, *d*) is a catuloid with the nictitating fold but with the complete Maltese cross type of vertebra. Thus the transitional stages of the two characters overlap but in general the families with the rudimentary or intermediate types of vertebra have the shorter folds, while *Atelomycterus* and *Triakis* have folds as long as the eye (Pl. III, *d* and *h*).

The complete membrane is found only in the Carcharinidae (Pl. III, *i*) and Sphyrnidae, which are the most specialized of the pelagic types. All stages in development are found, from those where the fold reaches the length of the eye, to those in which it reaches the lower lid and so folds under the upper lid to form a third eyelid. It is not essential to deep sea life, since in the Isurida, in which a similar pelagic development occurred, no membrane is found.

Dermal Denticles

Plates IV to XI

The dermal denticles (Pls. IV–VI), or placoid scales, of the elasmobranchs have the same structure as the teeth, and in this they differ from all other fishes. Because of the characteristic roughness which they give to the skin it has come to be known as shagreen. A simple denticle consists of a small cone of dentine surrounding a pulp cavity into which nerves and blood vessels enter. This is the pure dentine but into it often radiate small canaliculi from the pulp cavity and these compose what is known as vasodentine. The outer surface of the cone is covered with a hard, transparent layer, the vitrodentine.

At the base the cone spreads out under the epidermis to form a basal plate. This is composed of phosphate of lime but some fluoride and carbonate of lime contribute to the vitrodentine so that it is not a pure enamel even though partly secreted by the epidermis. The base of the denticle never sinks into the dermis but lies directly under the epidermis.

In the earliest known vertebrates, as suggested on page 45, the body was covered with a hard armor composed of four layers of tissue. The outer layer was of dentine and beneath it was a reticular layer into which nerves and blood vessels entered. This probably represents the pulp of the denticle, the basal layer, which often contained bone cells, having dropped out. Much discussion has arisen over the relation of the cones of the separate denticles to the plate-like placoid scale of the fossil elasmobranchs, and the answer probably lies in the breaking up of the Agnathan armor. Smith Woodward (1915) and Traquair (1898) favor the view that the armor was formed by the fusion of separate denticles. Jaekel (1901) and Kiaer (1932) believe that the solid plates are primitive and that the denticles have arisen by subdivision of the plates.

The Heterostraci, which have no bone cells in the armor and no appendages, are the probable ancestors of the elasmobranchs, and of them Kiaer suggests that the undivided dorsal shield of *Poraspis* is primitive.

On the theory of subdivision the denticles might be pictured as arising through some such series of processes as this. In *Anglaspis* (Fig. 1) the dorsal shield is undivided but has raised ridges of dentine forming a pattern on the surface. In *Cyathaspis* the shield is divided into four regions by distinct limits in the dentine layer. In *Pteraspis* the plates are separate and symmetrically arranged with fine concentric ridges, and in *Tolypaspis* the shield is broken into numerous small discs, each with an ornamental peak with stellate crenulations. In *Thelodus* and *Lanarkia* the plates are all small, separate tubercles resembling the shagreen of the elasmobranchs.

Traquair describes the plates of *Thelodus* as having flat and sculptured crowns. Those of *Lanarkia* are minute hollow cones without bases. Only the latter could be derived from such plates as those in *Tolypaspis*, but many Agnathans have small or even minute plates on their abdominal regions and frequently there are tubercles on the plates of the dorsal shield. In *Pteraspis* the tail is covered with rhombic scales which have close parallel ridges and frequent lateral crenulations. Traquair suggests that these were formed by the running together of the shagreen grains of *Thelodus*. Conversely, of course, the scales of *Thelodus* may represent the further subdivision of those of *Pteraspis*.

Ridges of dentine occur on many of the dorsal shields and are ridges of the dentine only, not affecting the lower layers. The earlier types in the Silurian had more bone than the later types and the Heterostraci

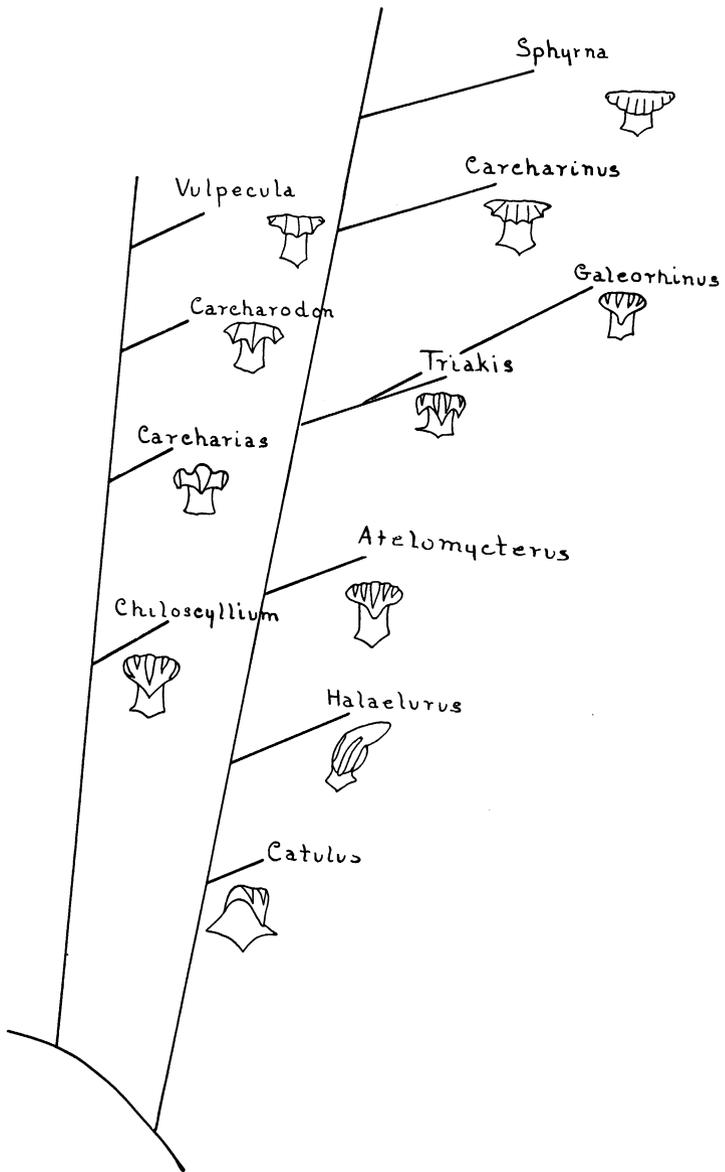


Fig. 63. Showing the possible development of the shell-like denticle from the incompletely keeled type in two parallel divisions of the order Galea.

have no bone cells at all. It is fairly well conceded at the present time that bony structures preceded cartilage development in vertebrates, and if the shagreen covering of the elasmobranchs followed on the loss of an underlying bony layer, then it is probable that the movements of muscular layers beneath might have caused crenulations in the surface layer of dentine, with subsequent subdivisions.

This would make the primitive elasmobranch denticle a flat plate on a thick base with a faintly crenulated crown. The crenulations may later have become keels. Typical modern sharks have scales with several keels on a flat surface rising from the base on a slender pedicel.

The course of development in the modern elasmobranchs has been paralleled in several groups so that there is a marked similarity between the denticles of widely separate species. The parallel development in the two suborders of the Galea is shown in Fig. 63, the Catuloidea forming the base from which the Carcharinidae develop, and the Orecto-loboidea the base for the Isuridae. The lower groups have similar denticles rising on pedicels with incomplete keels on a more or less flattened disc. Sometimes a single central keel is found and often the central keel is divided (Pls. IV-V). This often occurs on the denticles of the same individual. As the keels approach the margin it becomes lobed. At first the entire denticle is lobed deeply; later the disc becomes flatter and the margin shell-like, resembling a scallop shell. This type is found on all the large pelagic sharks of whatever division, including *Rhineodon typus* (Pl. IV, *l*), the whale shark, which is a pelagic form although retaining bottom-living specializations at the head end. The bulky basking shark, *Cetorhinus maximus* (Pl. IV, *f*), and the large Greenland shark, *Somniosus microcephalus* (Pl. IV, *c*), are exceptions to this, having denticles similar to those of *Chlamydoselachus anguineus* (Pl. IV, *i*), and *Scapanorhynchus owstoni* (Pl. IV, *e*), two elongate and very specialized sharks from the deep waters off the shores of Japan. These four sharks of such different relationships have in common an environment of cold deep waters. It is probable, therefore, that temperature as well as depth has determined denticle development.

The Squalea have had as much variation in denticle development as in other characters. The origin of the spiny type from the plate-like denticle is suggested in Fig. 64. *Squalus acanthias* has a denticle similar to that of *Carcharias taurus* (Pl. IV, *j*, *k*). This represents an intermediate type in the Galea and may be intermediate here, although no shell-like denticles have yet been formed. The flattened primitive scales of the Platosomeae have often been considered retrogressive

development from the squaloid line, but tracing their history back geologically it appears that the rays digressed from the main stock as early as the Jurassic, when the Squalea themselves were just getting established. Therefore, any primitive condition may as well be a retention as a loss.

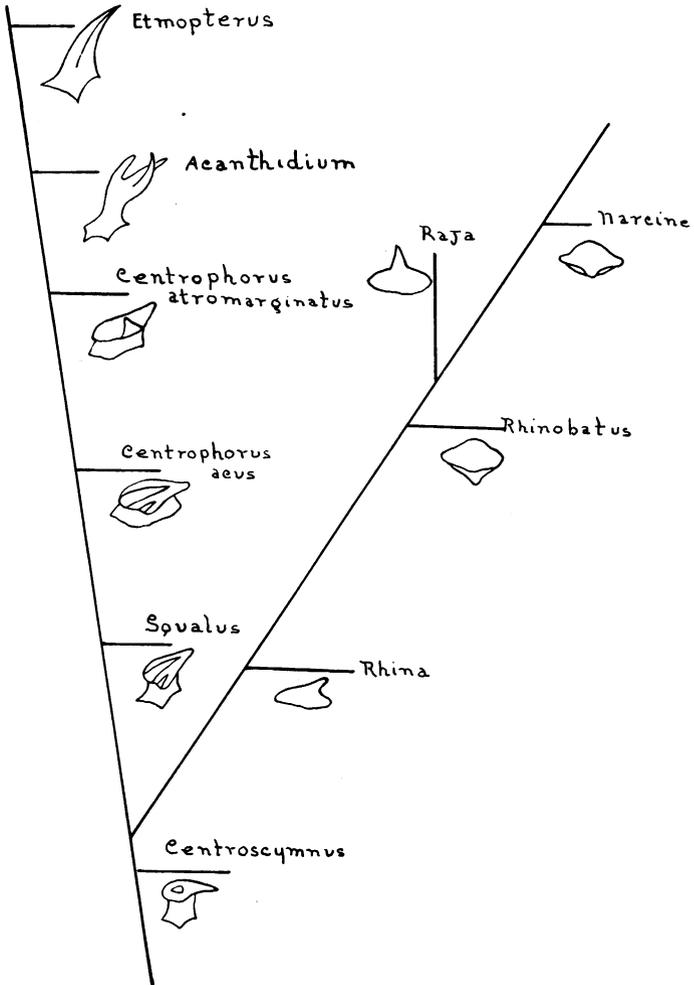


Fig. 64. Showing the possible development of the spine-like keel of the Squalea and of the spines, tubercles, and naked skins of the Platosomeae from the flat, un-keeled scale.

Looking also to the individual shark, we find that the denticles are flatter and less well keeled in the least exposed portions of the body, assuming the typical condition gradually as the flanks and dorsal surface are approached.

Modified denticles contribute to the elaborate feeding apparatus of the basking shark, *Cetorhinus maximus*, and of the whale shark, *Rhineodon typus*. These two sharks live in quite different environments and temperatures but have paralleled each other in their peculiar vertebral structure and in their feeding habits. They have large mouths, terminal in *Rhineodon*, with many minute useless teeth. When these sharks open their mouths large quantities of water enter without effort and from the water the shark must retrieve what minute forms of life may be present for food. This probably consists chiefly of small crustaceans and other similar forms of life which abound in the surface waters of the deep.

By great good fortune the esophagus of *Rhineodon* and the gills of both *Cetorhinus* and *Rhineodon* have been received in good condition. These have been photographed by the museum staff and are shown in Plates VII-XI. As the water passes through the pharynx it leaves by means of the gills, and the necessity for preventing the loss of food has resulted in two quite different but equally effective sieves, formed from the denticles. Plates VII and VIII show the gills of *Cetorhinus*. In the first plate the relation of the gills to the gill rakers can be seen, and this same relation prevails in *Rhineodon*, although the gill has been removed from the rakers because of the large size. In *Cetorhinus* the denticles have been prolonged into stiff, hair-like parallel threads resembling whalebone both in appearance and in feeling. This presents a forcible obstacle to the water as it leaves the pharynx, thus straining out the small forms of life. The gill rakers of *Rhineodon* are seen in Plates IX and X; the former an internal, and the latter an external view. From the inside it can be seen that the cartilaginous gill bar has been cut lengthwise, thus removing the gill. The specialization here includes the growth from the cartilaginous bar of parallel, oblique, and flat cartilaginous plates. Over the surface of these a veil of denticles is formed. From the inside can be seen the pattern formed by the modified denticles as the light shines through (Pl. IX). From the outside the form of the denticles can be seen, apparently fused into clumps. Through this veil can be seen the parallel bars, and in some parts the light shining through (Pl. X). Water would have to seep very slowly through such a sieve, and thus food is retained in the esophagus.

As the esophagus passes to the stomach in *Rhineodon* it is lined with large papillae, and these are covered with dermal denticles. The photograph in Plate XI shows the arrangement of these papillae in rows, also that the rows are arranged parallel with the furrows on the wall of the stomach. This mechanism is quite unusual in sharks and is probably an additional precaution for the passage of the food to the stomach. The Crustacea may be caught on the rough denticles and thus partly macerated as they pass from the pharynx to the stomach.

The history of denticles in general shows that their development is more directly affected by the environment than is that of other external characters. There is a definite similarity between the denticles of types in similar environments although in widely separated groups, and while it is impossible to test the conditions of the environment in all cases, it is probable that temperature, depth, and exposure are all concerned.

TABLE VII.—TYPES OF DENTICLES

	With flat surface unkeeled		Keels rising from a basal plate			Keels on a flat surface			
	With no rudiments of a central keel	With rudiments of a central keel	Keel a single central spine	Keel two or more lateral spines	Keel a single central cone	No keels complete	Central keel complete	All keels complete	
								Keels sharply marked off	Keels shell-like
Ichthyotomi									
<i>Cladodus</i>	X								
<i>Cladoselache</i>	X								
Hexanchea									
<i>Heptanchias perlo</i> (Pl. IV, m)								X	
<i>Chlamydoselachus anguineus</i> (Pl. IV, i)					X				
Heterodontea									
<i>Heterodontus</i> (Pl. IV, n)								X	
Squalea									
Squalida									
<i>Centroscymnus</i> (Pl. IV, a)		X							
<i>Centrophorus</i>						X			
<i>Somniosus</i> (Pl. IV, c)					X				
<i>Squalus acanthias</i>								X	
<i>Acanthidium rostratum</i> (Pl. IV, o)				X					
<i>Etmopterus lucifer</i> (Pl. IV, p)			X						
<i>Centroscyllium fabricii</i> (Pl. IV, q)			X						
Rhinida									
<i>Rhina californica</i> (Pl. IV, b)		X							
Platosomeae									
Narcobatea									
<i>Narcine</i> (Pl. IV, g)	X								
Batea									
<i>Rhinobatus</i>	X								
<i>Pristis clavata</i> (Pl. IV, d)	X								
Antaceae									
Galea									
Isurida									
Orectoloboidea									
<i>Nebrodes macrurus</i> (Pl. V, a)						X			
<i>Ginglymostoma</i> (Pl. V, b)						X			
<i>Orectolobus</i>						X			

TABLE VII—TYPES OF DENTICLES (Continued)

	With flat surface unkeeled		Keels rising from a basal plate			Keels on a flat surface			
	With no rudiments of a central keel	With rudiments of a central keel	Keel a single central spine	Keel two or more lateral spines	Keel a single central cone	No keels complete	Central keel complete	All keels complete	
								Keels sharply marked off	Keels shell-like
<i>Chiloscyllium griseum</i> (Pl. V, c)						X			
<i>Stegostoma tigrinum</i> (Pl. V, d)						X			
<i>Rhineodon typus</i> (Pl. IV, l)						X			
Odontaspoidea									
<i>Carcharias</i> (Pl. IV, j)								X	
<i>Scapanorhynchus</i> (Pl. IV, e)					X				
Isuroidea									
<i>Isurus</i>									X
<i>Vulpecula marina</i> (Pl. VI, e)									X
<i>Carcharodon</i>									X
<i>Cetorhinus maximus</i> (Pl. IV, f)					X				
Carcharinida									
Catuloidea									
<i>Catulus retifer</i> (Pl. V, i)						X			
<i>Catulus torazame</i> (Pl. V, f)							X		
<i>Parmaturus xaniurus</i> (Pl. V, j)							X		
<i>Parmaturus pilosus</i> (Pl. V, k)							X		
<i>Halaelurus bivius</i> (Pl. V, g)						X			
<i>Halaelurus burgeri</i> (Pl. V, h)							X		
<i>Calliscyllium</i>							X		
<i>Atelomycterus marmoratus</i> (Pl. V, e)							X		
Carcharinoidea									
<i>Triakis scyllium</i> (Pl. VI, a)						X			
<i>Triakis henlei</i>						X			
<i>Galeorhinus manazo</i> (Pl. VI, b)						X			
<i>Galeorhinus laevis</i> (Pl. VI, c)							X		
<i>Hemigaleus</i>									X
<i>Galeocerdo</i> (Pl. VI, d)									X
<i>Galeus glauca</i> (Pl. VI, h)									X
<i>Scoliodon</i>									X
<i>Aprionodon</i> (Pl. VI, f)									X
<i>Physodon</i>									X
<i>Carcharinus limbatus</i> (Pl. VI, g)									X
<i>Carcharinus japonicus</i> (Pl. VI, j)									X
<i>Sphyrna</i> (Pl. VI, i)									X

Teeth

Plates XII to XVII

The racial history of the elasmobranchs can be traced almost entirely through the history of the teeth, largely because the teeth were often the only parts preserved in the geological strata. This has been due in part to the structure of the vitrodentine covering the teeth, for while this is not a true enamel it contains enough calcium fluoride combined with the calcium phosphate and carbonate to make a hard resistant layer.

The teeth are specialized dermal denticles and so contain the same combination of dentine and vasodentine around a pulp cavity. Typically the dentine is in excess but in one group of Paleozoic elasmobranchs, the Bradyodonti, there is a preponderance of a very tubular vasodentine. This Jaekel (1901) calls palaeodentine, and it is found in a single group of modern elasmobranchs, the Chimaeras. Like the bradyodonts, the Chimaeras are mollusk eaters and some of the older ones are of a depressed grovelling form; a common derivation for the two groups is indicated, even though the bradyodonts became extinct in the Permian and the Chimaeras did not appear until the Jurassic. No doubt some undiscovered grovelling form persisted through the Triassic to carry on this ancient race.

The Chimaeras, or Holocephali, differ from all other elasmobranchs also in the fact that the teeth are statodont, that is, they are not shed and replaced. They consist of paired grinding plates with flattened basal regions which are in a state of perpetual growth. Palaeodentine predominates in its structure, and prominent grinding ridges on the surface, called tritors, are covered with vitrodentine. These may have been derived from the low-crowned teeth of the bradyodonts, which were slightly rounded in the middle and pressed so close together as to form crushing pavements.

Typically elasmobranch teeth are lyodont, each row being replaced by the one behind as the teeth wear away and drop off. They are arranged in series, and have two roots attached to the cartilaginous jaw by a layer of fibrous connective tissue. This type of tooth first appears in the Cretaceous, the Jurassic elasmobranchs having left no record of their teeth, but there is no doubt that these modern teeth have had their derivation through the hybodonts, which persisted through the Triassic. These are a heterodont type (Pl. XVI, *a, b*), the teeth in front being cuspidate and those on the sides flattened for

crushing although no pavements are formed. It was a kind of dentition of the utmost value to the elasmobranchs following the great wave of extinction which marked the close of the Paleozoic. The seas were practically cleared of both invertebrate and vertebrate life and only a few grovellers which could cling closely to the shores and forage for food by nibbling on the ocean bottom could make the most of whatever food remained.

They had their antecedents in the Permian, probably in such a type as *Orodus*. In *Orodus* (Pl. XVI, *c*, crown, *d*, side) the lateral teeth were obtuse and elongate with the dental crown raised in the middle. The surface was marked by more or less prominent wrinkles of dentine, which rose from each long margin or from a median longitudinal crest. It has been supposed that the lateral teeth of *Hybodus* and *Synechodus* (Pl. XVI, *b*) were formed by the flattening of the median cuspidate teeth, but the possibility exists that the cusps were the result of subdivision from the crests of an elongate tooth like that of *Orodus*.

The Paleozoic teeth were all broad-based. The earliest elasmobranch known is the stegoselachian, *Macropetalichthys primiensis* (Fig. 3). The teeth were merely flat dermal plates folded over the jaw. This may represent the broad base of the later Paleozoic teeth which became deeply embedded in the jaw tissue. Not until the late Devonian are cuspidate teeth found and these all run to one type, called the *Cladodus* type (Pl. XII, *m*, *n*). There is a large central upright cusp on a very wide base and numerous smaller but upright accessory cusps clustered about its base. Often the outermost lateral cusps are slightly higher than the intermediate ones.

From this type of tooth all of the Carboniferous and Permian teeth must have been derived. One type arose because of the difficulty of extruding the deeply embedded teeth as one series moved up on another. Fusion is seen even in the Devonian in *Protodus* (Pl. XII, *k*), and during the Carboniferous and Permian several types developed in which the symphyseal teeth fused and extended beyond the jaw in long spirals. These are the edestids, and include *Campodus* (Pl. XVI, *e*, *f*), *Edestus* (Pl. XVI, *g*), and *Helicoprion*. Such teeth were of no value in the open seas and there was a return to bottom-living habits. Probably crustaceans furnished the food.

The Permian also produced another specialized pelagic type, the pleuracanthids, which flourished for a relatively brief period and became extinct. The teeth (Pl. XII, *l*) are cuspidate and irregular. They bear some resemblance to the teeth of *Chlamydoselachus* (Pl. XVII,

a, b) but the structure of the pectoral fin is so aberrant as to make doubtful any direct connection. The Hexanchea, however, must have been derived from some Paleozoic type since they appear in the Jurassic with no resemblance to any of the contemporary forms. In the Hexeptranchidae the teeth on the two jaws are unlike. Typically there is a median symphyseal tooth row with minute surface cuspidations (Pl. XII, *d*). These give the appearance of subdivision rather than duplication. The lateral lower teeth have a series of cusps in increasing size on an elongate base (Pl. XVII, *c*). This, also, may be due to the subdivision of such an elongate tooth as that of *Orodus* (Pl. XVI, *d*) although Smith Woodward (1915) believes it to be a case of secondary polyisomerism from an original single cusp. The teeth of *Chlamydoselachus* (Pl. XVII, *a, b*) present another problem. Both jaws are alike but the teeth are irregularly cusped and curved. This also probably represents secondary polyisomerism from a *Cladodus* type tooth, multiplication being circular rather than in one plane. Both processes are common in fishes, and until more is known of its antecedents the origin of this group must remain in doubt. It is probable, however, that the origin lies in the Paleozoic rather than the Jurassic groups, as the modern types retain so many archaic features.

During the Triassic the seas were gradually repopulated with small bony fishes, and with the approach of the Jurassic conditions favorable to elasmobranch radiation were revived. All of the main modern groups were established during that period in about their present form and only the most highly specialized families had a later origin. Among the groups established were the Chimaeras, and the Hexanchea of Paleozoic origin. *Heterodontus* (Fig. 42) appears for the first time very little different from *Hybodus* (Fig. 6), except that the jaw articulation is less massive. The other modern groups appear to have owed their origin to a more modernized hybodont than *Hybodus*, *Palaeospinax priscus* (Fig. 7), which is found in the Liassic strata. It has a less overspecialized head region, and a more fusiform shape but it has retained the heterodont dentition and the enamelled dorsal fin spines. The central teeth are sharply cuspidate while the lateral teeth are only mildly obtuse.

The many small elasmobranchs which have been found in the Lithographic Stone of Bavaria have been most helpful in establishing the relationships of the modern groups. This is an Upper Jurassic formation, and the types found include the ancestral forms of the Squalea, the Platosomeae, the Orectoloboidea and the Catuloidea. Unfortu-

nately the teeth of these small forms have not been preserved, due doubtless to their small size and possibly to their fragility. In all of the Cretaceous and Eocene types the teeth agree in almost minute detail with those of existing species. There is no reason to think, therefore, that the teeth of the small Jurassic sharks would have been less like those of their existing relatives. On that basis it is safe to surmise that the Jurassic teeth were small, numerous, and multicuspidate. If these were derived from the symphyseal teeth of *Palaeospinax*, or some similar form, then the accessory cusps must have been derived by secondary polyisomerism, and the prevailing theory of Smith Woodward that the single-cusped teeth with the lateral serrations represent the central and accessory cusps of the multicuspidate teeth may be a correct explanation of the large carnivorous teeth found in the voracious sharks of the open waters.

The Cretaceous formations contain many small multicuspidate teeth of both Orectoloboidea (Pl. XII, *j*) and the Catuloidea, giving additional credence to the belief that the Jurassic teeth were of this type. The unicuspidate teeth of *Isurus* and *Carcharodon*, and of the Odontaspoidea are all present, showing that these groups were established at this time. Not until the Eocene do the teeth of the carcharinids and galeorhinids appear, so that the more highly specialized sharks have all had a late origin. During the Tertiary the sharks assumed great size, much greater than that of similar species today. A Cretaceous genus named *Corax*, however, is supposedly the forerunner of the modern *Cetorhinus*, which is found in its present form in the Pliocene. This is one of the largest of the modern types and is often considered degenerate, but its origin appears to have been as early as the Cretaceous. No fossil representatives of the enormous whale shark have been reported, but its teeth are so similar to those of *Cetorhinus* that they might easily be confused.

There is greater variation in the structure of the unicuspidate tooth than of any other type, and the large number of species in the Carcharinidae (Pl. XIII) are distinguished by minute differences in the serrations and slant of the teeth. They all agree, however, in the fundamental structure, in that there are few of them, there is but one series in function at one time, and they are never multicuspidate.

Flattening of the teeth for crushing is a specialization found in even the highly organized Carcharinoidea in the family Galeorhinidae. It is found in transition in the *Squalea*, and in its most extreme form in the *Platosomea*. It always indicates a return to extreme bottom-

living habits in groups already adapted to a littoral life. That the stages of flattening in the *Squalea* are antecedent to the flattening in the *Platosomeae* is not possible, since the rays branched from the squaloid line in the Jurassic before the modern types were developed. That we have here a parallel specialization, however, is quite probable. In the *Squalea* the teeth on the lower jaw often have the cusps bent obliquely so that the side faces the erect upper tooth (Pl. XIV, *d, g*). All stages can be found between the erect cusp and the completely flattened cusp. The roots become deeper as the flattening proceeds (Pl. XIV, *b*).

The t eth of *Raja* retain sharp cusps, but this group has probably had a separate origin from the Jurassic. In the *Platosomeae* typically the teeth are flattened and fitted over the jaws in pavements. When the bases of the teeth fuse the type is known as tessellate (Pl. XV). The type found in *Pristis* (Pl. XIV, *i*) is the most primitive type of pavement tooth. It is very similar to the type found in the Galeorhinidae (Pl. XIII, *p*), showing that this group has only begun its specialization toward bottom-living. In the *Dasybatoidea* a series can be seen showing the gradual broadening of the central plates (Pl. XV, *a*) to the extreme specialization found in *Aetobatus* (Pl. XV, *c*) where only the central plates remain. A modification of the specialization in this group is found in the *Mobulidae* (Pl. XIV, *j*) where the cusps are much broadened but have several peripheral cuspidations.

KEY TO THE TEETH OF THE MODERN ELASMOBRANCHS

- I.—Teeth unlike
 - A.—Upper teeth unlike lower teeth
 - Hexanchea (Pl. XVII, *a-d*)
 - B.—Central teeth unlike lateral teeth
 - Heterodontea (Pl. XVI, *a-b*)
- II.—Teeth alike and separate
 - A.—Teeth of both jaws cuspidate, erect
 - 1.—With more than one cusp
 - Antaceae
 - Galea
 - Orectoloboidea
 - Orectobidae (Pl. XII, *g-j*)
 - Catuloidea (Pl. XIII, *k-n*)
 - Carcharinoidea
 - Triakidae (Pl. XIII, *o*)
 - 2.—With a single prominent cusp
 - a.—With small lateral denticles
 - Antaceae

- Galea
 - Odontaspoidea (Pl. XII, c)
 - b.—With minute lateral denticles or none
 - ba.—Teeth large
 - baa.—Teeth not serrate
 - Antaceae
 - Galea
 - Isuroidea (Pl. XII, a-b)
 - Carcharinoidea
 - Carcharinidae
 - Scoliodon* (Pl. XIII, c, d)
 - Physodon*
 - Aprionodon*
 - bab.—Teeth serrate, at least at the base
 - Antaceae
 - Galea
 - Carcharinoidea
 - Carcharinidae
 - Galeus* (Pl. XIII, b)
 - Hemigaleus*
 - Carcharinus* (Pl. XIII, a, e,)
 - Sphyrnidae (Pl. XIII, f)
 - bb.—Teeth minute
 - Antaceae
 - Galea
 - Orectoloboidea
 - Rhineodontidae (Pl. XII, e)
 - Isuroidea
 - Cetorhinidae
- B.—Teeth of the upper jaw cuspidate, erect
 - 1.—Cusps of the lower teeth erect, at least in the center
 - a.—Teeth with more than one cusp
 - Antaceae
 - Squalea
 - Centroscyllium* (Pl. XIV, a)
 - b.—Teeth with one cusp only
 - Antaceae
 - Squalea
 - Scymnorhinus*
 - Isistius*
 - Pristiophorus*
 - 2.—Cusps of the lower teeth oblique
 - a.—Teeth serrate
 - Antaceae
 - Squalea
 - Oxymotus*
 - b.—Teeth not serrate
 - Antaceae

Squalea

*Centroselachus**Scymnodon**Heteroscymnus*

3.—Cusps of lower teeth bent at right angles, presenting a flat surface

a.—Upper teeth pluricuspid

Antaceae

Squalea

Etmopterus (Pl. XIV, b)

b.—Upper teeth unicuspid

Antaceae

Squalea

Centroscymnus (Pl. XIV, e)*Acanthidium* (Pl. XIV, d)*Centrophorus* (Pl. XIV, g)*Somniosus* (Pl. XIV, c)

c.—Cusps on both jaws bent at right angles

Antaceae

Squalea

*Echinorhinus**Squalus* (Pl. XIV, f)

III.—Teeth tessellate

A.—Teeth retaining cusps

1.—Cusps sharp, at least at the center

Platosomeae

Rajoidea

Raja (male)*Sympterygia**Malacorhina*

Dasybatoidea

*Pteroplatea**Aetoplatea**Urobatis* (in male only)

2.—Cusps flat, blunt

Antaceae

Galea

Carcharinoidea

Galeorhinidae (Pl. XIII, p)

Platosomeae

Rhinobatoidea

*Rhinobatus**Pristis* (Pl. XIV, i)

Rajoidea

Raja (female)

Dasybatoidea

*Disceus**Trygonoptera**Potamotrygon*

- 3.—Cusps flat, broader than long
 - a.—Teeth on both jaws
 - Platosomeae
 - Dasybatoidea
 - Mobula* (Pl. XIV, *j*)
 - Urotrygon*
 - Urolophus*
 - b.—Teeth on lower jaw only
 - Platosomeae
 - Dasybatoidea
 - Ceratobatis*
 - Manta*
 - B.—Teeth platelike
 - 1.—Teeth flat, without tritons
 - a.—Plates arranged in a quincunx
 - Platosomeae
 - Dasybatoidea
 - Dasybatus*
 - b.—Plates arranged in a series, median plates widest
 - Platosomeae
 - Dasybatoidea
 - Rhinoptera* (Pl. XV, *a*)
 - Myliobatis* (Pl. XV, *b*)
 - Pterymylaeus*
 - Aetomylaeus*
 - c.—Plates arranged in a single series
 - Platosomeae
 - Dasybatoidea
 - Aetobatus* (Pl. XV, *c*)
 - 2.—Teeth with rounded crowns, with tritons
 - Holocephali

INTERNAL CHARACTERS

Rostral Cartilages

Plates XVIII to XXI

In the elasmobranchs of Jurassic or more recent origin the rostrum is supported by cartilaginous rods which are outgrowths of the forward end of the skull. In the Galea the main rod is a prolongation of the median basal region; two rods which grow out from the walls of the olfactory capsules converge upward to meet the basal rod at the anterior tip of the snout and are slender or thick according to the size of the shark (Pl. XIX, *a*). In the Sphyrnidae, or hammerheads, where the skull is prolonged laterally the rostral cartilages are squared in front but the triangular structure is complete, and in *Scapanorhynchus*, in

which the snout is greatly elongated, the cartilages are prolonged anteriorly. This structure is consistent throughout the order except that in the Orecto-loboidea failure of the rods to chondrify fully results in an incomplete rostrum (Pl. XX). In *Stegostoma* (Pl. XX, a) there are no lateral rods and the median rod is incomplete; in *Chiloscyllium* (Pl. XX, b), the median rod is complete to the tip of the snout but there is no indication of lateral rods, and in *Orectolobus* (Pl. XX, c) two lateral knobs appear on the olfactory capsules.

So diagnostic is this character in the Galea that species which are externally difficult to place can be classified without question if the rostrum proves to be of this type. The acquisition in 1935 of the skull of a whale shark, *Rhineodon typus*, has made possible the examination of the rostrum (Pl. XXI, b). When thoroughly dried the skull was drawn for Mr. Denison (1937) in various views, two of which have been used here (Pl. XXI). The olfactory capsules were cut slightly on each side by the men who were removing the skin, but so little was removed that no question as to the general type of rostrum is possible. The front ventral margin forms a very thin shelf with two slight triangular processes on either side of the center, which is broad and straight. It rises with a gentle slope to the level of the dorsal surface and is continuous on the sides with the olfactory capsules. It does not look from the specimen at all likely that any knobs were present on the olfactory capsules, but that, of course, cannot be definitely determined.

In 1928 the author examined the vertebrae, jaws, denticles, teeth, and claspers of a whale shark and decided from these characters that the shark showed more characteristics of the Isuroidea than of the Orecto-loboidea. Subsequent observations have shown, however, that too much has been claimed in the literature for the claspers, as they vary too much in all the groups of the Galea to have any diagnostic value. The denticles of the shell-like type have been found in no other primitive group, but these also are of physiological rather than phylogenetic significance and may indicate merely the acquisition by this shark of the habitat of more specialized groups. The rostrum, however, is diagnostic, and *Rhineodon* may now be safely classified with the Orecto-loboidea.

In the other orders no such consistency exists, and the only character which can be assigned to them is the absence of any relation of the rostral cartilages to the olfactory capsules. The Heterodontea (Pl. XVIII, a) have no preoral cartilage, and the Paleozoic types show none,

so that the incomplete rostrum may be the initial form. In the Hexanchea (Pl. XIX, *e*) the rostrum is a short, broad, basal plate. In the Squalea and in the Platosomeae so much variation exists that no one form can be called typical. In the fossil *Protospinax* (Fig. 8) a fenestrated bar can be seen. In *Squalus* (Pl. XVIII, *b*) there is a single hollow trough with its sides attached to the cranium as well as the base. In *Rhinobatus* (Pl. XIX, *b*) two dorsal rods from the center of the cranium fuse with the basal rod, making a triradiate structure without any relation to the olfactory capsules. These groups vary greatly in other respects also, a fact which may be due to their early origin.

A peculiar condition is found in the Holocephali not paralleled by any other group. According to Schauinsland (1903), in the adult there are two rostral bars but in the embryo a ventral bar arises as a paired structure (Pl. XIX, *d*), one half of which later drops out or fuses with the other half (Pl. XIX, *c*). These bars are in no way homologous with the rostral bars of the typical elasmobranchs.

Fin Skeletons

Plates XXII to XXVIII

The endo-skeletal supports of the elasmobranch fins have been investigated from many angles, but there still remains some question as to the original structure. Thacher (1872), by examining the structure, and Balfour (1881), by studying the development, both arrived at the conclusion that the paired and unpaired fins are homologous structures. There can be, therefore, no connection between the paired fins and the visceral arches as predicated by Gegenbaur.

The fins are supported by a series of cartilaginous rods. Those within the body wall are called the basals, and those in the lobe of the fin, the radials. The basals serve to articulate the fin with the axial skeleton; the radials support the fin itself. The radials are typically segmented into three portions, and where the body of the fin is expanded, horny dermal rays (ceratotrichia) are attached to their distal ends. These are never calcified in the elasmobranchs and so they serve to distinguish between them and other fish groups. In the Osteopterygia they are calcified and are called lepidotrichia, although the ceratotrichia are typically retained in vestigial form.

Only the dorsal fins bear spines. When these are present they are typically pointed and approximately cylindrical. Their origin is similar to that of other denticles, and they come to lie on a process on the basal

cartilage (Pl. XXII, *c, d*). In those species where the spines are vestigial, or have disappeared, the shape of the basal may become modified (Pl. XXII, *a, e, f*). In the Galea, where the fin spines were irretrievably lost as early as the Jurassic, the basal is segmented into a series of parallel rods which give a greater flexibility to the fin (Pl. XXII, *b*). In the Paleozoic sharks the spines were variously ornamented with dentine ridges and tubercles. During the Triassic this was replaced by enamel and the fins became smooth, and in the modern forms all ornamentation has been lost. Spines are the last vestiges of the ancestral armor.

All fin skeletons have a similar development except that the paired fins develop girdles for articulation of the fin. In these a single cartilaginous bar forms on each side parallel to the long axis of the body. This is the basipterygium. Later the outer edge is continued into a plate which extends into the fin and becomes segmented into a series of parallel rays at right angles to the longitudinal bar. These are the radials and this process of segmentation is of importance because it throws some light upon the theory that the dermal denticles arose by the breaking up of the solid armor plates of the Agnatha.

In the pelvic fins the girdle segments off the anterior end of the bar and becomes fused to the bar from the opposite side. There is very little variation in the pelvics throughout the Antaceae, but in the rays, due to the extreme flattening and spreading of the body, there are some modifications.

The pectoral arch develops in a similar way but, because greater strength is required in this region, there is a stronger girdle and more complicated articulation. The basipterygium becomes the metapterygium, but is only one of three supporting basals. It rotates outward to form the posterior border of the fin skeleton. The mesopterygia and propterygia probably segment from the anterior end. Balfour's theory that they are formed by the fusion of radials is not supported by the embryological facts.

The basals of the pectorals serve to distinguish between large groups such as orders and superfamilies; the radials between families. The important question is to establish the primitive structure on the basis of geological precedence. The first true elasmobranchs appear in the early Devonian, and throughout the Paleozoic there was diverse radiation in body and fin form. The fins of *Cladodus*, *Cladoselache*, and *Pleuracanthus* give pictures quite different from those of any modern form. Curiously, however, there is a fin from the early Devonian, pre-

ceding all of these, which has a structure suggesting that of the fin of *Protospinax* in the Jurassic.

Macropetalichthys prumiensis E. Kayser, which possesses this fin (Pl. XXIII, *a*), is a Stegoselachian with a well-developed dermal armor of separate plates over the head and thorax. It has none of the typical unpaired fins and is a grovelling type depressed at the anterior end. In the specimen found the pectoral fin was so well preserved that with very little reconstruction the fin appears as a whole. The metapterygium was incomplete, but from the shape of the fragment as described by Broili in 1933, it must have had about the same expansion as the mesopterygium and the propterygium. Only three radials were found and these were all unsegmented rods. From their size it is apparent that about as many were inserted on one basal as on another.

Comparison of this fin with that of *Protospinax* (Fig. 8) shows only minor differences. The radials of *Protospinax* give no indication of segmentation and the three basals are of equal size and expansion. A quite similar fin is found in *Hybodus* (Fig. 6). This then is the primitive pectoral fin from which all of the modern fins can be derived, and those groups in which the radials are about equally distributed on the mesopterygium and metapterygium are the primitive modern groups. These include the Hexanchea (Pl. XXIII, *b*), the Heterodontea (Pl. XXV, *b*), the Squalia (Pl. XXVII, *a, b*), and the superfamily Orecto-*loboidea* (Pl. XXV, *a, d*) of the Galea. In all groups the propterygium is considerably reduced and often bears only one radial. In the Hexanchea it is so small that the mesopterygium reaches the free margin of the fin (Pl. XXIII, *b*). In the Isuroidea (Pl. XXIV, *c*), Catuloidea (Pl. XXIV, *d*, Pl. XXVI, *c, d*), and Carcharinoidea (Pl. XXIV, *a*, Pl. XXVI, *a, b*) the metapterygium is greatly expanded so that most of the radials are attached to it, and the mesopterygium is correspondingly reduced.

The radials undergo further segmentation, and there is more segmentation in the primitive groups than in the more specialized ones, where the number becomes stabilized at three segments to a radial. If the fins are elongated, the radials are lengthened but there is no further segmentation.

In the Platosomeae the pectoral fins are extended forward and back from the point of articulation and in the more specialized forms are fused with the skull in front. In the process of extension the basal cartilages are drawn out in either direction (Pl. XXVIII), with the result that the propterygium and metapterygium are greatly length-

ened and the mesopterygium is reduced. In the Dasybatidae the mesopterygium may segment into two or three pieces.

The fins of *Cladodus*, *Cladoselache*, and *Pleuracanthus* have long been looked to for the establishment of a primitive type of fin, but they must now pass out of the picture. They represent three attempts toward freer locomotion in the Paleozoic seas which were not sufficiently successful to be repeated in the later radiation of the elasmobranchs. Much work remains to be done on this problem but it opens up a field of great interest.

Vertebrae Plates XXIX to XXX

In the earliest elasmobranchs the notochord was unconstricted and the vertebrae were uncalcified. A somewhat similar condition is found in the Holocephali today. Hasse considered this the primitive type because it is also associated with the condition of polyspondyly in the tail.

In the body region there is always one myotome to each vertebra. Each neural plate is perforated or notched posteriorly for the exit of the ventral root of a spinal nerve and the interneural is similarly prepared for the exit of the dorsal root. Typically in the elasmobranchs the caudal region has twice as many vertebrae as myotomes (diplospondyly). In the Holocephali there are more than twice as many vertebrae as myotomes and Hasse believed this polyspondylic condition to have preceded the diplospondylic. Primitively, however, the monospondylic condition probably prevailed, and Tate Regan suggests that the multiplication of vertebrae in the caudal region may lead to greater flexibility of the tail. There is little doubt that the vertebrae of the Holocephali represent an archaic condition which has persisted unchanged since the Paleozoic. It does not mean, however, that the other elasmobranchs have been derived from them. They are an aberrant branch from an early ancestral stock.

Typically the notochord is constricted and the vertebrae take the shape of calcified double cones. This is the primary calcification which shows as rings in cross section. When no other calcification is present the type is known as cyclospondylic (Pl. XXIX, *b*, Pl. XXX, *a*, *d*, *f*). It precedes all other calcifications and so is primitive for the groups with calcified vertebrae.

Hasse (1879) recognized three types of vertebrae: the cyclospondylic, the tectospondylic, and the asterospondylic.

Asterospondylic vertebrae (Pl. XXIX, *g, i, k, l*, Pl. XXX, *c, g, h, i, j, k*) are those in which the secondary calcifications leave four main uncalcified areas, from the central double cone to the neural and haemal arches. The term tectospondylic as defined by Tate Regan (1908), is applied to all types not laid down on the asterospondylic plan. This would include not only the calcified concentric laminae around the primary ring but also those radiating rods which do not show any relation to the neural and haemal arches. This would then include the vertebrae of the Heterodontea, Squalea, and Platosomeae, and also those vertebrae in the tail of the Hexancha (Pl. XXIX, *e*) described as asterospondylic by Hasse. It probably also includes all those Mesozoic fossil types in which the vertebrae have been described in the literature as asterospondylic. It was the first type of secondary calcification to form and is found as early as the Triassic in *Synechodus*.

The Jurassic elasmobranchs laid the foundation for all the recent groups except the Hexancha and Holocephali mentioned above. It is unfortunate, therefore, that so little evidence is available of the secondary calcifications in the Triassic and Jurassic vertebrae. *Hybodus* is said to have uncalcified vertebrae, but *Palaeospinax priscus*, the modernized hybodont found in the Liassic, has vertebrae which Smith Woodward describes as faintly asterospondylic and Dean describes as strongly cyclospondylic.

Smith Woodward (1919) says of the Jurassic *Protospinax annectans* that the vertebrae show "much secondary calcification around the primary double cone and this seems to have been in concentric laminae." This would fit the tectospondylic type which is typical of many of the Squalea. Of *Crossorhinus jurassicus* he says that the vertebral centra are "much constricted and smooth, but where broken they seem to exhibit some secondary calcification round the primitive double cone."

Of *Crossorhinops minus* and *Palaeoscyllium formosum* there is no description of vertebrae, but *Pristiurus* in the upper Jurassic is said to have vertebrae of the cyclospondylic plan just as the modern *Pristiurus* has.

The conclusions from this meager data would seem to be that the uncalcified vertebrae precede the calcified; and the cyclospondylic, the tectospondylic. The asterospondylic is the latest development and does not appear until the Cretaceous, although the possibility exists of the Orectolobids having developed it in the Jurassic, since all modern Orectolobids have asterospondylic vertebrae.

The asterospondylic vertebrae are limited to the Order Galea, and

there are two types so definitely separated as to permit the splitting of the Galea into two suborders.

The first type may be called the radial type. The secondary calcifications are invaded by radiating rods, often branched, but never invading the four main uncalcified areas. This type is found throughout the Suborder Isurida, including the Orectoloboidea, the Odontaspoidea, and the Isuroidea. If *Protospinax* is the antecedent of this line, as is indicated by the close resemblance of *Crossorhinus jurassicus*, and if the concentric laminae in the vertebrae are the primitive tectospondylic type, then the radiating calcifications of the Isuroidea may have arisen from the tectospondylic direct, and not from the cyclospandylic. This might explain the appearance of concentric laminae in the vertebrae of *Cetorhinus maximus* (Pl. XXIX, *c*) and *Rhineodon typus* (Pl. XXIX, *m*). Here there are many concentric laminae in the calcified areas but in *Cetorhinus* these do not invade the four main uncalcified areas. In *Rhineodon* there is an exceptional development of very minute, branching rods extending for a short distance into the uncalcified areas. *Cetorhinus* is said to have been foreshadowed in the Cretaceous by a genus, *Corax*, whose teeth are somewhat similar. In that case the vertebrae may be primitive and developed direct from the Jurassic types. So far as known, *Rhineodon* has no fossil relatives.

The second type is the Maltese cross type which is found in the suborder Carcharinida. Here the secondary calcifications assume the shape of a Maltese cross and four short stiff calcified rods extend from the center into the four main uncalcified areas.

The only variations from the type are found in the Catuloidea (Fig. 65) where the primitive cyclospandylic type prevails but with a tendency in several species to extend the calcifications in four directions. Tate Regan believes this to be a retrogressive development returning to the primitive plan; but, considering that the Catuloidea originated in the Jurassic and that the grovelling types are now considered primitive, there is no reason to look upon the adaptations for bottom-living in the Catuloidea as retrogressive specializations, and the cyclospandylic vertebrae may be considered a retention of the ancestral plan rather than a return to it.

The transitional stages are represented in Figure 65, and while it would be impossible to suggest that the species mentioned represent a phylogenetic series, it is suggested that these species represent the retention of structures which played a part in the development of the type.

The Catulidae have the cyclospandylic vertebrae. *Catulus* has been

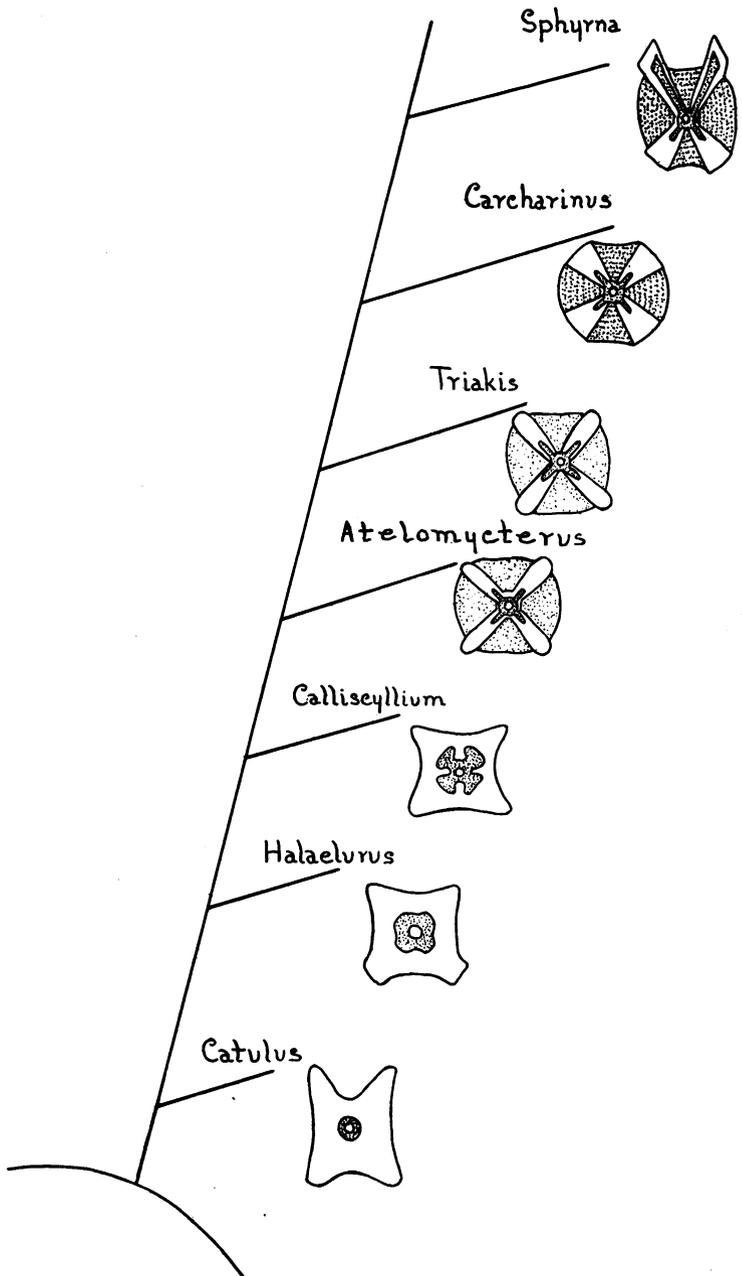


Fig. 65. Showing the development of the Maltese cross type of vertebral centra from the cyclospindlylic type in the suborder Carcharinida. In this type the calcified rods precede the secondary calcifications in development.

chosen as the type, since *Palaeoscyllium* is an earlier Jurassic form than *Pristiurus*. Both have the same vertebral structure (Pl. XXX, *a, d*).

The family Halaeluridae has been established to include all of those species formerly included in the Catulidae which have the intermediate vertebral structure (Pl. XXX *b, e*). This includes *Halaelurus*, *Haploblepharus* and *Calliscyllium*. Several species of *Catulus* have been attributed to *Haploblepharus* on the strength of Hasse's description of the vertebra of *Catulus capensis*. The other species included are so similar to this one in Garman's description that a possible correlation with the vertebral structure exists, although it has been impossible to examine the vertebrae in all cases.

The family Atelomycteridae includes the single genus *Atelomycterus* (Pl. XXX, *k*) which has attained the complete Maltese cross type of vertebra while retaining the primitive naso-oral grooves and the posterior dorsal fin. This family does not represent a transition toward the Triakidae, because of its elongation for a restricted environment, but it does represent the completion of the vertebral structure within the lower group.

On this theory the classification presented in this paper is determined, and the fact that certain physiological characters are found to be consistently correlated with the different vertebral structures gives credence to the divisions made and also leads to the suggestion that there exist in the elasmobranchs definite linkage groups as recognized by the geneticists. Such linkage is found between the nictitating membrane or fold and the Maltese cross type of vertebra. There is no consistent linkage between the incomplete membrane and incomplete fold, since the Atelomycteridae, the Triakidae, and Galeorhinidae, which have the complete vertebral structure, retain the fold. The types with complete membranes, however, all have complete vertebral structure and this again is correlated with the deepening of the body for open sea life.

A linkage exists in the radial type between the vertebral structure and the ring type of spiral valve. No exceptions have been found to this and no transitional stages exist. These linkage groups genetically may include other subordinal characters, but the two groups suggested are of importance in that they definitely link phylogenetic with physiological characters which have no possible functional relation.

Function has played no apparent part in vertebral development. *Atelomycterus*, which lives among the coral reefs of the Malay Archipelago and winds its way about the reefs, with its elongate body, has the complete vertebral structure, while *Halaelurus*, *Pristiurus*, and *Catulus*

are found in unrestricted environments off the coasts of Africa, Australia, and Japan and often in very deep water. They are small sharks and swim in schools, attacking schools of smaller fishes. Their vertebral structure is primitive or intermediate, however, and even *Calliscyllium*, in which the anterior dorsal has moved forward, adapting it to swifter swimming, has retained the intermediate vertebral type. It is obvious, therefore, that temperature, depth, and feeding habits have played no part in the development of vertebral structure and it is because of this apparent freedom from environmental influence that the vertebral structure forms a stable character on which to base relationships.

Spiral Valves

Plate XXXI

The spiral valve is a fold of tissue growing from the wall of the intestine and greatly increasing the area of its absorptive surface. With the exception of the teleosts, which are highly specialized bony fishes, the spiral valve is found in all fishes. Parker (1879) suggested that the valve has developed from the typhlosoles of invertebrates, but so little is known of the immediate invertebrate antecedents that any direct connection would be difficult to establish. In the elasmobranchs the typical valve has given rise to certain modifications which appear so consistently within the groups as to give them considerable value in classification. As there is no known environmental difference to account for the types, mutations and linkage are suggested to account for their consistency.

Type I.—This is the typical form of valve. It is wound spirally around a central axis which is completely free from the intestinal wall. The outer edges of the valves are attached to the wall and each valve is continuous with the adjacent valve and with the axis (Pl. XXXI, *b*). As a rule the valves range from two to twelve. The fewer the valves, the more pendulous the aspect, and when the valves are greatly increased in number they may lie so close together that the central axis will disappear, bringing about the second type of valve, which thus appears to have arisen from the spiral type by multiplication of valves. Parker divided the spiral type into several subtypes, which vary within families. For the purposes of this classification, however, the number of valves suffices.

Type II.—The valves are mainly separate sheets of tissue attached to the wall of the intestine all the way around. They are not rolled into

an axis at any point, the apparent axis being formed by the inpushing of the intestinal wall. In the less complete forms the upper valves retain connection with the adjacent valves forming a spiral but no axis. This form is found in *Carcharias* and *Scapanorhynchus*. When complete each valve is wholly separate as in *Chiloscyllium* (Pl. XXXI, c) and *Stegostoma*.

Type III.—The valve is a single fold of tissue rolled into a scroll. It is rolled on its own axis parallel to the axis of the intestine, and is attached to the wall on one side only throughout its entire length (Pl. XXXI, a). This is a specialization in the opposite direction from Type II and appears to have been formed by the reduction of valves and by the breaking of the attachment to the outer wall. Parker claimed that this type had a separate origin from the typhlosole, but the type is found in only two families, the Carcharinidae and Sphyrnidae, and these families have developed from families of earlier and more primitive origin which have valves of the spiral type, so that some direct connection with that type of valve is indicated.

Gegenbaur points to the small number of valves in *Chimaera monstrosa* as the primitive condition. The Holocephali have retained many archaic characters and this may be the primitive type. However, in the modern groups an intermediate number appears in the primitive families and the derived families show either a tendency toward multiplication or reduction (Tab. VIII).

Since the modified types occur consistently in closely related groups and do not occur as parallel specializations in widely separate groups, it is obvious that the conditions leading to their development must be deeper than the immediate environment. It is not possible to consider the condition of the viscera as phylogenetic characters, but the consistent appearance of visceral modifications with certain phylogenetic characters suggests the occurrence of linkage groups as mentioned in a previous section, the ring type of spiral valve being linked with the radial type of asterospondylic vertebrae and occurring in the Orectoloboidea, the Odontaspoidea, and the Isuroidea. No exceptions have been found. The scroll type is linked with the completed nictitating membrane. The Maltese cross type of vertebra is linked with either the fold or the membrane.

The spiral type is by far the most common but tendencies either toward multiplication or reduction may be noted within groups. For convenience the spiral type has been divided into three groups: those with few valves (from two to four); those with an intermediate number

(from five to ten); and those with numerous valves (from eleven to thirty).

In the Catuloidea the intermediate number is typical but both reduction and multiplication occur. *Calliscyllium venustum* has the reduced type which may be transitional, there being a similar reduction in *Triakis*. *Atelomycterus marmoratus* has a larger number, which may be correlated with its elongation. *Atelomycterus* is a specialized but not a transitional species, although it parallels in its development many of the characters attained by the Triakidae.

The Galeorhinidae are also variable, some species having few, some an intermediate number, and some numerous valves. This also is a specialized family. The Triakidae have the reduced number and in every respect the Triakidae lead direct to the Carcharinidae. Therefore reduction is suggested as the origin of the scroll type.

The Hexanchea have numerous valves but not the ring type. This may be correlated, as in *Atelomycterus*, with elongated body length, and with the multiplication in the Hexanchea of other characters, such as the gill slits and the heart valves.

The spiral type is found throughout the Heterodontea, the Squalea, and the Platosomeae, and the intermediate number is typical in all the groups, although some variation occurs in the direction of numerous valves. This is paralleled by the variation in the heart valves.

TABLE VIII.—TYPES OF SPIRAL VALVES

	Scroll type	Spiral type 2-4	Spiral type 5-10	Spiral type 11-30	Ring type
Holocephali					
<i>Chimaera monstrosa</i>		X			
Antaceae					
Hexanchea					
<i>Heptranchias perlo</i>					X
<i>Notorhynchus pectorosus</i>					X
<i>Chlamydoselachus anguineus</i>					X
Heterodontea					
<i>Heterodontus japonicus</i>			X		
Squalea					
<i>Squalus acanthias</i>			X		
<i>Squalus mitsukurii</i>			X		
<i>Acanthidium rostratum</i>				X	
<i>Etmopterus lucifer</i>			X		
<i>Somniosus microcephalus</i>				X	
<i>Pristiophorus japonicus</i>			X		
<i>Rhina californica</i>				X	
Platosomeae					
Batea					
<i>Raja</i>			X		
Antaceae					
Galea					
Isurida					
Orectoloboidea					
<i>Chiloscyllium griseum</i>					X
<i>Chiloscyllium indicum</i>					X
<i>Chiloscyllium tuberculatum</i>					X
<i>Stegostoma tigrinum</i>					X
Odontaspoidea					
<i>Carcharias taurus</i>					X
<i>Scapanorhynchus owstoni</i>					X
Isuroidea					
<i>Isurus punctatus</i>					X
<i>Vulpecula marina</i>					X

TABLE VIII.—TYPES OF SPIRAL VALVES (*Continued*)

	Scroll type	Spiral type 2-4	Spiral type 5-10	Spiral type 11-30	Ring type
Carcharinida					
Catuloidea					
<i>Catulus retifer</i>			X		
<i>Catulus torazame</i>			X		
<i>Parmaturus xaniurus</i>			X		
<i>Cephaloscyllium umbratile</i>					X
<i>Halaehurus burgeri</i>			X		
<i>Halaehurus bivius</i>			X		
<i>Calliscyllium venustum</i>		X			
<i>Atelomyclerus marmoratus</i>					X
Carcharinoidea					
<i>Triakis scyllium</i>		X			
<i>Galeorhinus mustelus</i>			X		
<i>Galeorhinus manazo</i>			X		
<i>Galeorhinus fasciatus</i>					X
<i>Hemigaleus pectoralis</i>					X
<i>Galeus glauca</i>		X			
<i>Galeocerdo</i>		X			
<i>Physodon mülleri</i>		X			
<i>Scoliodon wahlbeehmi</i>		X			
<i>Carcharinus limbatus</i>		X			
<i>Carcharinus sorrah</i>		X			
<i>Carcharinus commersonii</i>		X			
<i>Carcharinus porosus</i>		X			
<i>Carcharinus acronotus</i>		X			
<i>Carcharinus milberti</i>		X			
<i>Carcharinus spallanzani</i>		X			
<i>Carcharinus dussumieri</i>		X			
<i>Carcharinus borneensis</i>		X			
<i>Sphyrna zygaena</i>		X			
<i>Sphyrna blochii</i>		X			

Heart Valves

Plates XXXII to XLIII

The heart valves of the elasmobranch fishes (Fig. 66) have been the subject of discussion from time to time, and have been somewhat extensively described by Garman (1913). A great many have been examined in the preparation for this paper, with results which do not entirely agree with those of past authors.

In all fishes the conus arteriosus of the heart is functional and contains a varying number of valves. In the higher Osteopterygia there is a separation between the two regions of the conus, the anterior portion being strengthened and the valves restricted to a single row in the posterior portion. In the lower Osteopterygia, and in the elasmobranchs there is no such division, the entire conus being valvular. The development within the elasmobranchs, therefore, does not parallel that of the typical fishes, but the conditions found in the lower Osteopterygia (see *Ceratodus forsteri*, Pl. XXXII, *i*) is reminiscent of some of the higher elasmobranchs, and may represent the continuation of a process begun in the lower group.

In the elasmobranchs the number of valves varies from three series of valves in two rows, as found in the Orectoloboidea, to four series in five rows in the Hexanchea, and to six or seven rows in some of the rays. Although variation occurs even between members of the same species in some cases, the variation tends to fall within limits characteristic of a group or to show transitional tendencies toward a higher group, and for that reason the heart valves may be used as one of the contributing characters in establishing a classification.

The question is whether the small number or the large number is primitive. Garman (1885) suggests that the large number is primitive and that reduction has occurred in the elasmobranchs with the increase of specialization. He admits, however, that the opposite seems to be true in the rays. Lankester (1878) suggests that duplication occurs in some cases in a longitudinal direction. In the opinion of the author the tendency in the elasmobranchs is for duplication of valves rather than reduction, and this duplication may take place transversely as well as longitudinally. In some cases valves arising by longitudinal division in one row may be pushed downward and thus give rise to an additional row.

In the Hexanchea the tendency is toward a large number of valves, usually in four series of four or five rows. Garman's figure of *Heptranchias perlo* shows three series of five rows, the row directly beneath the

Heart Valves
in

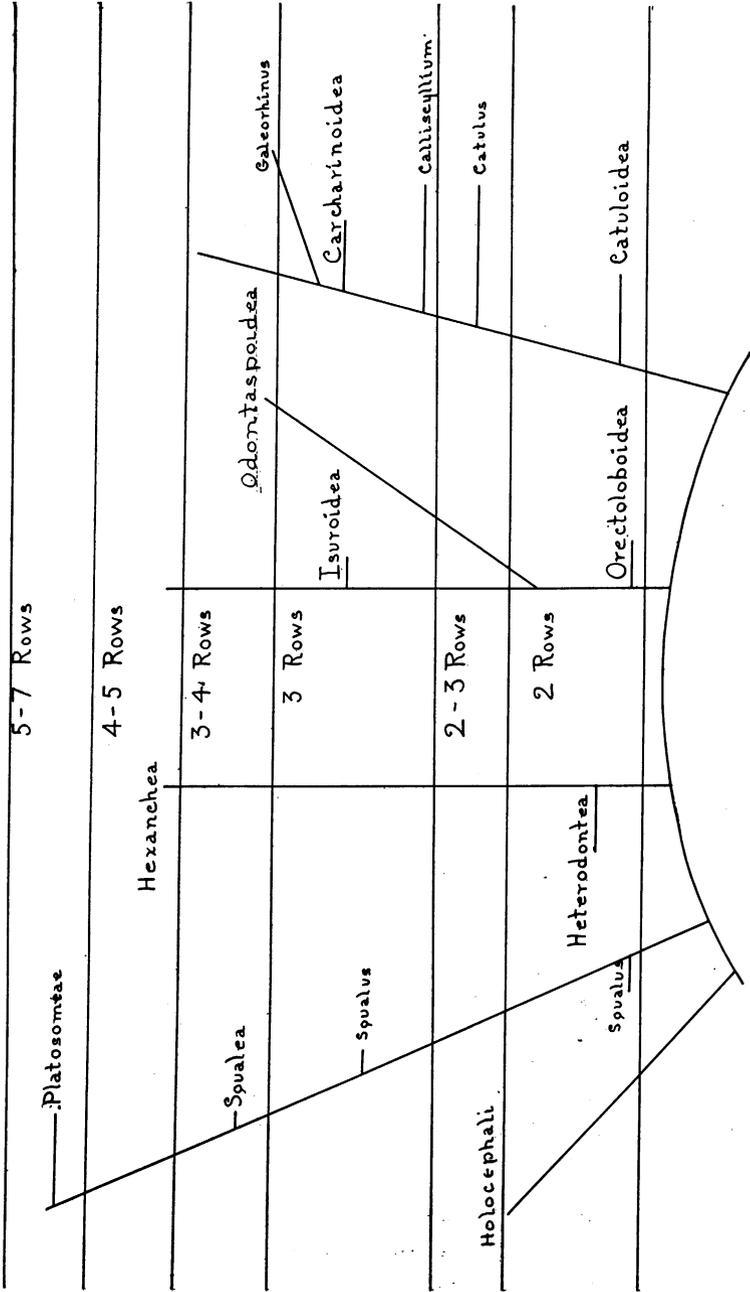


Fig. 66. Groups arranged to show relationships based on the number of rows of valves in the bulbous. Genera showing transitional conditions are shown in smaller type. In this characteristic the Hexanthea and the Carcharioidea have shown extreme specialization.

membranous valves being very minute. In 1885 Garman quoted Owen as saying that both *Hexanchus* and *Heptanchias* have four rows of valves. He himself describes two species, a young *Notorhynchus pectorosus* (formerly *Heptanchias*) with five rows, and a large *Heptanchias maculatus* with only three rows, but with traces in the middle of the conus as of two rows which he calls obsolete.

I find a mature specimen of *Notorhynchus pectorosus* with only four rows but in four series, which would seem to indicate duplication rather than reduction (Pl. XXXII, a). A specimen of *Chlamydoselachus anguineus* shows four distinct series with five rows, the fourth row in the process of duplication (Pl. XXXII, d). This varies considerably from Garman's figure (1885), in which he shows only three series of valves. The fourth series has been found in no other group of the elasmobranchs but is frequently found in the Osteopterygia (Pl. XXXII, i).

The valves of *Chlamydoselachus* are more membranous than those of other types but there is a general resemblance between them. The conus is long and the upper row of valves is membranous in all. The valves extend down by a chord to the lower row, some of which have thickened walls. A distinct tendency to duplication is apparent in all members of the order, and it is reasonable to look upon Garman's vestigial fifth row as a rudimentary fifth in *Heptanchias*.

On the theory of duplication it will be apparent that the Hexanchea have exceeded their usual speed of development. This is not unexpected, however, since it is a well-known fact that this group is highly specialized in certain characters while retaining others in archaic condition. This duplication is paralleled in the Hexanchea in the spiral valves and in the gill openings.

The same appears to be true in the Odontaspoidea. In a specimen of *Scapanorhynchus owstoni* examined by the author (Pl. XXXII, g) the valves do not differ from the one figured by Garman in 1913. It is clear that duplication in the transverse direction is in progress, for the chordae tendineae in the upper row of valves mark off a decidedly thickened area at the base of the membranous valves. These have not yet separated off, as no cleavage of the tissue has taken place. The same condition is found in a young specimen of *Carcharias taurus* (Pl. XXXII, f), except that here the duplication is occurring in the second instead of the first row of valves. In both species the conus is shorter than in the Hexanchea.

Two rows are characteristic of the Holocephali, the Orectoloboidea, and the Catuloidea, but are the exception in other groups. Three rows

are characteristic of the Odontaspoidea, although duplication is in progress, and of the Isuroidea and the Carcharinoidea. The only tendency to duplication in the latter groups was found in one species of the Galeorhinidae: in *Galeus glauca* of the Carcharinidae there are but two rows, the upper row being excessively elongate.

One of the most interesting types was found in *Catulus torazame* (Pl. XL, *d*). The heart was taken from a mature female with complete egg cases in the oviduct, and is not, therefore, a transitional stage in the life of the individual. There is an obvious transverse duplication in progress here, and, since the typical number for the group is two rows, this condition bears out the author's conclusion that *Catulus torazame* is a transitional type approaching the stable condition prevailing throughout the Carcharinoidea.

In *Calliscyllium venustum* (Pl. XL, *b*) three definite rows are already established in a group in which two rows are typical. This species, also, shows other transitional characters, bridging the gap between *Catulus torazame* and the Carcharinoidea. *Triakis scyllium* has three complete rows established and has, therefore, reached the condition characteristic of its group, and is not transitional as it is in so many of its characters.

The recent acquisition of the heart of a thirty-foot whale shark, *Rhineodon typus* (Pl. XXXVI), gives an interesting picture of duplication in progress. Here there are two definite rows, the upper membranous and the lower row attached to the upper by chords. Additional pockets are formed on some of the lower valves and between them are two completely formed additional valves. These represent longitudinal multiplication, and if later pushed down would form a third row.

The Heterodontea (Pl. XXXIII, *a*) and the Holocephali (Pl. XXXIII, *d*) have both typically two rows, although three occur in some specimens of *Chimaera* (Pl. XXXIII, *e*). These are groups of low development and ancient origin. The Squalea show variable tendencies even within the species, *Squalus acanthias* (Pl. XXXIV, *a, c*) having two rows in some specimens and three in others. This is unusual and may indicate a mutating species. Other species of *Squalus* and of *Etmopterus* (Pl. XXIV, *e, g*) have four rows and this means that the group as a whole is in an unstable condition. Instability is characteristic of transitional groups. The Platosomeae, which are derived from the Squalea, show even more extreme duplication of valves, reaching six and sometimes even seven rows (Pl. XLIII).

The condition commonly found among the lower Osteopterygia and

shown in *Ceratodus forsteri* (Pl. XXXII, *i*) may well be carrying on a condition of duplication already well under way among the elasmobranchs, even though reduction occurs in the higher fishes.

TABLE IX.—HEART VALVES

	Number of Rows					
	2	3	4	5	6	7
Chismopnea						
<i>Callorhynchus callorhynchus</i> (Pl. XXXIII, <i>d</i>)	X					
<i>Chimaera monstrosa</i> (Goodrich)	X					
<i>Chimaera monstrosa</i> (Lankester) (Pl. XXXIII, <i>e</i>)		X				
Antacea						
Heterodontea						
<i>Heterodontus japonicus</i> (Pl. XXXIII, <i>a</i>)	X					
Squalea						
<i>Squalus acanthias</i> (Pl. XXXIV, <i>c</i>)	X					
<i>Squalus acanthias</i> (Pl. XXXIV, <i>a</i>)		X				
<i>Pristiophorus japonicus</i> (Garman)		X				
<i>Squalus fernandinus</i> (Pl. XXXIV, <i>g</i>)			X			
<i>Etmopterus lucifer</i> (Pl. XXXIV, <i>e</i>)			X			
Platosomeae						
Narcobatoidea						
<i>Narke japonica</i> (Garman)	X					
<i>Narcacion marmoratum</i> (Garman)		X				
Rhinobatoidea						
<i>Rhinobatus percellens</i> (Garman)			X			
<i>Discobatus sinensis</i> (Garman)			X			
Dasybatoidea						
<i>Discus thayeri</i> (Garman)			X			
<i>Pteroplatea altavela</i> (Garman)				X		
<i>Aetobatus narinari</i> (Garman) (Pl. XLIII, <i>a</i>)					X	
<i>Mobula hypostoma</i> (Garman) (Pl. XLIII, <i>f</i>)						X
<i>Rhinoptera jussieuvi</i> (Garman) (Pl. XLIII, <i>c</i>)						X

TABLE X.—HEART VALVES (Continued)

	Number of Rows					
	2	3	4	5	6	7
Antacea						
Galea						
Orectoloboidea						
<i>Orectolobus japonicus</i> (Garman) (Pl. XXXV, <i>f</i>)	X					
<i>Chiloscyllium griseum</i> (Pl. XXXV, <i>e</i>)	X					
<i>Chiloscyllium indicum</i> (Pl. XXXV, <i>g</i>)	X					
<i>Chiloscyllium plagiosum</i> (Pl. XXXV, <i>a</i>)	X					
<i>Stegostoma tigrinum</i> (Pl. XXXV, <i>b</i>)	X					
<i>Rhineodon typus</i> (Pl. XXXVI-XXXVII)	X					
Odontaspoidea						
<i>Carcharias taurus</i> (Pl. XXXII, <i>f</i>)		X				

	Number of Rows					
	2	3	4	5	6	7
<i>Scapanorhynchus owstoni</i> (Pl. XXXII, g)		X				
Isuroidea						
<i>Isurus punctatus</i> (Garman) (Pl. XXXVIII, c)		X				
<i>Carcharodon carcharias</i> (Parker)						
(Pl. XXXVIII, f)		X				
<i>Vulpecula marina</i> (Goodrich)		X				
Hexanchea						
<i>Hexanchus</i> (Owen)				X		
<i>Hepranchias perlo</i> (Garman)				X		
<i>Notorhynchus pectorosus</i> (Pl. XXXII, a)				X		
<i>Notorhynchus pectorosus</i> (Garman)					X	
<i>Hepranchias maculatus</i> (Garman)					X	
<i>Chlamydoselachus anguineus</i> (Garman)				X		
<i>Chlamydoselachus anguineus</i> (Pl. XXXII, d)						X

TABLE XI.—HEART VALVES (Concluded)

	Number of Rows					
	2	3	4	5	6	7
Antacea						
Galea						
Catuloidea						
<i>Halaehurus burgeri</i> (Pl. XXXIX, f)		X				
<i>Halaehurus bivius</i> (Pl. XXXIX, a)		X				
<i>Parmaturus xaniurus</i> (Pl. XL, f)		X				
<i>Pristiurus eastmani</i> (Pl. XXXIX, d)		X				
<i>Cephaloscyllium umbratile</i> (Garman)		X				
<i>Atelomycterus marmoratus</i> (Pl. XXXIX, b, c)		X				
<i>Catulus retifer</i> (Pl. XL, a)		X				
<i>Catulus torazame</i> (Pl. XL, d)					X	
<i>Calliscyllium venustum</i> (Pl. XL, b)					X	
Carcharinoidea						
<i>Triakis scyllium</i>				X		
<i>Galeorhinus mustelus</i> (Pl. XLI, b)				X		
<i>Galeorhinus laevis</i> (Pl. XLI, a)				X		
<i>Galeorhinus manazo</i> (Pl. XLI, d)					X	
<i>Galeorhinus fasciatum</i> (Pl. XLI, e)				X		
<i>Galeus glauca</i>		X				
<i>Eugaleus galeus</i> (Pl. XXXVIII, a)				X		
<i>Carcharinus sorrah</i> (Pl. XLII, d, f)				X		
<i>Carcharinus porosus</i>				X		
<i>Carcharinus commersonii</i> (Pl. XLII, e)				X		
<i>Carcharinus milberti</i> (Pl. XLII, a)				X		
<i>Carcharinus acronotus</i>				X		
<i>Carcharinus spallanzani</i>				X		
<i>Scoliodon wahlbeehmi</i>				X		
<i>Physodon mülleri</i>				X		
<i>Sphyrna zygaena</i> (Pl. XLII, c)				X		

Male Claspers and Myxopterygia

Plates XLIV to L

The claspers of the male elasmobranchs are specialized organs adapted to the internal fertilization of the egg and are peculiar to the cartilaginous fishes. They are not found in the Paleozoic elasmobranchs, their first appearance being in the Triassic hybodonts, so that internal fertilization must be considered a late development. From time to time authors have claimed that consistent tendencies exist in well-recognized groups which are of aid in classification. Leigh-Sharpe (1920-1926) has emphasized the external structure and function of the organs, and Huber (1901) the internal structure of the skeletal supports, the myxopterygia, which are modified basals and radials of the pelvic fins.

Leigh-Sharpe has grouped the elasmobranchs according to the external structure of the claspers as follows:

I.—Those without claspers and presumably without siphons and glands. These are exclusively fossil.

II.—Those having a blindly ending cavity in the proximal portion of the clasper. The Holocephali and *Chlamydoselachus*.

III.—Those having a true abdominal siphon in addition to a cavity in the proximal portion of the clasper. The Heterodontea.

IV.—Those having an abdominal siphon only and no cavity in the clasper (unless it is represented by the parasiphon of *Scyllium* (*Catulus*)¹). All the Selachians except *Heterodontus*, *Chlamydoselachus*, *Isurus*, and *Rhina*.

V.—Those in which a clasper gland has been developed inside the original siphon sac. *Isurus*, *Rhina*, and the Platosomeae.

The position of *Isurus* is the only strange exception. *Rhina* links the Squalea with the Platosomeae, and may, therefore, be expected to show specialization in their direction, but no apparent reason exists for a parallel structure in the most specialized family in one branch of the Galea.

Leigh-Sharpe (1924) suggests the relationship of the Carcharinidae to the Scylliidae (Catuloidea) through an intermediate form, *Triakis*. This relationship he bases on the length of the siphons and the presence of pseudosiphons and parasiphons. The parasiphon is found in the Catuloidea as a functioning structure; is vestigial in *Triakis*, and absent

¹ Note —Leigh-Sharpe's genus *Scyllium* includes *Catulus* and *Halaclurus* of this paper.

in *Carcharinus*. He suggests a relationship of *Chiloscyllium* to this group, but this is doubtful.

Huber's groups show that the number of basal cartilages serving to attach the axial cartilages to the pelvic arch are consistent within large groups. The Holocephali have one cartilage; Hexanchea, the Heterodontea, and the Squalea, two; the Galea one, and the Platosomeae a larger number varying from two to four. He holds that the accessory structures of the myxopterygia tend to follow the same grouping.

The general structure of the axial cartilages upholds this point. In the Holocephali they are undifferentiated (Pl. XLIV, *a*) and show no homology with similar structures in the other groups. This type may have existed in the Paleozoic, although no fossil forms of that period indicate it. In the Hexanchea they are cylindrical and pointed but undifferentiated. A slight projection at the distal end possibly represents a rudimentary ventral cartilage (Pl. XLIV, *b*). In the Heterodontea, Squalea, and Platosomeae, the dorsal cartilage is elongate and cylindrical, while the ventral cartilage is small and limited to the distal end (Pl. XLV).

In the Galea, however, an entirely different structure persists. The dorsal and ventral cartilages are both elongate and flattened dorsoventrally. There is no variation from this structure throughout the order, so that the general structure of the axial cartilages may prove a deciding factor in classification. They tend to vary within the order, however, and so inconsistently that they are of little value in establishing relationships. In some the two cartilages are open like a leaf; in others the edges are slightly curled in toward the center, and in other types the two cartilages are rolled into a tight scroll. It has been suggested that the open type may be a temporary state in young individuals, but this is not the case. Where the cartilages are rolled in the adult they are rolled in the young specimens in which the terminal cartilages have not even chondrified, and where the open type exists, it has been found to be as flatly open in a specimen fourteen feet long as in an immature one. Variations of this type are shown on Pls. XLVI-L.

Fusion is more complete and the cartilages more elongate in the Catuloidea than in any other group. Especially is this true in *Atelomycterus marmoratus* (Pl. XLVIII, *b*), and in *Halaaelurus burgeri* (Pl. XLVII, *c*), types chosen by Leigh-Sharpe as transitional to the condition found

in *Triakis*. In *Triakis scyllium* the cartilages are open and leaf-like (Pl. XLIX, *a, b*), a condition not following that of the Catuloidea unless the development has been one of unfolding the scroll instead of rolling it up. That this is a possible explanation is indicated by the rolled condition in the Orectoloboidea (Pl. XLVIII, *e*, Pl. XLVI, *c*), in the Catuloidea (Pl. XLVII), and in the Isuroidea (Pl. XLVI, *a, b*). More variability is found among the Carcharinoidea than in the more primitive groups, which is unusual since this group is more stable in most of its characters rather than less so. All stages are found, from the tightly rolled scroll to the completely open type. In the Sphyrnidae (Pl. L, *e, f*) the scrolls are tightly rolled, however, which does not bear out a tendency to unrolling the scroll, this family being more highly specialized than the Carcharinidae (Pl. L, *a-d*). *Calliscyllium venustum* (Pl. XLVII, *d*) has an open, leaflike cartilage which may be transitional to the character in *Triakis* (Pl. XLIX, *a, b*). Any definite conclusions on this matter, however, must be reserved for more adequate information.

It is not unexpected to find that the basals of the myxopterygia and the general plan of the axial cartilages are more stable factors than the rolling of the cartilages. The latter condition is probably more under the control of the environment, while the former are of phylogenetic significance.

Reproduction

Plate LI

The modern sharks are often thought to be typically viviparous because this condition exists in the large pelagic sharks, which are the most familiar. As a matter of fact, many sharks are oviparous and this habit probably preceded viviparity. Moreover, the kind of viviparity found in the elasmobranchs is really an ovoviviparous condition and the organs do not differ essentially in the two types.

In the oviparous types leathery egg cases are secreted around the large eggs in the long oviducts. The reproductive organs of *Catulus torazame* are shown in the photograph on Pl. LI, *a*, with two egg cases intact in the oviducts. When these are laid, long twisting threads are secreted from the four corners and are twined around some object which

serves as an anchor. Two of these egg cases from the same species are shown in figure *b* of the same plate, fastened to a branching colony of the hydroid, *Sertularia*. This beautiful specimen and several others were loaned to the author for photographing by Kuma Aoki, the well-known collector at the Misaki Marine Biological Laboratory in Japan. In figure *c* is shown an egg case of *Cephaloscyllium*, which has been opened to disclose the embryo developing within it, and in figure *d* a similar case from *Heterodontus japonicus*.

The oviparous habit is found in the Holocephali, the Heterodonta, the Orectoloboidea (with the exception of *Chiloscyllium* and *Hemiscyllium*), the Catuloidea, and in the Rajoidea of the rays. This last group is puzzling, since the Squala and all the other Platosomeae are viviparous. *Zanobatus*, one of the rhinobatids, is said to be oviparous because an egg in its shell has been observed in its oviduct, and this has been offered as explanation for the development of the oviparous Rajoidea from the Rhinobatoidea. Garman, however, believes that the egg found in *Zanobatus* was one in which the embryo is developed before extrusion and so is a specialized ovoviviparity. *Raja*-like forms have been reported from the Jurassic, so it is possible that this group branched from the squaloid line before the viviparous habit had been established.

In the viviparous types the uterus is slightly enlarged and ridges and furrows develop on its surface. The uterus of a female *Calliscyllium venustum* shows a slightly ridged surface, indicating that this may be a viviparous species in an otherwise oviparous group. No specimens with either eggs or embryos have been taken, however, so that it is impossible to decide definitely.

The eggs in viviparous types are large and have as much yolk as the oviparous ones. Villi develop from the walls of the oviduct for the nourishment of the embryo, and many curious specializations are found for transferring the nourishment to the embryo. In the Carcharinoidea the villi fit into crypts in the wall of the yolk sac, thus forming a pseudo-placenta, and transitory threads from the gill lamellae appear to have some absorptive as well as respiratory power. In the Platosomeae the strangest arrangements are found in the Myliobatidae, where contact with the embryo is often made through the spiracles. In *Pteroplatea* the maternal villi actually penetrate through the spiracles to the embryonic digestive tract.

Such specializations in themselves indicate that the habit is a derived

one, and claspers are not known in the Paleozoic elasmobranchs, except in the Permian *Pleuracanthus*, which seems to have some such organ but is in no way ancestral to the modern forms. Claspers are necessary for the internal fertilization of the egg, and it is inferred that these early vertebrates must have laid the eggs in the water, where they were fertilized much as in the higher fishes today. Doubtless the elasmobranchs retained the egg-laying habit long after the development of internal fertilization, but because of this the eggs were laid in a much more protected condition. The ovoviviparous habit would then have been a later development from the egg-laying habit.

This is the more plausible because the oviparous habit is found in the more primitive groups and those which were established in the Jurassic or earlier. The Squalea are the only viviparous group established as early as the Jurassic, and it is possible that this habit was not begun so early since the oviparous Rajoidea branched from the squaloid line during the Jurassic, as did also the Orectoloboidea. In all the oviparous groups there is shown some tendency toward ovoviviparity and in all the groups established in the Cretaceous or later we find it well developed.

CHARACTERISTICS OF THE CLASSES, SUBCLASSES, SUPERORDERS, ORDERS, ETC., OF THE ELASMOBRANCHS

(See Table I)

CLASSES OF THE SUPERCLASS PISCES

CHONDROPTERYGIA	ACANTHODIA	OSTEOPTERYGIA
Exoskeleton of dermal denticles, structurally identical with teeth	Exoskeleton of small plates covered with ganoine, not structurally identical with teeth	Exoskeleton of bony plates or scales, not structurally identical with teeth
Spines primitively present	Spines always present	Spines primitively absent
Ceratotrichia present	Ceratotrichia reduced	Ceratotrichia vestigial (actinotrichia)
Lepidotrichia absent	Lepidotrichia absent	Lepidotrichia predominant
Endoskeleton cartilaginous, often calcified	Endoskeleton cartilaginous with some bony cells	Endoskeleton typically replaced by bone

CHONDROPTERYGIA	ACANTHODIA	OSTEOPTERYGIA
Membrane bones absent	Membrane bones few	Membrane bones dominant
Elements of skull not separated by sutures	Elements of skull not separated by sutures	Elements of skull separated by sutures
Primary lower jaw (Meckel's cartilage) principal element	Primary lower jaw principal element	Primary lower jaw sheathed with membrane bone
Spines of pectoral arch absent	Spines of pectoral arch present	Spines of pectoral arch typically absent
No bone cells in arch	Bony tissue with endoskeletal base	Membrane bones of girdle predominate
Ribs typically of dorsal type		Ribs typically of ventral type (both types in Polypteri)
Notochord more or less persistent	Notochord persistent	Notochord replaced
Vertebral column with neural and haemal arches only	Vertebral column with neural and haemal arches only	Supraneural and infra-neural arches added
Branchial arches 5-7	Branchial arches 5	Branchial arches 5-4 1/2 or less
Openings separate, without opercula (except Holocephali)	Openings separate with small opercula	Openings covered by operculum
Paired nasal organs, each with one external opening		Paired nasal organs each with two external openings
No air bladder or lungs		Air bladder or lungs typically present
Modern forms with internal fertilization		External fertilization typical
Myxopterygia in male of modern forms		No myxopterygia in male

SUBCLASSES OF THE CHONDROPTERYGIA

PLAGIOSTOMI	HOLOCEPHALI
Gill clefts open to the exterior	Gill clefts open to a chamber with one external opening
No erectile spine	Erectile spine
Pterygoquadrate distinct from the cranium	Pterygoquadrate fused with cranium
Teeth numerous, without tritons	Teeth few, with tritons
No frontal tenaculum	Frontal tenaculum
Rectal gland	No rectal gland

SUPERORDERS OF THE PLAGIOSTOMI

ANTACEAE (Pleurotremata)	PLATOSOMEAE (Hypotremata)
Body fusiform	Body, head, and pectorals depressed
Eyes with margins free	Superior margins of eyes not free
Eyes lateral	Eyes superior
Gill openings lateral	Gill openings ventral
Teeth cuspidate, rarely in pavements	Teeth in bands or pavements
Dorsals 1 to 2	Dorsals 0 to 2
Pterygoquadrate with a palatobasal process attached by ligament to cranium	No palatobasal process; not attached to cranium
Preorbitals not attached to olfactory capsules	Preorbitals attached to olfactory capsules

The rays (Hypotremata) split from the Squalea during the Jurassic, probably from Rhinidae.

ORDERS OF THE PLATOSOMEAE

	NARCOBATEA	BATEA
Rostral cartilage	Paired or branched	Unpaired or absent
Preorbital cartilage		
Form	Reticulate or branched	Simple
Extent	To anterior margin snout	Not extended forward
Articulation, proximal	Anterior wall nasal capsules	Posterior wall
Articulation, distal	Propterygium	Absent
Suprascapulae united	Above vertebral column	To vertebral column
Electric organs	Present	Absent

SUPERFAMILIES OF THE BATEA

	RHINOBATOIDEA	RAJOIDEA	DASYBATOIDEA
Dorsal fins	Two, anterior middle of tail	Two, posterior middle of tail	Present or absent
Tail	Strong	Medium	Whip-like
Rostral cartilage	Present	Present or absent	Absent
Pelvis	Transverse	Transverse	Arched
Prepelvic process	Absent	Lateral	Median
Reproduction	Ovoviviparous	Oviparous	Ovoviviparous

ORDERS OF THE ANTACEAE

	HEXANCHEA	HETERODONTEA	SQUALEA	GALEA
Dorsal fins	1	2	2	2
Dorsal fin spines	Absent	Present	Present	Absent
Anal fin	Present	Present	Absent	Present
Gill openings	5 to 7	5	5 to 6	5
Sixth gill arch	Complete	Absent	Absent or complete	Rudimentary
Jaw suspension	Amphihyostylic	Amphihyostylic to hyostylic	Hyostylic	Hyostylic
Pterigoquadrate articulation	Loose	Extensive	Absent	Loose or absent
Palatobasal process	Present	Present	Absent	Reduced
Rostral cartilages	Single	Absent	Single	Triradiate
Pectoral fin				
Mesopterygium	On margin of fin	Not on margin	Not on margin	Not on margin
Radials on propterygium	None	1	1 to several	1 to several
Radials on meso- and metapterygium	Equal	About equal	About equal	Unequal
Notochord	Unconstricted anteriorly	Constricted	Constricted	Constricted
Vertebrae	Diplospondylic	Monospondylic	Monospondylic	Monospondylic
Vertebral centra	Undifferentiated anteriorly, tectospondylic posteriorly	Tectospondylic	Cyclo- or tectospondylic	Asterospondylic
Myxopterygia				
Elements of stem	2	2	1 to 2	1
Axial cartilage	Cylindrical and pointed	Cylindrical and pointed	Cylindrical and pointed	Dorso-ventrally flattened
Ventral marginal	Short and distal	Short and distal	Short and distal	Elongate

The origin and relationships of the Heterodontea and the Hexanchea have been noticed above (pp. 48, 49).

The Squalia retain the great variability of a stem group. The variations involve both the phylogenetic and the physiological characters and include dorsal fin spines, denticles, teeth, gill slits (reduplication in *Pliotrema*), rostral cartilages, spiral valves, heart valves.

This variation is found not only in families but in members of a genus and even of a species, showing that the Squalia is a group of great instability. Variability within a species may mean a species in a mutating condition. *Squalus acanthias* presents this picture, and without doubt other species will be found to be in the same condition.

SUBORDERS OF THE SQUALIA

	SQUALIDA	RHINIDA
Body	Compressed	Depressed
Pectoral fins	Not expanded	Expanded forward and back
Dorsal fins	Forward of tail	Far back on tail
Spines	Present or absent	Absent
Neural spines	Not attached to dorsals	Attached to dorsals
Pelvis	Transverse	Curved backward

SUBORDERS OF THE GALEA

ISURIDA	CARCHARINIDA
Nictitating membrane absent	Nictitating fold or membrane present
Vertebral centra with calcifications radiating and often branching in the calcified areas	Vertebral centra with secondary calcifications in form of a Maltese cross, or rudimentary
No rod-like calcifications in the uncalcified areas	Typically four rod-like calcifications in the uncalcified areas
Spiral valves of ring type	Spiral valves of spiral or scroll type

Development within these two suborders has followed the same general trend because in each group the radiation was from a littoral to a pelagic life. Many parallel structures have been developed in the higher types of the two groups, therefore, so that a general similarity in external form is noticeable.

The Squalia form the stem group for the Isurida but not for the Carcharinida, which I believe to have developed independently from the Hybodontidae.

SUPEREAMILIES OF THE ISURIDA

	ORECTOLOBOIDEA	ODONTASPOIDEA	ISUROIDEA
Dorsals	Subequal, small	Subequal, large	Unequal
Anterior dorsal	Posterior pelvics	Between pectoral and pelvic	Anterior pelvic
Caudal axis	Low	Little raised	Much raised
Caudal keels	Absent	Variable	Present
Caudal pits	Variable	Absent	Present
Gill openings	Narrow	Wide	Wide
Last two	Close together over base pectoral	Separate anterior base pectoral	Separate anterior to or over base pectoral
Spiracles	Large	Small	Small or absent
Nasoral grooves and cirri	Present	Absent	Absent
Denticles, keels	Incomplete	Complete	Complete
Central keel	Prominent	Prominent	Not prominent
Teeth	Small	Large	Large
Cusps	More than one	One	One
Lateral denticles	Large	Small	Minute
Spiral valves	Ring type	Ring type	Ring type
Heart valves	In 2 rows	In 3-4 rows	In 3 rows
Rostral cartilages	Not united	United	United
Pectoral fin			
Mesopterygium	Expanded	Small	Small
Radials on meso- and metapterygium	Equal	Unequal	Unequal
Segments of radials	3 or more	2 or more	3 or more
Claspers			
Siphon	Present	Primitive	Present
Gland	Absent	Absent	Present
Myxopterygia			
Axial cartilages	Coiled into tube		Coiled

The Orectoloboidea show less variation than the Catuloidea, probably because the Catuloidea are closer to the Hybodontidae, and therefore a more variable stem group like the Squalea. Variation in the Orectoloboidea includes teeth, nasal valves, segments of the radials in the pectoral fins, myxopterygia.

The heart valves and spiral valves are peculiarly stable (see pp. 83, 89).

SUPERFAMILIES OF THE CARCHARINIDA

	CATULOIDEA	CARCHARINOIDEA
Dorsals	Subequal	Subequal
Anterior dorsal	Posterior to pelvics (rarely anterior)	Anterior to pelvics
Caudal axis	Little raised	Little raised
Caudal pits and keels	Absent	Absent
Nictitating membrane	Rudimentary	More or less complete
Nasoral grooves and cirri	Absent	Absent
Gill openings	Narrow	Medium
Last two	Over base of pectoral	Over base of pectoral
Denticles	Keels incomplete	Keels incomplete or complete
Central keel	Prominent	Not prominent
Teeth	Small, pluricuspid	Large, unicuspid, compressed to plate-like
Roots	2	2
Series	Several	1-several
Spiral valves	Intermediate	Few
Type	Spiral	Spiral or scroll
Heart valves	2-3	2-4
Rostral cartilage	3 united	3 united
Pectoral fin		
Radials	Mostly on metapterygium	Mostly on metapterygium
Segments	3	3
Vertebral centra	Cyclospondylic to intermediate type	Maltese cross type
Claspers		
Siphon	Large	Large
Gland	Absent	Absent
Groove	Closed	Open or closed
Reproduction	Oviparous	Ovoviviparous

VARIATION IN THE CATULOIDEA

In the Catuloidea variation is so great as to make even the establishment of a genus difficult. No two species have the fins in quite the same position, of quite the same length or size, and there are wide variations in the mouth and nasal region. Moreover, no two variations coincide, so that in establishing a genus no two characters can safely be correlated. For that reason there has been a tendency to place all species in one large and variable family, and to link as one genus many quite different types. By separating the group on the basis of vertebral centra I have attempted to make a natural grouping. This will be criticized, no doubt, by observers who wish to identify a specimen quickly, but when taxonomists learn to correlate internal with external structures

in their original descriptions a much simpler task will await the later observers.

The important variations in the Catuloidea include:

- Length and shape of body (typically shorter than tail, occasionally eel-like);
- Position of first dorsal fin (typically over or posterior to pelvis, rarely anterior);
- Size and shape of all fins;
- Armature on caudal (rare and primitive condition);
- Size of eye and spiracle;
- Length of nictitating fold;
- Extent of labial folds;
- Nasal valves and cirri (occasional nasoral grooves);
- Dermal denticles;
- Teeth (typically small, numerous, and five-cusped);
- Heart valves (typically two rows, rarely three; phylogenetic);
- Spiral valves (typically five to ten rows, tendency to reduction and to reduplication, phylogenetic);
- Vertebral centra (cyclospondylic, intermediate, and rarely Maltese cross; phylogenetic);
- Marginal axial cartilages of myxopterygia (typically rolled, tending to open);
- Radials of pectoral fin skeleton (length, and rarely number of segments; phylogenetic).

The transitional species chosen are those which combine primitive catuloid characters with characters approaching or parallel to carcharinoid characters. The transitional characters are of more importance if concerned with the phylogenetic characters of which only the vertebral centra, heart valves, and spiral valves vary to any considerable extent.

The characters of these species are listed below. The retained characters are those typical of the more primitive catuloids; the transitional characters are those which lead in the direction of the stable carcharinoid condition; the advanced characters those which parallel the carcharinoid conditions, and the peculiar characters those which adapt the species to an environment not typical of either the catuloid or carcharinoid sharks.

Catulus torazame

Retained characters:

- Body short
- First dorsal posterior
- Nictitating fold rudimentary
- Denticles incompletely keeled
- Teeth five-cusped
- Vertebral centra cyclospondylic (phylogenetic)
- Marginal axial cartilages rolled into a scroll, loosely
- Oviparous

Transitional characters:

Heart valves forming a third row (phylogenetic)

Calliscyllium venustum

Retained characters:

Denticles incompletely keeled

Teeth five-cusped

Oviparous

Transitional characters:

Nictitating fold intermediate

Marginal axial cartilage open

Vertebral centra intermediate (phylogenetic)

Advanced characters:

First dorsal anterior

Marginal axial cartilages open

Third row of heart valves complete (phylogenetic)

Peculiar characters:

Body lengthened but not deepened anteriorly

Atelomycterus marmoratus

Retained characters:

First dorsal posterior

Nictitating fold shorter than eye

Denticles with incomplete keels

Marginal axial cartilages coiled

Oviparous

Transitional characters:

Denticles not lobed

Teeth three-cusped

Advanced characters:

Vertebral centra of Maltese cross type (phylogenetic)

Peculiar characters:

Body eel-like

Nasoral grooves

Slight reduplication of radials in pectoral fin skeleton (phylogenetic)

Reduplication in spiral valves

Within the carcharinoids, *Triakis scyllium* represents a transitional stage between the catuloid and the complete carcharinoid structure. This species has already been recognized by Leigh-Sharpe (1920) as transitional because of the presence of a retained clasper siphon and parasiphon. My examination shows it to be transitional in many other respects also, and so decidedly leading to the stable condition of the carcharinoids that I have separated it from the specialized Galeorhinidae with which it has been associated in the literature and have made a new family, the Triakidae, to accommodate its transitional nature.

Triakis scyllium

Transitional characters:

- Body spotted and striped
- Spiracles small
- Teeth three-cusped
- Labial folds retained
- Nictitating fold as long as eye
- Denticles with incomplete keels
- Spiral valves with few spirals (phylogenetic)

Advanced characters:

- Body deepened anteriorly
- First dorsal anterior
- Vertebral centra of Maltese cross type (phylogenetic)
- Heart valves in three rows (phylogenetic)
- Marginal axial cartilages open
- Ovoviviparous

Carcharinus

Variable characters:

- Spiracle minute or absent
- Teeth serrated or smooth
- Marginal axial cartilages coiled or open

Stable characters:

- Color uniform, darker above
- Body deepened anteriorly
- First dorsal anterior
- Nictitating membrane complete
- Labial folds absent
- Denticles completely keeled, shell-like
- Vertebral centra of Maltese cross type (phylogenetic)
- Heart valves in three rows (phylogenetic)
- Spiral valves of scroll type (phylogenetic)
- Ovoviviparous

Carcharinus milberti (subspecies *japonicus*)

- Spiracle absent
- Teeth serrate, triangular on both jaws, lower teeth erect
- Marginal axial cartilages open

In basing family divisions on phylogenetic characters several new families have been established, and new definitions compiled. These were published in 1936 (Novitates, No. 879) and are listed below.

Catulidae

Catulidae of Garman, in part; Galeidae of Tanaka, in part; Scyliorhinidae of Regan, in part.

DEFINITION.—Body shorter than tail; anterior dorsal posterior to or just over pelvics; eyes large, lateral, nictitating fold shorter than

eye; spiracles prominent; teeth small, pluricuspid, in several series; nasal valves nearer mouth than snout, occasionally reaching the mouth; denticles with prominent central keels, and lateral keels incomplete; vertebral centra cyclospondylic; heart valves in two rows; spiral valves with from five to ten valves.

CATULUS VALMONT, 1768

C. retifer Garman, 1913, (*Scyllium retiferum* Garman, 1881; *Scylliorhinus retifer* Jordan and Gilbert, 1883; Jordan and Evermann, 1896; Goode and Bean, 1896; *Scylliorhinus retifer* Regan, 1908).

HABITAT.—Atlantic coast.

SPECIMEN.—Young male from the collection of The American Museum of Natural History, New York.

C. torazame Tanaka, March 15, 1908 (*Scylliorhinus rudis* Pietschmann, March 19, 1908; *Halaaelurus rudis* Tanaka, 1911; *H. torazame* Tanaka, 1912).

HABITAT.—Sagami Sea, Japan. Locally known as Torazame, tiger shark.

SPECIMENS.—Adult male and female (female with mature egg cases in oviduct) presented by Dr. Shigeo Tanaka from the collection of the Imperial University at Tokyo, Japan, 1930.

Halaeluridae White, 1936

Catulidae of Garman, in part; Galeidae of Tanaka, in part; Scylliorhinidae of Regan, in part.

DEFINITION.—Body shorter than tail; anterior dorsal over or anterior to pelvics; eyes medium, lateral, nictitating folds shorter than eye; spiracles prominent; teeth small, pluricuspid, in several series; nasal valves closer to mouth than snout, rarely reaching mouth; denticles with prominent central keels, lateral keels incomplete; vertebral centra of intermediate types; heart valves in two to three rows; spiral valves in five to ten rows.

HALAELURUS GILL, 1861

Scyllium Müller and Henle, 1841.

H. burgeri Gill, 1861, Garman, 1913; *Scyllium burgeri* Müller and Henle, 1841; Schlegel, 1850; Bleeker, 1856; Duméril, 1865; Günther, 1870.

HABITAT.—Coastal waters from Japan to East Indies.

SPECIMENS.—Adult male and female presented by Dr. Shigeo Tanaka from the collection of the Imperial University of Tokyo in 1930.

CALLISCYLLIUM TANAKA, 1912 (in Family Galeidae)

Triakis Garman, 1913 (in Family Galeorhinidae).

C. venustum Tanaka, 1912; *Triakis venusta*, Garman, 1913.

HABITAT.—Sagami Sea, Japan. Locally known as H̄yozame, leopard shark.

SPECIMENS.—Adult male and female presented by Dr. Shigeo Tanaka from the collection of the Imperial University in Tokyo, 1930.

Atelomycteridae White, 1936

Catulidae of Garman, in part; Scyliorhinidae of Tate Regan, in part.

DEFINITION.—Body elongate; anterior dorsal posterior to pelvics; eyes large, lateral; spiracles prominent; nictitating fold as long as eye; teeth three-cusped; denticles with prominent central keels, lateral keels incomplete; vertebral centra of complete Maltese cross type; heart valves in two rows; spiral valves numerous; radials of pectoral fin slightly reduplicated.

ATELOMYCTERUS GARMAN, 1913

Scyllium Bennett, 1830; *Scyliorhinus* Regan, 1908.

Scyllium marmoratum Bennett, 1830; *Scyllium maculatum* Gray and Hardwicke, 1832; Müller and Henle, 1841; Richardson, 1846; T. Cantor, 1849; Bleeker, 1852; Duméril, 1865; Günther, 1876; *Scyliorhinus marmoratus* Regan, 1908; *Atelomycterus marmoratus* Garman, 1913.

HABITAT.—Coral reefs of Malay Archipelago.

SPECIMEN.—Adult male presented by Dr. Verwey from the collection of the Laboratorium voor het Onderzoek der Zee, Batavia, Java in 1931.

Triakidae White, 1936

Galeorhinidae of Garman, in part; Carcharidae of Regan, in part.

DEFINITION.—Body longer than tail, deepened anteriorly; first dorsal anterior to pelvics; eyes large, lateral; spiracles small; nictitating fold as long as eye; teeth small, numerous, three-cusped; denticles without prominent central keel, lateral keels incomplete; vertebral centra of complete Maltese cross type; heart valves in three rows; spiral valves few in number.

TRIAKIS MÜLLER AND HENLE, 1838

T. scyllium Müller and Henle, 1841; Duméril 1865; Günther, 1870; Ishikawa and Matsura, 1897; Snyder, 1900; Jordan and Fowler, 1903; Pietschmann, 1908; Garman, 1913.

HABITAT.—Coastal waters of Japan.

SPECIMENS.—Male and female adults and young from open markets in Tokyo, Japan.

Carcharinidae Garman

Carcharidae Regan.

DEFINITION.—Body fusiform, deepened anteriorly; first dorsal anterior to pelvics; eyes small with more or less complete nictitating membrane; spiracles minute or absent; teeth large, few, with a single

triangular cusp, with or without lateral serrations; denticles completely keeled, shell-like, without prominent central keel; vertebrae of complete Maltese cross type; heart valves in three rows; spiral valves of scroll type.

CARCHARINUS BLAINVILLE, 1816

Carcharias Cuvier, 1817.

HABITAT.—Open oceans, universal.

Carcharinus milberti Jordan and Gilbert, 1883; *Carcharias (Prionodon) milberti* Müller and Henle, 1841. Subspecies *C. japonicus* Schlegel, 1850.

SPECIMEN.—Fresh adult male, Misaki market, Japan.

KEY TO THE ORDER GALEA¹

- (1) Nictitating membrane absent; vertebral centra with four main uncalcified areas without calcified rods; radiating calcifications in the calcified areas, frequently branching, or rarely, with concentric laminae.
 Suborder ISURIDA.....See (2).
 Nictitating membrane present or rudimentary; vertebral centra with calcified rays extending into each of the four main uncalcified areas; secondary calcifications in the form of a Maltese cross, or vertebral centra showing all stages of development of type; rostral cartilages three, united; pectoral fin with well-developed propterygium and mesopterygium; caudal axis low.
 Suborder CARCHARINIDA.....See (30).
- (2) First dorsal posterior to the pelvics; rostral cartilages short, not united; pectoral fins with radials about equal on the mesopterygium and metapterygium.
 Caudal axis low; expanded propterygium and mesopterygium.
 Superfamily ORECTOLOBOIDEA.....See (3).
 First dorsal anterior to the pelvics; rostral cartilages three, united; pectoral fins with radials mostly on the metapterygium....See (21).
- (3) Teeth small, pluricuspid, several series in function; denticles with incomplete keels; last two gill-slits close together and over pectoral base; nasoral grooves and nasal cirri present.
 Family ORECTLOBIDAE.....See (4).
 Teeth minute, unicuspid, several series in function; denticles with 3-7 complete keels, shell-like; gill openings wide, last two over base of pectorals.

¹ The author desires to express grateful acknowledgment to Mr. John T. Nichols, Curator of Recent Fishes at The American Museum of Natural History, for revising this key and recasting it in a more convenient form than that of her original.

Family RHINEODONTIDAE.

Caudal keels extended along length of body; pectoral fin at least twice as long as wide; gill-rakers from clumps of modified denticles.

Genus 1.—*Rhineodon* Jordan and Fowler, 1903 (*Rhincodon* A. Smith, 1829; *Rhinodon* Müller and Henle, 1841; *Microstomus* Gill, 1867).

Body dark, spotted and striped with white.

Species a.—*R. typus* White, 1928 (*Rhincodon typus* A. Smith, 1829; *Rhinodon typicus* Müller and Henle, 1841; *Rhineodon typicus* Jordan and Fowler, 1903).

- (4) Body short; tail long.....See (5).
 Body long; tail short to long.....See (16).
 (5) Caudal short.....See (6).
 Caudal long.....See (14).
 (6) First dorsal behind pelvics.....See (7).
 First dorsal above pelvics.

Genus 1.—*Hemiscyllium* A. Smith, 1837.....See (12).

- (7) Transgenial fold present.

Genus 2.—*Chiloscyllium* Müller and Henle, 1837 (*Synchismus* Gill, 1861).....See (8).

Transgenial fold lacking.

Genus 3.—*Parascyllium* Gill, 1861.....See (11).

- (8) One dermal ridge on back.....See (9).
 Three dermal ridges on back.

All fins small. Grayish rusty brown with narrow streaks or series of brown spots.

Species a.—*Chiloscyllium indicum* Günther, 1870 (*Squalus indicus* Gmelin, 1780; *S. tuberculatus* Schneider, 1801; *Chiloscyllium tuberculatum* Müller and Henle, 1841; *C. phyngmatodes* Bleeker, 1852).

- (9) Dorsals larger than pelvics.

Brown with ten or more broad bands of darker, often spotted.
 Front edge of gill openings white.

Species b.—*C. punctatum* Müller and Henle, 1841 (*C. griseum* *ibid.*, 1841).

Dorsals smaller than pelvics.....See (10).

- (10) Grayish brown with transverse bands and white spots. Spotting varies with age.

Species c.—*C. plagiosum* Müller and Henle, 1841 (*Scyl-*

lium plagiosum Bennett, 1839; *Chiloscyllium indicum* Günther, 1870).

Olivaceous with indistinct transverse bands and dark spots. Whitish below.

Species d.—*C. griseum* Müller and Henle, 1841 (*C. plagiosum* *ibid.*, 1841; *C. obscurum* Gray, 1851; *C. hasseltii* Bleeker, 1852; *C. indicum* Günther, 1870).

- (11) Brown with black spots on fins and white on body. A transverse dark band on nape.

Species a.—*Parascyllium variolatum* Gill, 1863.

Yellowish with eight cross bands and black spots on fins and body.

Species b.—*P. collare* Ramsay and Ogilby, 1889.

- (12) Ocellate spot above pectoral. See (13).
Spot above pectoral non-ocellate. Reddish brown with irregular rounded spots of darker.

Species a.—*Hemiscyllium freycineti* Regan, 1908.

- (13) First dorsal above end pelvic base; spots black, round, and scattered.

Species b.—*H. ocellatus* Bonnaterre, 1788.

First dorsal slightly further back, grayish with brown spots grouped.

Species c.—*H. trispeculare* Richardson, 1843.

- (14) Anal long.

Genus 4.—*Brachaelurus* Ogilby, 1907 (*Cirriscyllium* Ogilby, 1908). See (15).

Anal short, caudal very long.

Genus 5.—*Stegostoma* Müller and Henle, 1837.

Anterior nasal valves fused, forming a pad; brown with twelve cross bands of yellow on body and twenty-two on tail.

Species a.—*S. tigrinum* Günther, 1870 (*S. varium* Garman, 1913).

- (15) Base of anal near caudal; brownish to grayish, yellowish below.

Species a.—*Brachaelurus modestus* Garman, 1913 (*Chiloscyllium modestum* Günther, 1871; *Hemiscyllium modestum* Waite, 1901).

Base of anal far from caudal; ashy gray, white below.

Species b.—*B. colcloughi* Ogilby, 1908 (*Heteroscyllium colcloughi* Regan, 1908).

- (16) Dermal lobes absent. See (17).
Dermal lobes few.

- Genus 6.—*Orectolobus* Bonaparte, 1834 (*Crossorhinus* Müller and Henle, 1837)..... See (20).
 Dermal lobes numerous.
 Genus 7.—*Eucrossorhinus* Regan, 1908 (*Crossorhinus* Bleeker, 1867).
 Body brown, profusely marked with small spots of white; a white spot behind each spiracle; caudal region with transverse bands of dark.
 Species a.—*E. dasypogon* Bleeker, 1867.
- (17) Tail and caudal medium.
 Genus 8.—*Ginglymostoma* Müller and Henle, 1837.
 See (18).
 Tail and caudal long; one or two series of teeth function; brownish.
 Genus 9.—*Nebrodes* Garman, 1913 (*Nebrius* Rüppell, 1837)..... See (19).
- (18) Fin angles rounded; anal small; cirrus long; brown with scattered spots.
 Species a.—*Ginglymostoma cirratum* Müller and Henle, 1841.
 Fin angles rounded; anal large; cirrus short; uniform brown.
 Species b.—*G. brevicaudatum* Günther, 1866.
 Fin angles sharp; cirrus very short; uniform rusty brown.
 Species c.—*G. ferrugineum* Jordan and Snyder, 1906 (*Scyllium ferrugineum* Lesson, 1830; *G. concolor* Müller and Henle, 1841; *G. mülleri* Günther, 1870).
- (19) Fin angles sharp; cirrus short; brownish.
 Species a.—*Nebrodes concolor* Rüppell, 1837 (*Ginglymostoma concolor* T. Cantor, 1849; *G. rüppellii* Bleeker, 1852).
 Fin angles blunt; cirrus long; rusty brown, white scales.
 Species b.—*N. macrurus* Garman, 1913.
- (20) No orbital papilla; dermal lobes simple; grayish brown with irregular blotches of brown, lighter spot above each eye.
 Species a.—*Orectolobus ornatus* Regan, 1908 (*Crossorhinus ornatus* De Vis, 1883).
 No orbital papilla; dermal lobes bifid or trifid; rusty marbled brown with light edged spots and transverse blotches, white spot behind each spiracle.
 Species b.—*O. japonicus* Regan, 1906 (*Crossorhinus barbatus* Müller and Henle, 1841).

One orbital papilla; one dermal lobe at side of throat; yellowish gray with light edged blotches of darker, dark spots on fins.

Species c.—*O. tentaculatus* Regan, 1908 (*Crossorhinus tentaculatus* Peters, 1864).

Two orbital papillae; two dermal lobes at side of throat, a few lobes below chin; grayish brown spotted and mottled with darker.

Species d.—*O. maculatus* Garman, 1913 (*Squalus maculatus* Bonnaterre, 1788; *O. barbatus* Jordan and Fowler, 1903).

- (21) Caudal axis low; small propterygium and mesopterygium. Superfamily ODONTASPOIDEA..... See (22).

Caudal axis raised; propterygium and mesopterygium well developed.

Vertebrae with secondary calcifications subdivided and branching; teeth compressed; third upper tooth smaller than second.

Superfamily ISUROIDEA..... See (25).

- (22) Snout not produced; tail short; denticles with three complete keels.

Family CARCHARIIDAE.

Teeth with long, slender cusps; roots deeply bifid.

Genus 1.—*Carcharias* Rafinesque, 1810 (*Odontaspis* Agassiz, 1853; *Triglochis* Müller and Henle, 1837; *Eugomphodus* Gill, 1861)..... See (23).

Snout produced, tail long; denticles with a single minute, upright spine.

Family SCAPANORHYNCHIDAE (Mitsukurinidae).

Teeth with slender, awl-shaped cusps.

Genus 1.—*Scapanorhynchus* Woodward, 1898 (*Mitsukurina* Jordan, 1898; *Rhinognathus* Davis, 1887).

Lateral teeth with one denticle on each side of cusp. First lower tooth smaller than second.

Species a.—*S. owstoni* Woodward, 1899 (*Scapanorhynchus jordani* Hussakof, 1909).

- (23) Teeth without lateral denticles. Species a.—*Carcharias owstoni* Garman, 1913.

Teeth with one denticle on each side of cusp..... See (24).

Teeth with two denticles on each side of cusp.

Species b.—*C. ferox* Risso, 1826 (*Squalus ferox* Risso, 1810; *Galeorhinus ferox* Blainville, 1816).

- (24) First upper tooth smaller than second.

Species c.—*C. taurus* Rafinesque, 1819 (*C. griseus* Ayres, 1843; *Odontaspis americanus* Abbott, 1861; *Eugomphodus griseus* Gill, 1861).

First upper tooth equal to second.

Species d.—*C. tricuspидatus* Day, 1873 (*Odontaspis americanus* Abbott, 1861; *Eugomphodus griseus* Gill, 1861).

- (25) Body massive anteriorly; snout subconical; mouth inferior; gill openings medium; gill-rakers absent; denticles with 3 to 7 complete keels, shell-like..... See (26).
Body extremely massive and clumsy forward; snout subconical; mouth inferior; gill openings excessively wide, anterior to pectorals; gill-rakers present; denticles with a single, minute, upright spine.

Caudal axis deep; caudal keels and pits present; gill-rakers like whalebone.

Family CETORHINIDAE.

Pectoral fin less than twice as long as wide, teeth numerous, minute.

Genus 1.—*Cetorhinus* Blainville, 1816 (*Selache* Cuvier, 1817).

Color uniform.

Species a.—*C. maximus* Gunner, 1765.

- (26) Caudal axis moderately raised; caudal pits present; caudal keels absent.

Family VULPECULIDAE (Alopeciidae).

Caudal fin half or more of total length.

Genus 1.—*Vulpecula* Valmont, 1768 (*Alopias* Rafinesque, 1810; *Alopecias* Müller and Henle, 1837).

Dark brown above; white below.

Species a.—*V. marina* Aldrovandi, 1613 (*Alopecias vulpes* Müller and Henle, 1837).

Caudal axis deep; caudal keels and pits present.

Family ISURIDAE (Lamnidae)..... See (27).

- (27) Teeth large, triangular, serrate, without denticles at base.

Genus 1.—*Carcharodon* Müller and Henle, 1838 (*Lamia* Rondelet, 1554; *Canis* Aldrovandi, 1613).

A black spot in the axil of the pectoral.

Species a.—*C. carcharias* Jordan and Gilbert, 1883 (*Canis carcharias* Aldrovandi, 1613).

Teeth large or small, subulate; with or without denticles at base.

Genus 2.—*Isurus* Rafinesque, 1810 (*Lamna* Cuvier, 1817; *Isuropsis* Gill, 1861)..... See (28).

(28) Teeth with denticles at each side of base.

Species a.—*Isurus nasus* Gray, 1851 (*Squalus nasus* Bonnaterre, 1788; *Squalus cornubicus* Gmelin, 1789; *Lamna cornubica* Cuvier, 1817).

Teeth without lateral denticles..... See (29).

(29) First dorsal above pectorals; second dorsal above anal.

Species b.—*I. punctatus* Garman, 1888 (*Lamna punctata* Storer, 1839; *Lamna cornubica* Jordan and Gilbert, 1883; *Isuropsis glaucus* Gill, 1864).

First dorsal above pectorals; second dorsal in front of anal.

Species c.—*I. tigris* Garman, 1913 (*Lamna punctata* DeKay, 1842; *Carcharias tigris* Atwood, 1869).

First dorsal above end of pectoral base; second dorsal in front of anal.

Species d.—*I. oxyrhyncus* Garman, 1913 (*I. oxyrinus* Rafinesque, 1810; *Lamna oxyrhina* Owen, 1840).

First dorsal above end of pectoral base; second dorsal above front of anal.

Species e.—*I. glaucus* Garman, 1913 (*Oxyrhina glaucus* Müller and Henle, 1841; *Isuropsis glaucus* Gill, 1861; *Lamna spallanzani* Day, 1878).

First dorsal behind pectoral; second dorsal in front of anal; teeth small, numerous.

Species f.—*I. güntheri* Murray, 1884.

(30) Nictitating membrane rudimentary; vertebral centra showing all stages of development of type; oviparous; teeth small, pluricuspid, several series in function; denticles with incomplete keels.

Superfamily CATULOIDEA..... See (31).

Nictitating membrane more or less perfectly developed; vertebral centra of complete Maltese cross type; ovoviviparous.

Superfamily CARCHARINOIDEA..... See (55).

(31) Vertebral centra cyclospodylic; external characters variable but anterior nasal valves not reaching the mouth.

Family CATULIDAE (Scyliorhinidae in part, Galeidae in part). Note: vertebrae of starred(*) genera have not been examined..... See (32).

- Vertebral centra intermediate in type.
 Family HALAELURIDAE White..... See (46).
- Vertebral centra of complete Maltese cross type.
 Family ATELOMYCTERIDAE White.
- Tail elongate; anterior nasal valves reaching mouth.
 Genus 1.—*Atelomycterus* Garman, 1913 (*Scyllium* Bennett, 1830).
- Nasal valves form rounded lobes.
 Species a.—*A. marmoratus* Garman, 1913 (*Scyllium marmoratus* Bennett, 1830; *Scyllium maculatum* Gray and Hardwicke, 1832; *Scyliorhinus maculatus* Regan, 1908).
- (32) Median fins lobate..... See (33).
 Median fins elongate; first dorsal base extends far beyond the anterior margin of pelvic base.
 Snout depressed, tapering, tail short.
 Genus 1.—*Pseudotriakis* Capello, 1867..... See (45).
- (33) First dorsal fin present..... See (34).
 First dorsal fin lost.
 *Genus 2.—*Pentanchus* Smith and Radcliffe, 1912.
 Pelvics, anal, and caudal close together; a deep sea modification.
 Species a.—*P. profundicolus* Smith and Radcliffe, 1912.
- (34) Pectoral fins small..... See (35).
 Pectoral fins large..... See (40).
- (35) Labial folds absent or rudimentary.
 *Genus 3.—*Cephaloscyllium* Gill, 1861 (*Scyliorhinus* Blainville, 1816)..... See (36).
 Labial folds distinct but not prominent..... See (37).
 Labial folds prominent.
 *Genus 4.—*Proscyllium* Hilgendorf, 1904.
 Scattered small black spots; row of white spots along the sides.
 Species a.—*P. habereri* Hilgendorf, 1904 (*Scyllium proscyllium habereri* *ibid.*, 1904).
- (36) Band across head reaches to last gill opening.
 Species a.—*Cephaloscyllium isabellum* Garman, 1913 (*Squalus isabella* Bonnaterre, 1788; *Scyliorhinus laticeps* Duméril, 1853).
 Band across head not reaching to gill region.

* Vertebrae of starred (*) genera not examined.

Species b.—*C. ventriosum* Garman, 1880 (*Catulus cephaloscyllium uter* Jordan and Evermann, 1896; *Scyliorhinus ventriosus* Regan, 1908).

Band across head obsolete.

Species c.—*C. umbratile* Jordan and Fowler, 1903 (*Scyllium laticeps* Nyström, 1887; *Scyliorhinus umbratilis* Regan, 1908).

(37) Nasal cirri rudimentary.

Genus 5.—*Catulus* Valmont, 1768 (*Scyllium* Cuvier, 1817)..... See (38).

Nasal cirri well developed.

Genus 6.—*Poroderma* A. Smith, 1837..... See (39).

(38) Second dorsal mainly behind anal; body marked by a network of brown lines.

Species a.—*Catulus retifer* Garman, 1913 (*Scyllium retiferum* Garman, 1881; *Scyliorhinus retifer* Jordan and Gilbert, 1883).

Second dorsal mainly behind anal; body marked by blotches of brown and white.

Species b.—*C. boa* Garman, 1913 (*Scyliorhinus boa* Goode and Bean, 1896; *Scyliorhinus retifer* Regan, 1908).

Species c.—*C. torazame* Tanaka, March 15, 1908 (*Scyliorhinus rudis* Pietschmann, March 19, 1908; *Halaelurus rudis* Tanaka, 1911; *Halaelurus torazame* Tanaka, 1911).

Species d.—*C. cephalus* Gilbert, 1891 (*Scyliorhinus cephalus* Regan, 1908).

(39) Nasal cirrus not reaching lip.

Species a.—*Poroderma africanum* A. Smith, 1837 (*Scyllium africanus* Cuvier, 1817; *Scyliorhinus africanum* Regan, 1908).

Nasal cirrus reaching beyond lip.

Species b.—*P. pantherinum* A. Smith, 1837 (*Scyllium pantherinum* Müller and Henle, 1837; *Scyliorhinus pantherinus* Regan, 1908).

(40) No special armature on caudal.

Genus 7.—*Apristurus* Garman, 1917..... See (41).

Special armature on caudal; no nasal cirri..... See (42).

- (41) Pelvics, anal, and subcaudal close together; first dorsal smaller than second.

Species a.—*Apristurus indicus* Garman, 1913 (*Scyliorhinus indicus* Brauer, 1906).

Anal far from pelvics, close to caudal; first dorsal base longer than second.

Species b.—*A. platyrhynchus* Garman, 1913 (*Scyliorhinus platyrhynchus* Tanaka, 1909).

Anal far from pelvics; first dorsal equal second.

Species c.—*A. macrorhynchus* Garman, 1913 (*Scyliorhinus macrorhynchus* Tanaka, 1909).

Anal close to pelvics, far from caudal; first dorsal equal second.

Species d.—*A. profundorum* Garman, 1913 (*Scyliorhinus profundorum* Goode and Bean, 1896).

Anal close to pelvics, far from caudal; first dorsal smaller than second.

Species e.—*A. brunneus* Garman, 1913 (*Scyliorhinus brunneus* Regan, 1908).

- (42) Eye small.

Genus 8.—*Parmaturus* Garman, 1906..... See (43).

Eye large.

Genus 9.—*Pristiurus* Bonaparte, 1831 (*Galeus Rafinesque*, 1810)..... See (44).

- (43) Anal fin larger than the pelvics; inner angles of pectorals blunt.

Species a.—*Parmaturus pilosus* Garman, 1906.

Anal fin smaller than the pelvics; inner angles of pectorals sharp.

Species b.—*P. xaniurus* Garman, 1913 (*Catulus xaniurus* Gilbert, 1891; *Scyliorhinus xaniurus* Regan, 1908).

- (44) Colors on body not uniform; marked by faint cross bands; base of anal three times that of first dorsal.

Species a.—*Pristiurus melastomus* Garman, 1913 (*Scylliorhinus melastomus* Blainville, 1830; *Galeus melastomus* Rafinesque, 1810).

Colors on body not uniform; marked by faint cross bands; base of anal more than twice that of first dorsal.

Species b.—*P. eastmani* Jordan and Snyder, 1904.

Colors on body uniform; base of anal more than twice that of second dorsal.

Species c.—*P. sauteri* Jordan and Richardson, 1910.

Colors on body uniform; base of anal two and one-seventh that of second dorsal.

Species d.—*P. spongiceps* Garman, 1913 (*Catulus spongiceps* Gilbert, 1905; *Scyliorhinus spongiceps* Regan 1908).

- (45) Brown with hind edges of pelvics, second dorsal, and caudal darker.

Species a.—*Pseudotriakis microdon* Capello, 1867 (*Pseudotriacis microdon* Günther, 1870).

Uniform brown.

Species b.—*P. acrales* Jordan and Snyder, 1904 (*P. acrages* Garman, 1913; *Pseudotriacis acrales* Regan, 1908).

- (46) First dorsal posterior to pelvics..... See (47).
First dorsal anterior to pelvics.

First dorsal base about twice that of anal.

Genus 1.—*Calliscyllium* Tanaka, 1912 (*Triakis* Garman, 1913).

Form elongate; snout tapering; tail long. Light brown with cross bands of darker thickly sprinkled with dark spots.

Species a.—*C. venustum* Tanaka, 1912 (*Triakis venusta* Garman, 1913).

- (47) Anterior nasal valves not reaching the mouth.

Genus 2.—*Halaelurus* Gill, 1861..... See (48).

Anterior nasal valves reaching the mouth in angular flaps.

Genus 3.—*Haploblepharus* Garman, 1913 (*Scyllium* Cuvier, 1817). Note: starred(*) species uncertain.

Vertebrae not examined..... See (53).

- (48) First dorsal about equal to second..... See (49).

First dorsal larger than second..... See (51).

First dorsal smaller than second..... See (52).

First dorsal base about equal anal base.

Origin of first dorsal above hind end pelvics; dark brown with scattered small black spots.

Species a.—*Halaelurus labiosus* Garman, 1913 (*Squalus maculatus* Schneider, 1801; *Scyllium maculatum* Günther 1870; *Catulus labiosus* Waite, 1905; *Scyliorhinus maculatus* Regan, 1908).

- (49) Origin of first dorsal above middle pelvic base..... See (50).

Origin of first dorsal above hinder third pelvic bases.

Anal base one and one half that of second dorsal; transverse bands broad, marbled, and reticulate.

Species b.—*H. natalensis* Garman, 1913 (*Scyllium natalense* Regan, 1904; *Scyliorhinus natalensis* Regan, 1908).

Origin of first dorsal little in advance of hind ends pelvic bases.

Anal base little longer than either dorsal base; transverse bands narrow, numerous, separated by light.

Species c.—*H. quagga* Garman, 1913 (*Scyllium quagga* Alcock, 1899; *Scyliorhinus quagga* Regan, 1908).

- (50) Anal base little longer than that of second dorsal; transverse bands of darker spotted with black.

Species d.—*H. burgeri* Gill, 1861 (*Scyllium burgeri* Müller and Henle, 1841; *Scyliorhinus burgeri* Regan, 1908).

Anal base one and one half times that of second dorsal; transverse blotches of darker, and faint dark spots.

Species e.—*H. chilensis* Garman, 1913 (*Scyllium chilense* Guichenot, 1848; *Scyliorhinus chilensis* Smitt, 1898).

- (51) Origin of first dorsal little forward of pelvic bases.

Species f.—*H. hispidus* Garman, 1913 (*Scyllium hispidum* Alcock, 1891; *Scyliorhinus hispidus* Regan, 1908).

Origin of first dorsal above hind ends pelvic bases; brown with scattered dark spots.

Species g.—*H. analis* Garman, 1912 (*Scyllium anale* Ogilby, 1885; *Scyliorhinus analis* *ibid.*, 1889; *Catulus analis* Waite, 1899).

- (52) Origin of first dorsal at ends first two-thirds pelvic bases; brown with faint cross bands, and spots of lighter and darker.

Species h.—*H. bivius* Garman, 1913 (*Scyllium bivium* A. Smith, 1837; *Scyliorhinus chilensis* Smitt, 1898; *Scyliorhinus brevicolis* Delfin, 1901; *Scyliorhinus bivius* Regan, 1908).

Origin of first dorsal above middle pelvic bases; uniform blackish.

Species i.—*H. alcockii* Garman, 1913 (*Scyllium canescens* Alcock, 1896).

Origin of first dorsal above middle pelvic bases; grayish, caudal tipped with black, other fins with white.

Species j.—*H. canescens* Garman, 1913 (*Scyllium canescens* Günther, 1878; *Scyliorhinus canescens* Regan, 1908).

- (53) Posterior nasal valves present.....See (54).
Posterior nasal valves absent.

Body light yellowish brown with irregular dark-edged transverse bands of darker, and reticulations of yellow.

Species a.—*Haploblepharus edwardsii* Garman, 1913 (*Squalus catulus* Edwards, 1764; *Scyllium d'edwards* Cuvier, 1817; *Scyllium edwardsii* Voigt, 1832; *Scyliorhinus edwardsii* Regan, 1908).

- (54) Second dorsal partly above anal base.

*Species b.—*H. caniculus*, nom. nov. (*Galeus caniculus* Rafinesque, 1810; *Scyliorhinus caniculus* Blainville, 1816; *Catulus caniculus* Garman, 1913).

Second dorsal wholly above anal base; length of anal base less than its distance from caudal.

Species c.—*H. capensis*, nom. nov. (*Scyllium capense* A. Smith, 1837; *Catulus capensis* Garman, 1913).

Second dorsal half its length behind anal base, scattered spots of varying sizes.

*Species d.—*H. stellaris*, nom. nov. (*Scyllium catulus* Cuvier, 1817; *Galeus stellaris* Belon, 1553; *Scyliorhinus stellaris* Blainville, 1830; *Catulus stellaris* Garman, 1913).

- (55) Nictitating fold present; several series of teeth in function.

Family TRIAKIDAE.....See (56).

Nictitating membrane complete; one series of teeth in function.....See (67).

- (56) Teeth cuspidate.....See (57).

Teeth in a pavement; cusps flattened. Spiracles present; no caudal pits.....See (63).

- (57) Spiracles absent.....See (58).

Spiracles present; no caudal pit.

Genus 1.—*Triakis* Müller and Henle, 1838....See (60).

- (58) Subcaudal lobe produced; caudal pit present.

Genus 2.—*Triaenodon* Müller and Henle, 1841.....
.....See (59).

* Starred species uncertain. Vertebrae not examined.

Subcaudal lobe slight; no caudal pit.

Genus 3.—*Leptocharia* Müller and Henle, 1838.

Median tooth of lower jaw smaller, erect.

Species a.—*L. smithii* Gray, 1851 (*Triaenodon smithii* Müller and Henle, 1841; *Leptocarcharias smithii* Günther, 1870).

- (59) First dorsal far from pectorals; second dorsal little larger than anal.

Species a.—*Triaenodon obesus* Müller and Henle, 1841 (*Carcharias obesus* Rüppell, 1835; *Leptocarcharias obesus* Gray, 1851).

First dorsal close behind base pectorals; second dorsal about equal anal.

Species b.—*T. obtusus* Day, 1878.

- (60) Cusps of teeth sharp; median cusp pointed..... See (61).

Cusps of teeth short; median cusp wide based..... See (62).

- (61) Grayish with cross bands and large spots of brown.

Species a.—*Triakis semifasciatus* Garman, 1913 (*T. californica* Gray, 1851; *T. semifasciatum* Girard, 1854).

Brown with cross bands of darker, and scattered spots of black.

Species b.—*T. scyllium* Müller and Henle, 1841.

- (62) Slaty brown with scattered small black spots.

Species c.—*T. maculata* Kner and Steindachner, 1867 (*Mustelus maculatus* Günther, 1870).

Grayish brown, uniform.

Species d.—*T. henlei* Putnam, 1863 (*Rhinotraxis henlei* Gill, 1862; *Pleurocromylon laevis* Jordan and Gilbert, 1889).

- (63) Teeth blunt or with rudimentary cusps. Anterior nasal valves short; far from mouth.

Genus 4.—*Galeorhinus* Blainville, 1816 (*Mustelus* Valmont, 1768; *Cynias* Gill, 1903)..... See (64).

Teeth with flattened crowns; anterior nasal valves reaching mouth.

Genus 5.—*Scylliogaleus* Boulenger, 1902.

Tail longer than body; caudal two-ninths of total length.

Species a.—*S. quecketii* Boulenger, 1902.

- (64) Teeth without notches, smooth..... See (65).

Teeth concave on edge..... See (66).

Teeth with notches or denticles.

Teeth not diverse; upper labial fold equal.

Species a.—*Galeorhinus laevis* Garman, 1913 (*Galeus laevis* Rondelet, 1554; *Mustelus laevis* Risso, 1826; *Squalus canis* Mitchill, 1815; *Mustelus canis* DeKay, 1842; *Mustelus hinnulus* Jordan and Gilbert, 1882; *Cynias canis* Ribeiro, 1907).

(65) Upper labial fold longer.

Species b.—*G. mustelus* (*Galeus asterias* Rondelet, 1554; *Mustelus laevis* Salviani, 1554; *Galeus laevis* Gesner, 1558; *Galeus stellatus* Valmont, 1768; *Galeus mustelus* Rafinesque, 1810; *Squalus* (*Galeorhinus*) *mustelus* Blainville, 1816).

Upper labial fold shorter.

Species c.—*G. fasciatus* Garman, 1913.

(66) Tooth concavity on hind edge; upper labial fold longer.

Species d.—*G. manazo* Garman, 1913 (*Mustelus vulgaris* Schlegel, 1850; *Mustelus manazo* Bleeker, 1854; *Cynias mustelus* Tanaka, 1911).

Tooth concavity on inner edge; upper labial fold longer.

Species e.—*G. antarcticus* Günther, 1870.

Tooth concavity on outer edge; upper labial folds equal.

Species f.—*G. californicus* Garman, 1913 (*Mustelus californicus* Gill, 1864; *Mustelus hinnulus* Jordan and Gilbert, 1881; *Galeus californicus* Jordan and Evermann, 1896).

Tooth concavity on each side; upper labial fold shorter.

Species g.—*G. lunnulatus* Jordan and Gilbert, 1882 (*Galeus lunnulatus* Jordan and Evermann, 1895).

(67) Skull not expanded laterally.

Family CARCHARINIDAE..... See (68).

Skull expanded laterally across frontal region.

Family SPHYRNIDAE (Cestraciontidae).

Spiracles absent.

Genus 1.—*Sphyrna* Rafinesque, 1810 (*Cestracion* Klein, 1742; *Zygaena* Cuvier, 1817)..... See (97).

(68) Spiracles small; caudal pits rudimentary.

Teeth serrated, notched, oblique.

Genus 1.—*Eugaleus* Gill, 1864 (*Galeorhinus* Blainville, 1816; *Galeus* Cuvier, 1817)..... See (69).

Spiracles minute..... See (70).

- Spiracles absent.....See (76).
- (69) Snout produced; anterior nasal valve with two points.
 Species a.—*Eugaleus galeus* Gill, 1864 (*Galeus canis* Rondelet, 1554; *Galeorhinus galeus* Blainville, 1816; *Carcharias galeus* Risso, 1826; *Galeus chilensis* Perez, 1886; *Galeus japonicus* Jordan and Evermann, 1905).
 Snout short, nasal valve with rounded lobe.
 Species b.—*E. japonicus* Müller and Henle, 1841.
- (70) Teeth serrate.....See (71).
 Teeth not serrate.
 Genus 2.—*Loxodon* Müller and Henle, 1838.
 Form slender; uniform gray above, white below; edges of fins lighter.
 Species a.—*L. macrirhinus* Müller and Henle, 1841.
- (71) Teeth serrate on upper jaw only.
 Genus 3.—*Hemigaleus* Bleeker, 1852.....See (72)
 Teeth serrate on both jaws; upper teeth oblique.
 Genus 4.—*Thalassorhinus* Müller and Henle, 1841.....See (75).
 Teeth serrate on both jaws; oblique on both jaws.
 Genus 5.—*Galeocerdo* Müller and Henle, 1837.
 Form massive; young marked by numerous irregular dark spots fusing into transverse bands; markings fade with age.
 Species a.—*G. arcticus* Müller and Henle, 1838.
- (72) Snout broadly rounded.....See (73).
 Snout tapering.....See (74).
- (73) Caudal longer than space between dorsals.
 Species a.—*Hemigaleus pectoralis* Garman, 1906.
 Caudal equal to space between dorsals.
 Species b.—*H. microstoma* Bleeker, 1852.
- (74) Caudal equal to space between dorsals.
 Species c.—*H. macrostoma* Bleeker, 1852.
 Caudal shorter than space between dorsals.
 Species d.—*H. balfouri* Day, 1878.
- (75) Snout rather pointed; anal exactly below second dorsal.
 Species a.—*Thalassorhinus rondeletii* Gray, 1851 (*Squalus rondeletii* Risso, 1810; *Thalassorhinus vulpecula* Müller and Henle, 1841).
 Snout broad, rounded; anal below end of second dorsal.

Species b.—*T. platyrhynchus* Müller and Henle, 1841
(*Squalus platyrhynchus* Walbaum, 1784).

- (76) Teeth serrate..... See (77).
Teeth not serrate..... See (92).

- (77) Teeth all serrate; cusps oblique; first dorsal near pelvics.

Genus 6.—*Galeus* Valmont, 1768.

Body elongate, slender; dark blue above, white below.

Species a.—*G. glaucus* Rondelet, 1554 (*Squalus glaucus* Linné, 1758; *Carcharias glaucus* Cuvier, 1817; *Prionodon glaucus* Müller and Henle, 1841; *Prionace glauca* Jordan and Evermann, 1896).

Some or all teeth serrate on base and cusps; first dorsal near pectorals.

Genus 7.—*Carcharinus* Blainville, 1816 (*Carcharias* Cuvier, 1817; *Prionodon* Müller and Henle, 1841; *Eulamia* Gill, 1861)..... See (78).

Teeth with serrations on the base on upper jaw only.

Genus 8.—*Hypoprion* Müller and Henle, 1841 (*Hypoprionodon* Gill, 1861)..... See (90).

- (78) Teeth in both jaws oblique, serrate.

Species a.—*Carcharinus sorrah* Müller and Henle, 1841.

Teeth in upper jaw triangular, oblique..... See (79).

- (79) Teeth in lower jaw triangular, narrower than upper. Teeth serrate in both jaws..... See (80).

Teeth in lower jaw awl-like to lanceolate, erect..... See (84).

Teeth nearly erect in both jaws..... See (87).

- (80) Pectoral less than twice as long as wide..... See (81).

Pectoral nearly twice as long as wide..... See (82).

Pectoral more than twice as long as wide..... See (83).

- (81) Second dorsal smaller than anal; origin over anal.

Species b.—*C. falciformis* Jordan and Evermann, 1896
(*Carcharias (Prionodon) falciformis* Müller and Henle, 1841; *Platypodon tiburo* Poey, 1868).

Second dorsal about equal to anal; origin over anal.

Species c.—*C. dussumieri* Garman, 1913 (*Carcharias (Prionodon) dussumieri* Müller and Henle, 1841; *Carcharias (Prionodon) javanicus* Bleeker, 1852).

Second dorsal about equal to anal; origin forward of anal.

Species d.—*C. amboinensis* Garman, 1913 (*Carcharias (Prionodon) amboinensis* Müller and Henle, 1841).

Second dorsal equal to anal; origin forward of anal; lower teeth erect.

Species e.—*C. milberti* Jordan and Gilbert, 1883 (*Carcharias (Prionodon) milberti* Müller and Henle, 1841).

Subspecies *C. japonicus* Schlegel, 1850.

- (82) Second dorsal smaller than anal; origin behind anal.

Species f.—*C. porosus* Garman, 1913 (*Carcharias porosus* Ranzani, 1839; *Carcharias (Prionodon) henlei* Müller and Henle, 1841).

Second dorsal about equal to anal; origin over anal.

Species g.—*C. spallanzani* Garman, 1913 (*Squalus spallanzani* Lesueur, 1822; *Carcharias (Prionodon) bleekeri* Duméril, 1865).

- (83) Second dorsal about equal to anal; origin over anal.

Species h.—*C. menisorrh* Garman, 1913 (*Carcharias (Prionodon) menisorrh* Müller and Henle, 1841).

Second dorsal about equal anal; origin forward of anal.

Species i.—*C. melanopterus* Garman, 1913 (*Carcharias melanopterus* Quoy and Gaimard, 1824; *Carcharias (Prionodon) melanopterus* Müller and Henle, 1841).

Second dorsal smaller than anal; origin forward of anal.

Species j.—*C. platyodon* Jordan and Evermann, 1896 (*Squalus platyodon* Poey, 1861).

- (84) Teeth serrate in both jaws.....See (85).

Teeth serrate on upper jaw; not serrate on lower jaw.....See (86).

- (85) Second dorsal equal anal; origin over anal; lower teeth nearly erect.

Species k.—*C. brachyurus* Garman, 1913 (*Carcharias (Prionodon) brachyurus* Günther, 1870).

Second dorsal smaller than anal; origin over anal; lower teeth erect, awl-like.

Species l.—*C. amblyrhynchus* Garman, 1913 (*Carcharias (Prionodon) amblyrhynchus* Müller and Henle, 1841).

Second dorsal smaller than anal; origin behind anal; teeth of lower jaw erect, awl-like.

Species m.—*C. velox* Jordan and Evermann, 1898 (*Carcharias velox* Gilbert and Starks, 1903).

Second dorsal smaller than anal; origin behind anal; cusps of lower teeth lanceolate, nearly erect.

Species n.—*C. acronotus* Jordan and Evermann, 1896
(*Squalus acronotus* Poey, 1860).

- (86) Second dorsal larger than anal, origin behind anal.

Species o.—*C. borneensis* Garman, 1913 (*Carcharias*
(*Prionodon*) *borneensis* Bleeker, 1858).

Second dorsal larger than anal, origin forward of anal.

Species p.—*C. glyphys* Garman, 1913 (*Carcharias*
(*Prionodon*) *glyphys* Müller and Henle, 1841).

- (87) Teeth serrate on both jaws.....See (88).

Teeth serrate on upper jaw only.....See (89).

Teeth not serrate.

Teeth triangular, smooth; second dorsal larger than anal;
origin behind anal.

Species q.—*C. maou* Garman, 1913 (*Squalus* (*Car-*
charias) *maou* Lesson, 1830; *Carcharias* (*Prionodon*)
maou Müller and Henle, 1841).

- (88) Lower teeth serrate on bases only; second dorsal smaller than
anal.

Species r.—*C. limbatus* Garman, 1913 (*Carcharias*
(*Prionodon*) *limbatus* Müller and Henle, 1841).

Teeth narrow, erect; second dorsal behind anal.

Species s.—*C. remotus* Garman, 1913 (*Carcharias*
(*Prionodon*) *remotus* Duméril, 1865).

Teeth nearly erect, subtriangular; second dorsal larger than
anal; origin forward of anal.

Species t.—*C. commersonii* Blainville, 1816 (*Squalus*
carcharias Risso, 1810; *Carcharias* (*Prionodon*) *leucas*
Müller and Henle, 1841; *Eulamia lamia* Jordan and
Gilbert, 1882).

Upper teeth nearly erect; lower teeth narrower, erect; second
dorsal larger than anal; origin forward of anal.

Species u.—*C. albimarginatus* Garman, 1913 (*Car-*
charias albimarginatus Rüppell, 1835).

Lower teeth lanceolate, erect, with a distal swelling on base; second
dorsal larger than anal; origin forward of anal.

Species v.—*C. ellioti* Garman, 1913 (*Carcharias ellioti*
Day, 1878).

- (89) Second dorsal equal anal; origin over anal.

Species w.—*C. pleurotaenia* Garman, 1913 (*Carcharias*
(*Prionodon*) *pleurotaenia* Bleeker, 1852).

Teeth narrow, erect; second dorsal larger than anal; origin above anal.

Species x.—*C. temminckii* Garman, 1913 (*Carcharias* (*Prionodon*) *temminckii* Müller and Henle, 1841).

Teeth narrow, erect; upper teeth serrate near apices; second dorsal larger than anal; origin forward of anal.

Species y.—*C. oxyrhynchus* Garman, 1913 (*Carcharias* (*Prionodon*) *oxyrhynchus* Müller and Henle, 1841; *Isogomphodon oxyrhynchus* Gill, 1861).

Upper teeth triangular, serrate; lower teeth lanceolate, smooth; second dorsal larger than anal; origin above anal.

Species z.—*C. munsing* Garman, 1913 (*Carcharias* (*Prionodon*) *munsing* Bleeker, 1849).

- (90) Second dorsal larger than anal; origin a little behind anal; snout short, broad.

Species a.—*Hypoprion brevirostris* Poey, 1868 (*Carcharias* (*Hypoprion*) *brevirostris* Günther, 1870).

Second dorsal smaller than anal; origin above hinder third anal base; snout elongate, pointed.

Species b.—*H. macloti* Garman, 1913 (*Carcharias* (*Hypoprion*) *macloti* Müller and Henle, 1841).

Second dorsal smaller than anal; origin a little behind anal; snout moderate.

Species c.—*H. hemiodon* Garman, 1913 (*Carcharias* (*Hypoprion*) *hemiodon* Müller and Henle, 1841).

Second dorsal equal anal; origin above anal. See (91).

- (91) Snout broad, rounded at end.

Species d.—*H. playfairii* Garman, 1913 (*Carcharias* (*Hypoprion*) *playfairii* Günther, 1870).

Snout elongate, sharp.

Species e.—*H. signatus* Garman, 1913 (*Hypoprion* *signatus* Poey, 1868).

- (92) Bases of teeth swollen; cusps slender, pointed; one median tooth on upper jaw; two on lower.

Genus 9.—*Scoliodon* Müller and Henle, 1841. . . See (93).

Teeth narrow on broad bases, nearly erect.

Genus 10.—*Aprionodon* Gill, 1861 (*Aprion* Müller and Henle, 1841). See (96).

- (93) Base of anal more than twice that of second dorsal.

Labial folds short, on lower jaw only.

Species a.—*Scoliodon sorrakowah* Garman, 1913 (*Sorrakowah* Russell, 1803; *Carcharias sorrakowah* Cuvier, 1829; *Carcharias (Scoliodon) laticaudus* Müller and Henle, 1841).

Base of anal not more than twice that of second dorsal. . . . See (94).

- (94) Labial folds short, on lower jaw only.

Species b.—*S. palasorrah* Garman, 1913 (*Pala sorra* Russell, 1803; *Carcharias acutus* Rüppell, 1835; *Carcharias (Scoliodon) acutus* Müller and Henle, 1841).

Labial folds in the angles of both jaws.

Species c.—*S. dumerilii* Garman, 1913 (*Carcharias (Scoliodon) dumerilii* Bleeker, 1856).

Labial folds in the angles, and slightly on the lower jaw. . . . See (95).

Labial folds on both jaws; fully one-third the length of jaws.

Species d.—*S. longurio* Garman, 1913 (*Carcharias (Scoliodon) longurio* Jordan and Gilbert, 1882).

Labial folds on both jaws; less than one-third length of jaws.

Species e.—*S. terrae-novae* Garman, 1913 (*Aprionodon punctatus* Gill, 1861; *Scoliodon terrae-novae* Gill, 1861).

Labial folds on both jaws, less than one-third length of jaws; snout rounded.

Species f.—*S. intermedius* Garman, 1913.

Labial folds subequal, elongate; teeth with fine serrations.

Species g.—*S. vagatus* Garman, 1913.

- (95) Second dorsal smaller than anal; origin behind anal.

Species h.—*S. wahlbeehmi* Garman, 1913 (*Carcharias (Scoliodon) wahlbeehmi* Bleeker, 1865).

Second dorsal equal to anal; origin above anal.

Species i.—*S. lalandii* Garman, 1913 (*Carcharias (Scoliodon) lalandii* Müller and Henle, 1841).

- (96) Second dorsal smaller than anal; origin behind anal.

Species a.—*Aprionodon brevipinna* Gill, 1861 (*Carcharias (Aprion) brevipinna* Müller and Henle, 1841).

Second dorsal larger than anal; origin a little forward of anal.

Species b.—*A. acutidens* Garman, 1913 (*Carcharias (Aprionodon) acutidens* Duméril, 1865).

Second dorsal nearly equal anal; origin at end of anal base.

Species c.—*A. isodon* Poey, 1876 (*Carcharias (Aprion) isodon* Müller and Henle, 1841)..

- (97) Lateral expansions of head heart-shaped.

Eyes and nostrils not widely separated.

Species a.—*Sphyrna tiburo* Rafinesque, 1810 (*Cestracion tiburo* Klein, 1776; *Zygaena tiburo* Valenciennes, 1882).

Lateral expansions of head hammer-shaped.....See (98).

(98) Eyes and nostrils close together.....See (99).

Eyes and nostrils widely separated; lateral expansion long, slender.

Species b.—*S. blochii* Müller and Henle, 1841 (*Zygaena blochii* Cuvier, 1817).

(99) Hind angles of hammer at right angles to long axis body..See (100).

Hind angles of hammer oblique.....See (101).

(100) Outer edges of hammer straight.

Species c.—*S. mokarran* Müller and Henle, 1841 (*Zygaena mokarran* Rüppell, 1835).

Outer edges of hammer rounded.

Species d.—*S. tudes* Müller and Henle, 1841 (*Zygaena tudes* Valenciennes, 1787).

(101) Concavity above nostril deep; cusps of teeth erect.

Species e.—*S. zygaena* Rafinesque, 1810 (*Squalus zygaena* Linné, 1758; *Cestracion zygaena* Klein, 1776; *Zygaena malleus* Valenciennes, 1822).

Concavity above nostril moderate; cusps of teeth oblique.

Species f.—*S. oceanica* Garman, 1913.

SUMMARY

The results of this investigation tend to show that the characters of phylogenetic value are those not easily affected by the immediate environment or by the habits of a species. These characters have determined the main lines of development and are of value in determining groups of the grade of class, order, or suborder. They are deep-seated characters and include the vertebral structure, the basals of the paired fins and of the myxopterygia, the jaw attachment, and the rostral cartilages.

The physiological characters are those which appear to have direct application to the environment or habits of the species. They cause wide variation within the groups determined by the phylogenetic characters and may be used in determining family, genus, or species relationships. These characters include the radials of the pectoral fin, the axial cartilages of the myxopterygia, the position of the dorsal fins, the teeth and denticles, the mouth and nostrils, the general body form, and all modifications of the skin such as folds, keels, pits, etc.

The phylogenetic characters determine the lines of adaptive radiation and the physiological characters determine the adaptive radiation within the subgroups. The phylogenetic characters were laid down during the geological age of origin and when present today have been retained. The physiological characters may continue to vary at the present time.

Certain physiological characters have become linked to the phylogenetic so consistently that linkage groups are suggested. Slight variations from the linkage may mean crossing over.

The modern groups which were separated from the main stock more recently have proved to be more stable than those originating at an earlier time. Variation is, therefore, found in the more primitive groups and these may be supposed to be still in a varying or mutating condition. Certain species have been found to vary in characters otherwise typical of a group and these may represent mutating species.

Feeding habits seem to have determined the direction of tooth development; temperature and water pressure, denticle development; depth and water pressure, the general body form, position of the dorsal fins, and numerous dermal specializations. Bottom and shallow water habits have determined the movement of the nostrils toward the mouth, the width of the mouth gape, the size of the spiracles, and the spreading of the pectoral fins. Restricted environments have tended to lengthen the body and free environments to deepen the body and increase bulk, leading in either direction to over-specialization in some cases.

The intermediate grovelling type has been primitive in any group because of the fundamental need for securing food, which would have been primarily more abundant close to the shores.

The Hexanchea and Holocephali branched from the ancestral stock during the Paleozoic; the Hybodonts, in the Triassic; the Squalea, Platosomeae, Orectoloboidea and Catuloidea, in the Jurassic; the Odontaspoidea and Isuroidea, in the Cretaceous; the Carcharinoidea, in the Eocene. The groups established in the Jurassic have been less stable than those of later origin and appear to be still in mutating condition.

An hypothetical ancestral shark may be constructed on the basis of characters found to be primitive:

A grovelling shore type depressed anteriorly, tapering toward the tail.

Mouth wide, nearly terminal and ventral.

Nostrils very near the mouth with a nasoral groove.

Eyes large, lateral, with large spiracle behind them and without a nictitating fold or membrane.

Gill slits five in number, lateral and wide, all open to the exterior, all anterior to the pectoral fins and at equal distances apart.

Two spiny dorsal fins of equal size with ridges and ornamentations on the spines; the first over or just back of the pelvic fins.

A large anal fin.

A caudal fin with axis not raised and without notches, keels, or pits.

Denticles as flat plates with bases fitted together.

Teeth small, multicuspid, with a broad base deeply embedded in the jaw.

Coloration uniform, lighter below.

The rostral support absent.

The jaw suspension amphihyostylic and the pterygoquadrate articulation extensive.

The basals of the pectoral fins of equal size and expansion. The radials unsegmented rods about equally distributed on the basals.

The notochord uncontracted, the vertebrae with no secondary calcifications.

A condition of diplospondyly in the tail.

The spiral valves of the spiral type with from five to ten valves.

The heart valves in three series arranged in two rows.

The myxopterygia absent indicating an oviparous habit with external fertilization.

The fish probably lived in the early Devonian and followed the armored *Stegoselachians*.

The results of the present investigation show the need of reorganization in the order Galea. Previous classifications have either included the *Orectolobidae* with the *Catulidae* or given them parallel standing. There are two types of vertebral structure in the Galea: the *Orectoloboidea* have one type, and the *Catuloidea* have the transitional stages approaching the other. I believe the two types of vertebrae to have had a separate origin in the Jurassic, and the two groups to represent, therefore, fundamentally distinct groups. These I have called suborders, within which the *Orectoloboidea* form the stem group of one, and the *Catuloidea* the stem group of the other. Therefore superfamilies have been established and the members of the order Galea have been distributed according to the foregoing key (p. 109).

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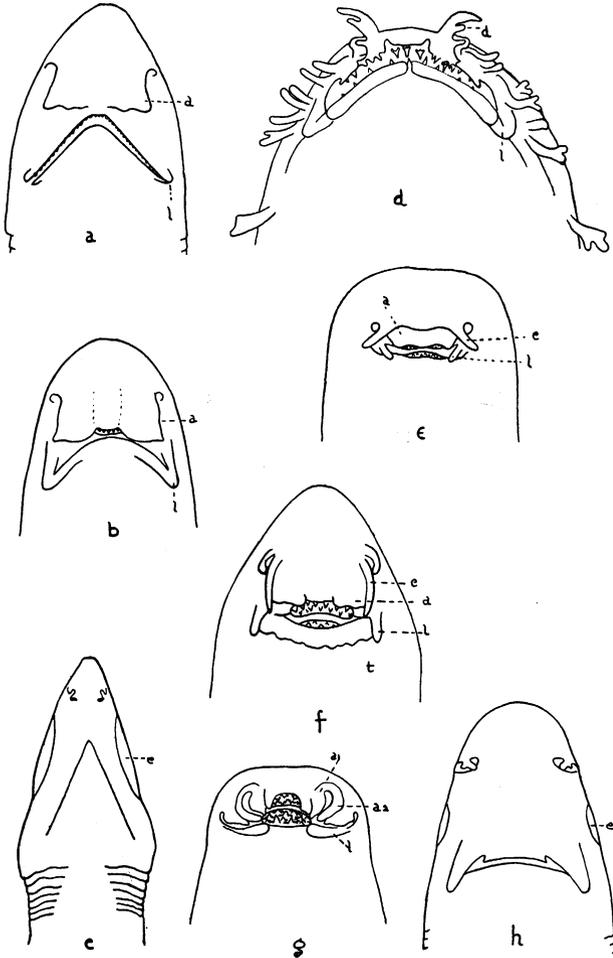
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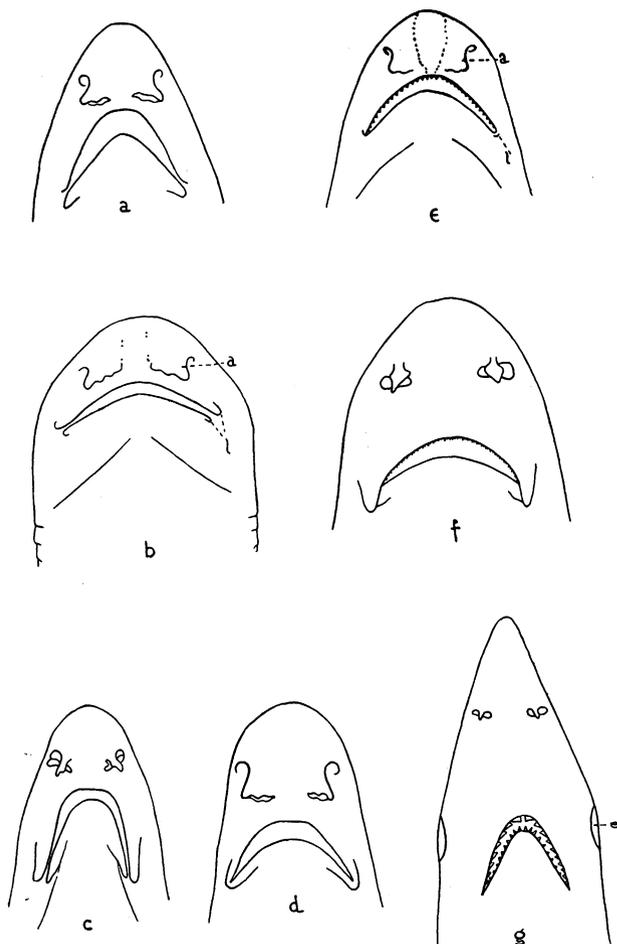
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Heads, showing the shape of the snout and the relation of the nostrils to the mouth.

Ventral view.

a, *Calliscyllium venustum*; b, *Atelomycterus marmoratus* (note anterior nasal flaps reaching the mouth); c, *Hepranchias perlo*; d, *Orectolobus japonicus* (note numerous dermal lobes), after Müller and Henle; e, *Stegostoma tigrinum*; f, *Chiloscyllium griseum*; g, *Heterodontus japonicus* (note that the anterior nasal flaps divide the lips into four lobes on each half); h, *Squalus mitsukurii*.

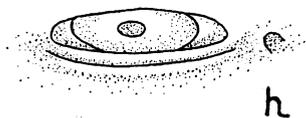
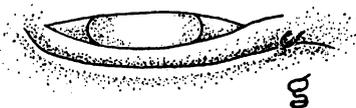
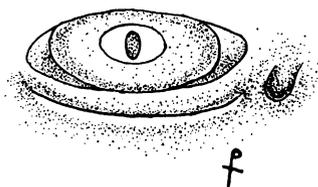
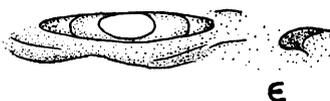
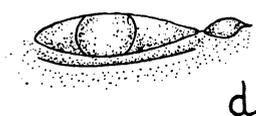
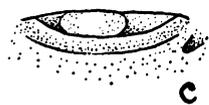
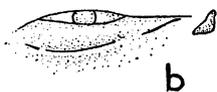


Heads, showing the shape of the snout and the relation of the nostrils to the mouth.

Ventral view.

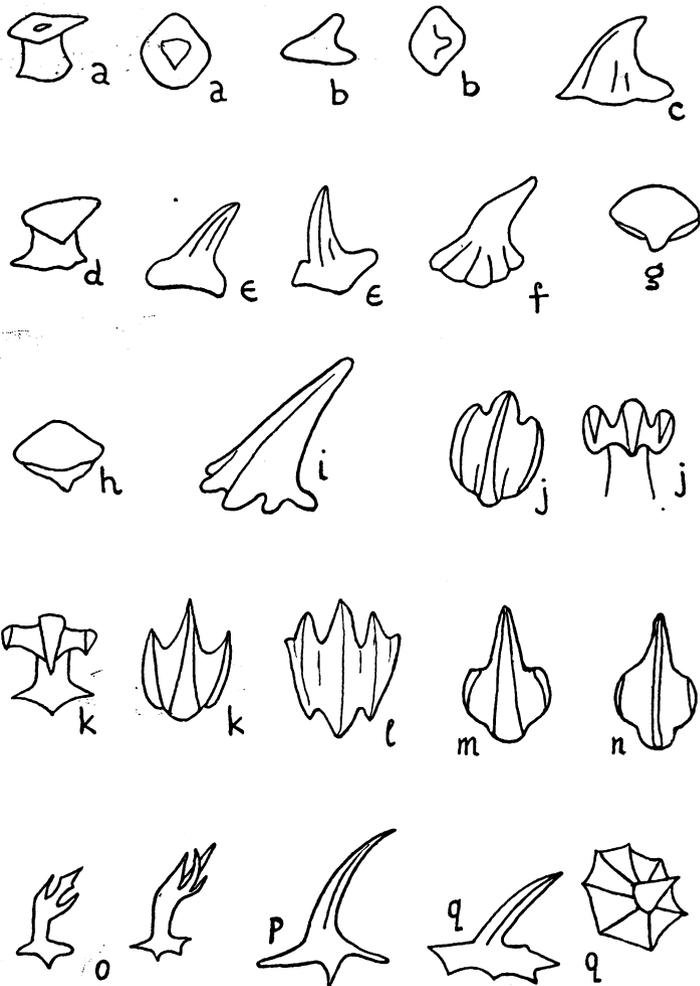
a, anterior nasal flap; *l*, labial folds.

a, *Catulus retifer*; *b*, *Catulus torazame*; *c*, *Halaelurus bivius*; *d*, *Parmaturus xaniurus*; *e*, *Halaelurus burgeri*; *f*, *Triakis scyllium*; *g*, *Galeus glauca*.



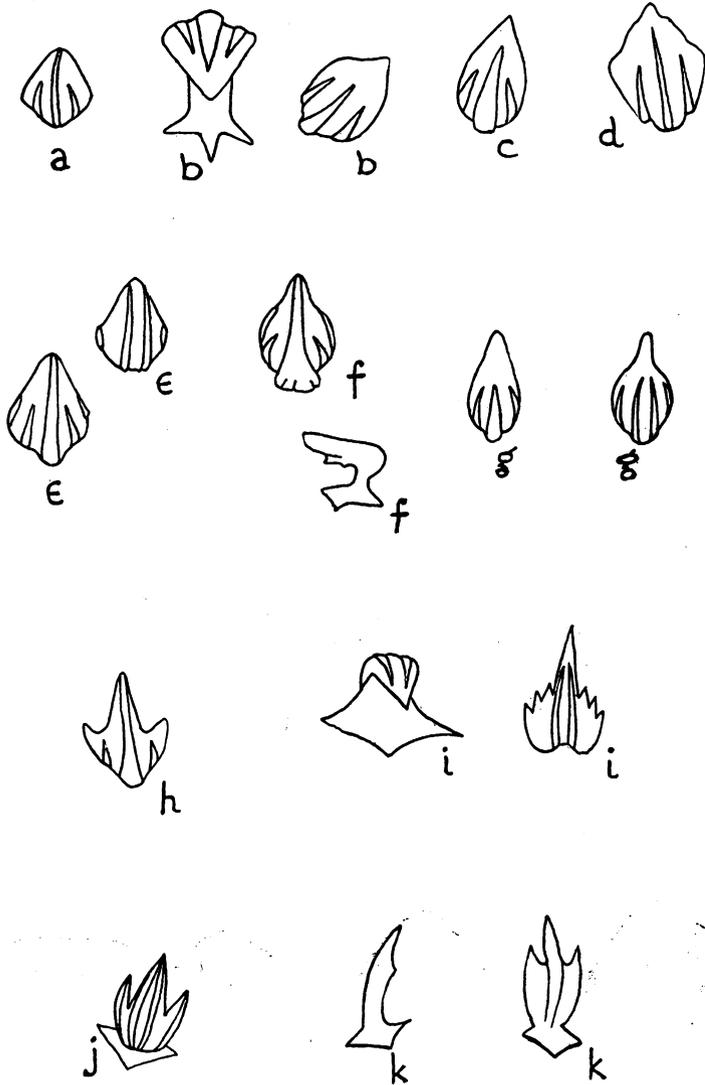
The nictitating fold and nictitating membrane in the Carcharinida. Spiracle at right of eye.

a, *Halaelurus burgeri*; b, *Catulus torazame*; c, *Catulus retifer*; d, *Atelomycterus marmoratus*; e, *Halaelurus bivius*; f, *Calliscyllium venustum*; g, *Parmaturus xaniurus*; h, *Triakis scyllium*; i, *Carcharinus sorrah*.



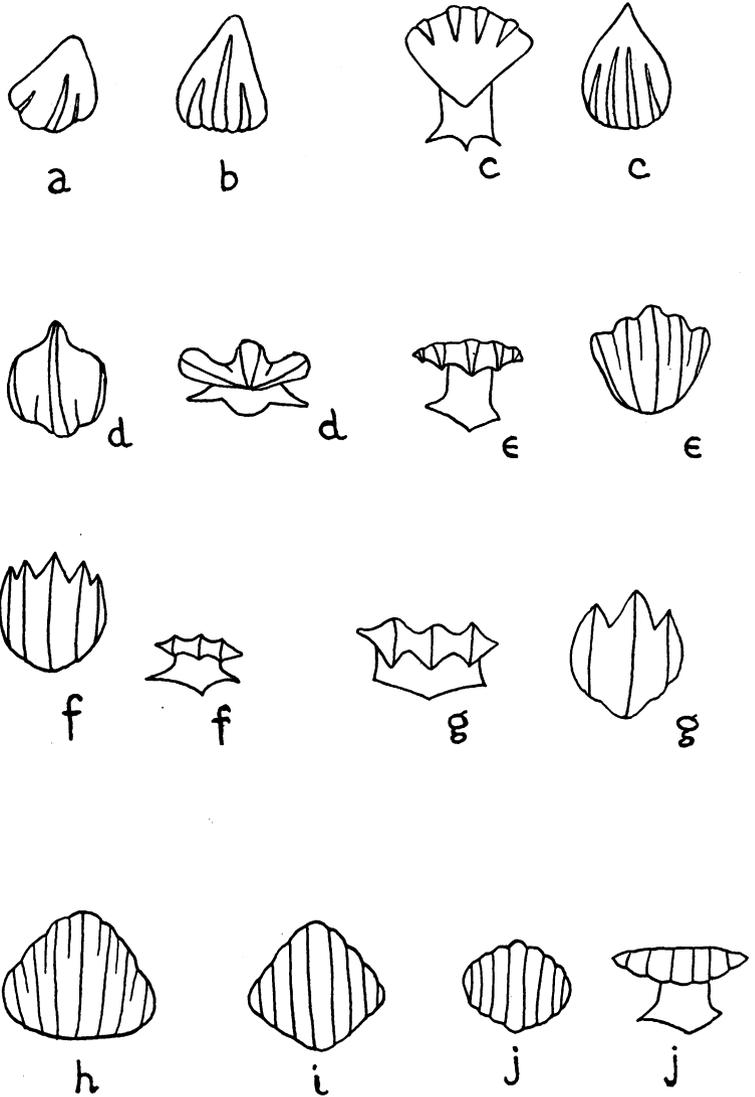
Denticles from the latero-dorsal surface of the thorax.

a, *Centroscyrnus owstoni*, after Garman; b, *Rhina californica*, after Garman; c, *Somniosus microcephalus*, after Garman; d, *Pristis clavata*, after Garman; e, *Scapanorhynchus owstoni*; f, *Cetorhinus maximus*, after Radcliffe; g, *Narcine*, after Radcliffe; h, *Rhinobatus*, after Radcliffe; i, *Chlamydoselachus anguineus*, after Röse; j, *Carcharias taurus*; k, *Squalus acanthias*, after Radcliffe; l, *Rhineodon typus*; m, *Heptranchias perlo*; n, *Heterodontus japonicus*; o, *Acanthidium rostratum*, after Garman; p, *Etmopterus lucifer*; q, *Centroscyllium fabricii*, after Garman.



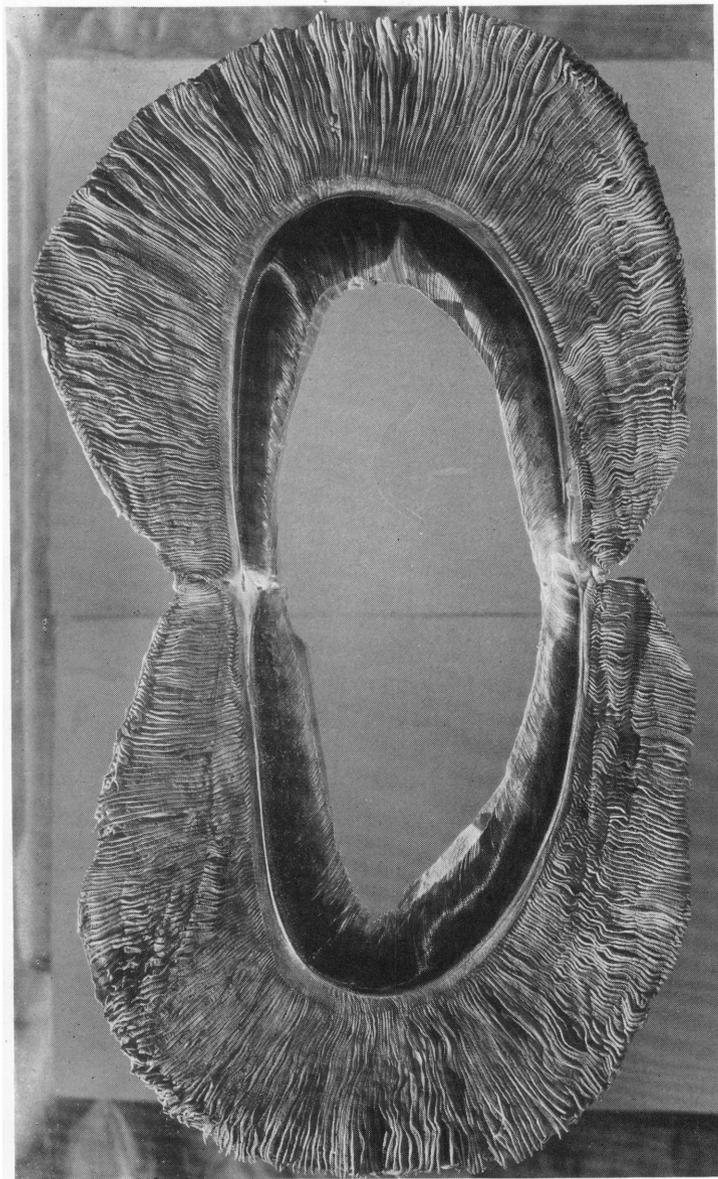
Denticles from the latero-dorsal surface of the thorax.

a, *Nebrodes macrurus*, after Garman; b, *Ginglymostoma*, after Radcliffe; c, *Chiloscyllium griseum*; d, *Siegostoma tigrinum*; e, *Atelomycterus marmoratus*; f, *Catulus torazame*; g, *Halaelurus bivius*; h, *Halaelurus burgeri*; i, *Catulus retifer*, after Radcliffe; j, *Parmaturus xaniurus*, after Garman; k, *Parmaturus pilosus*, after Garman.



Denticles from the latero-dorsal surface of the thorax.

a, *Triakis scyllium*; b, *Galeorhinus manazo*; c, *Galeorhinus laevis*; d, *Galeocerdo*, after Radcliffe; e, *Vulpecula marina*, after Radcliffe; f, *Aprionodon*, after Radcliffe; g, *Carcharinus limbatus*, after Radcliffe; h, *Galeus glauca*; i, *Sphyrna zygaena*; j, *Carcharinus japonicus*.

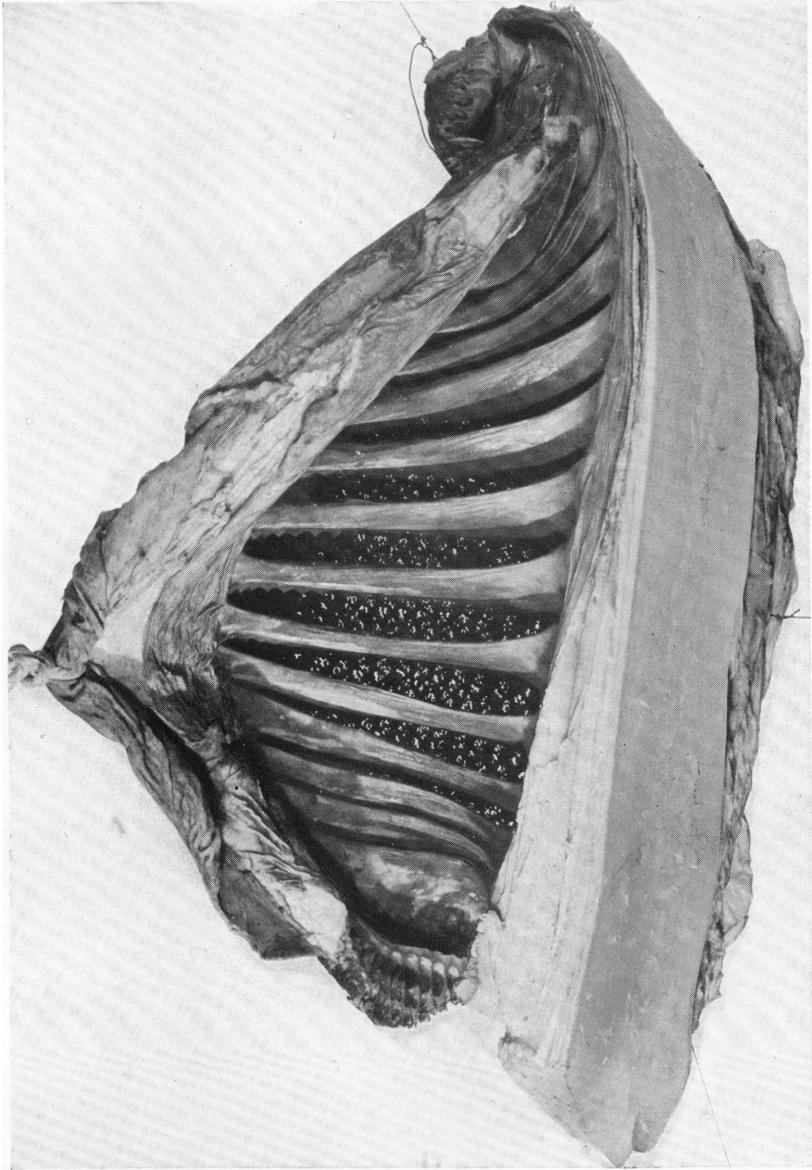


Gills of basking shark, *Cetorhinus maximus*, showing gill rakers in position.
Photograph by A. M. N. H.



Detail of gill rakers, *Cetorhinus maximus*.

Photograph by A. M. N. H.

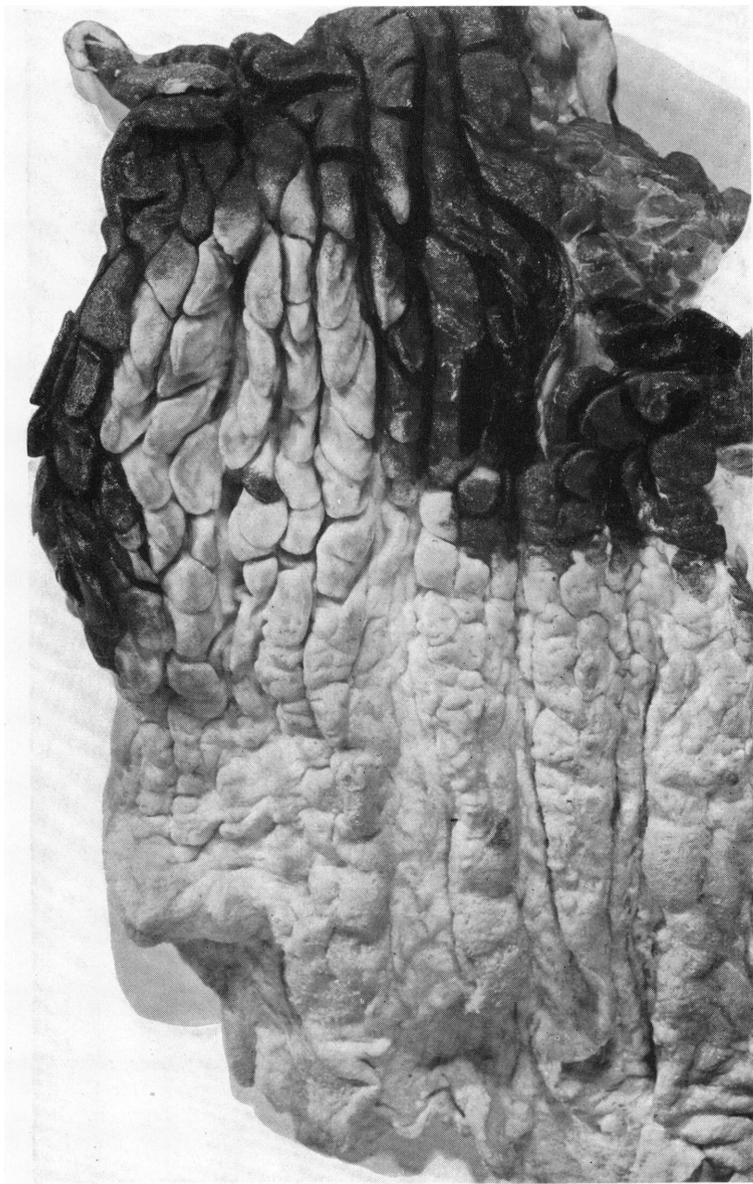


Gill rakers of whale shark, *Rhineodon typus*, inner view.
Photograph by A. M. N. H.



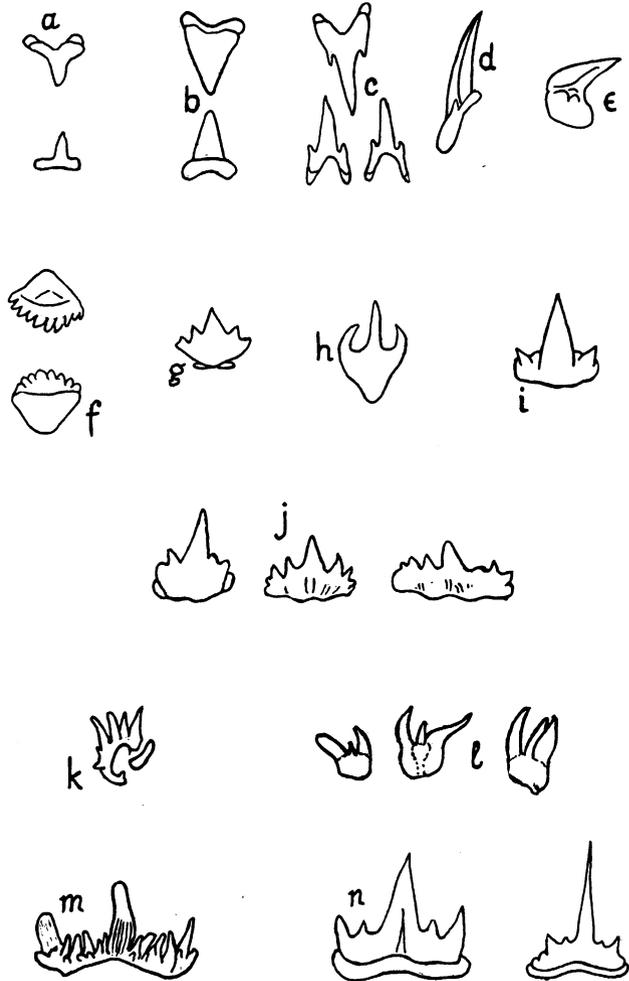
Gill rakers of whale shark, *Rhineodon typus*, outer view.

Photograph by A. M. N. H.



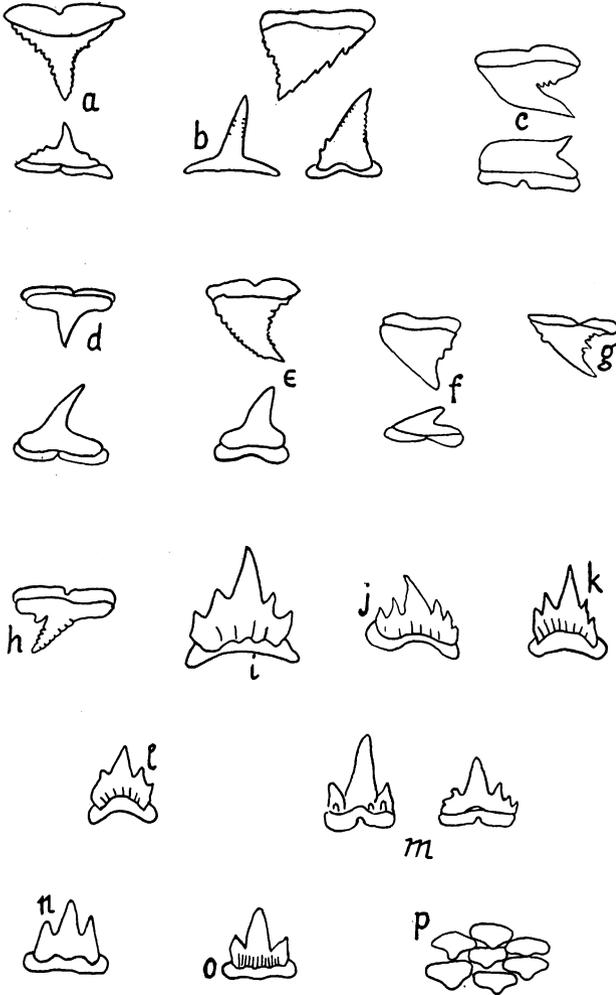
Lining of esophagus of whale shark, *Rhineodon typus*, to show papillae covered with denticles continuous with ridges on stomach wall.

Photograph by A. M. N. H.



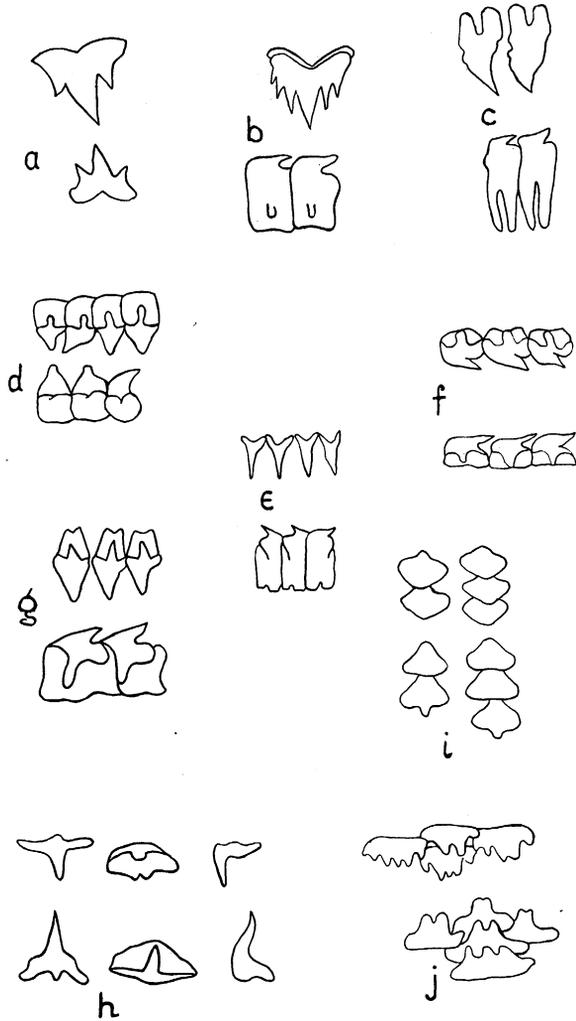
a-j, Teeth of the Isurida; k-o, fossil teeth. Where only one tooth of a species is shown, the teeth on both jaws are alike.

a, *Isurus punctatus*, after Garman; b, *Carcharodon carcharias*, after Garman; c and d, *Carcharias taurus*, after Garman; e, *Rhineodon typus*, after E. G. White; f, *Nebrodes concolor*, after Garman; g, *Ginglymostoma cirratum*; h, *Stegostoma tigrinum*; i, *Chiloscyllium griseum*; j, *Ginglymostoma africanum*, anterior lateral and more lateral teeth (Paleocene), after Leriche; k, *Protodus scoticus* Newton, from the Devonian, after Smith Woodward; l, *Pleuracanthus*, from the Permian, after Romer; m, *Cladodus striatus* Agassiz, from the Carboniferous, after Dean; n, *Cladodus*, from the Devonian, after Goodrich.



Teeth of the Carcharinida.

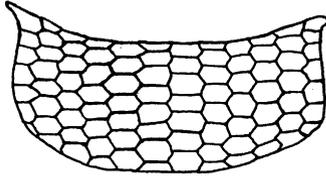
a, *Carcharinus limbatus*; b, *Galeus glauca*; c, *Scoliodon terrae novae*, after Garman; d, *Scoliodon wahlbeehmi*; e, *Carcharinus japonicus*; f, *Sphyrna zygaena*; g, Upper tooth of *Hemigaleus pectoralis*, after Garman; h, Upper tooth of *Carcharinus mülleri*; i, *Calliscyllium venustum*; j, *Parmaturus xaniurus*; k, *Catulus torazame*; l, *Halaelurus burgeri*; m, Anterior and lateral teeth of *Catulus capensis* from the Paleocene, after Leriche; n, *Atelomycterus marmoratus*; o, *Triakis scyllium*, after Garman; p, *Galeorhinus laevis*.



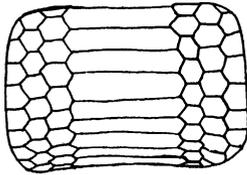
Variations in the teeth of, a-h, the Squalea, i-j, the Platosomia.

a, *Centroscyllium fabricii*; b, *Etmopterus hildani*; c, *Somniosus brevipinna*.
 d, *Acanthidium rostratum*; e, *Centroscymnus owstoni*; f, *Squalus acanthias*; g,
Centrophorus atomarginatus; h, *Rhina californica*, front, top, and side views;
 i, *Pristis clavata*, flattened pavement teeth showing parallel specialization with the
 Galeorhinidae; j, *Mobula hypostoma*.

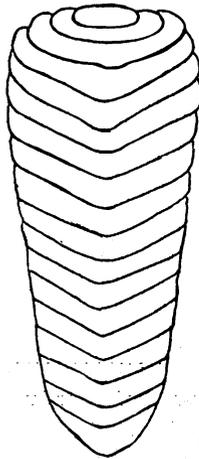
All after Garman.



a



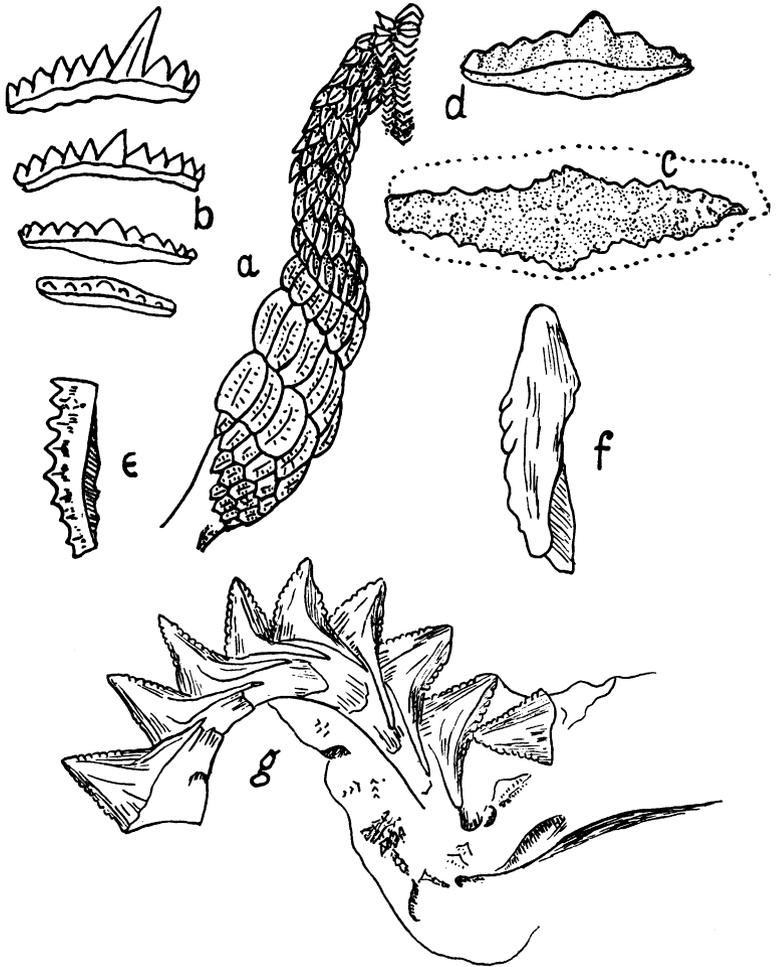
b



c

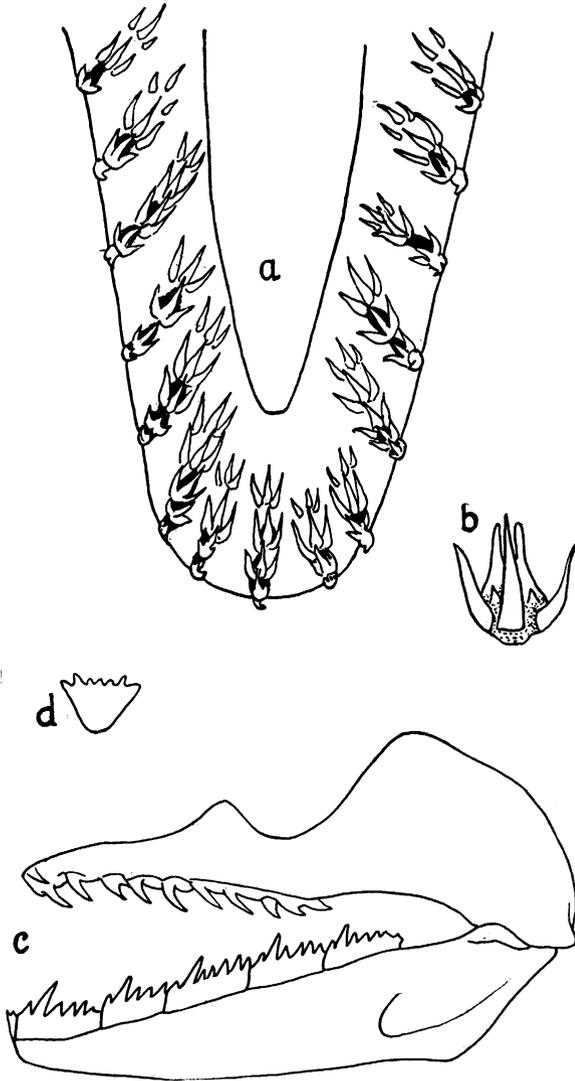
Tessellate teeth of the Dasybatoidea, showing the gradual broadening of the central plates.

a, *Rhinoptera polyodon*, from Goodrich, after Günther; b, *Myliobatis aquila*, from Goodrich, after Owen; c, *Aetobatus narinarius*, after Garman.



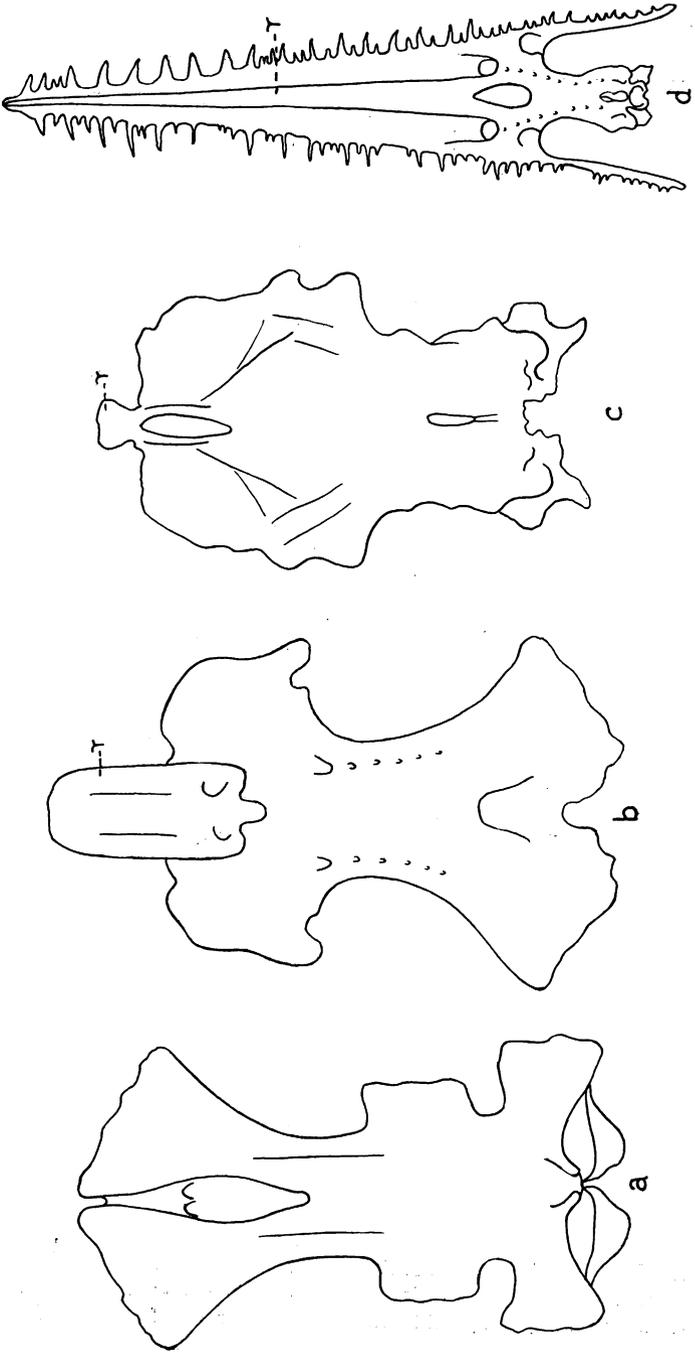
Heterodont teeth.

a, *Heterodontus philippi*, one-half of lower jaw, after Zittel; b, *Synechodus* from the Cretaceous, four teeth from the upper jaw showing gradations from the central cuspidate teeth to the lateral crushing teeth, after Smith Woodward; c, *Orodus ramosus* Agassiz from the Carboniferous, crown view of lateral tooth, after Davis; d, *Orodus*, side view, after Romer; e, *Campodus variabilis*, half of a lateral tooth; f, symphyseal tooth, after Smith Woodward; g, *Edestus newtoni*, symphyseal teeth, after Smith Woodward.



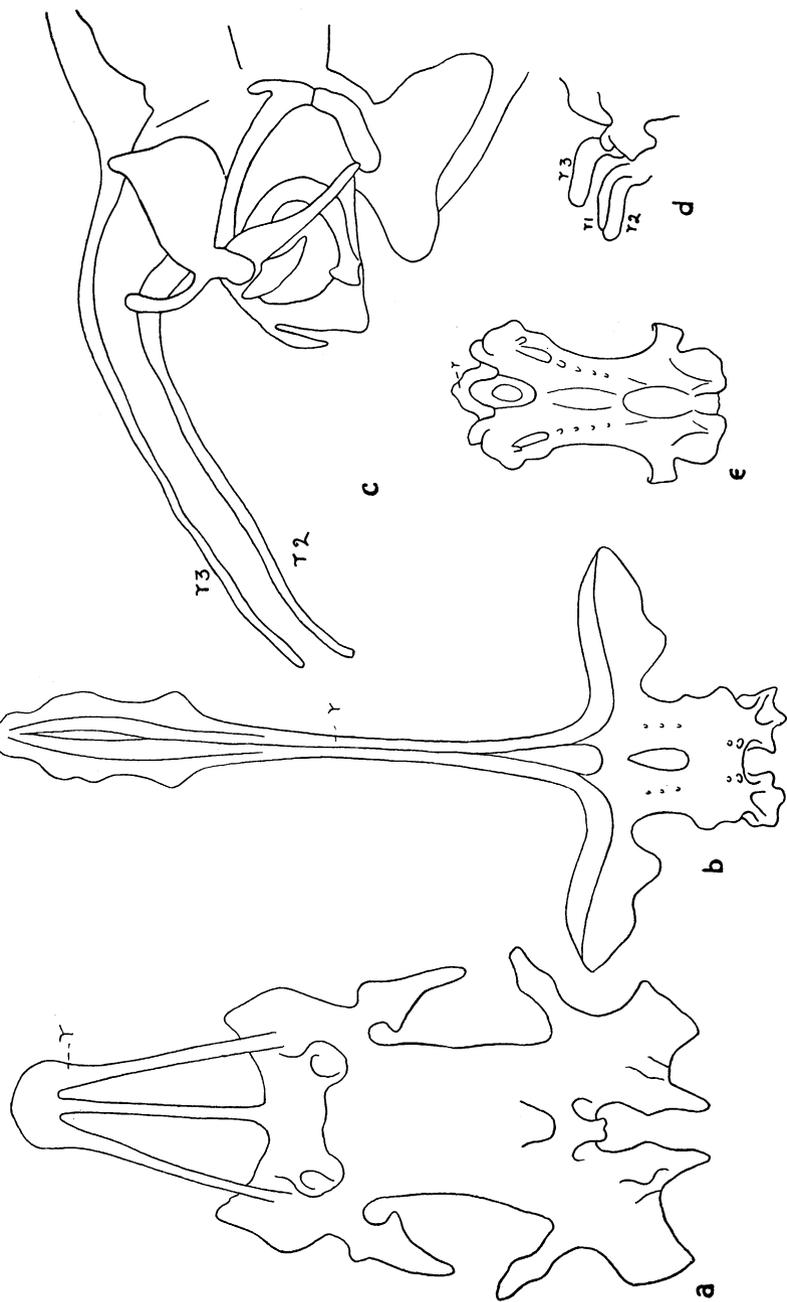
Hexanchoid teeth.

a, Lower jaw of a 340-mm. embryo of *Chlamydoselachus anguineus*, from B. G. Smith, after Rose; b, single tooth of *Chlamydoselachus anguineus*, from B. G. Smith, after Garman; c, jaws of *Heptanchias perlo*, showing the differentiation of the teeth in the two jaws; d, a symphyseal tooth from the lower jaw of *Heptanchias perlo*.



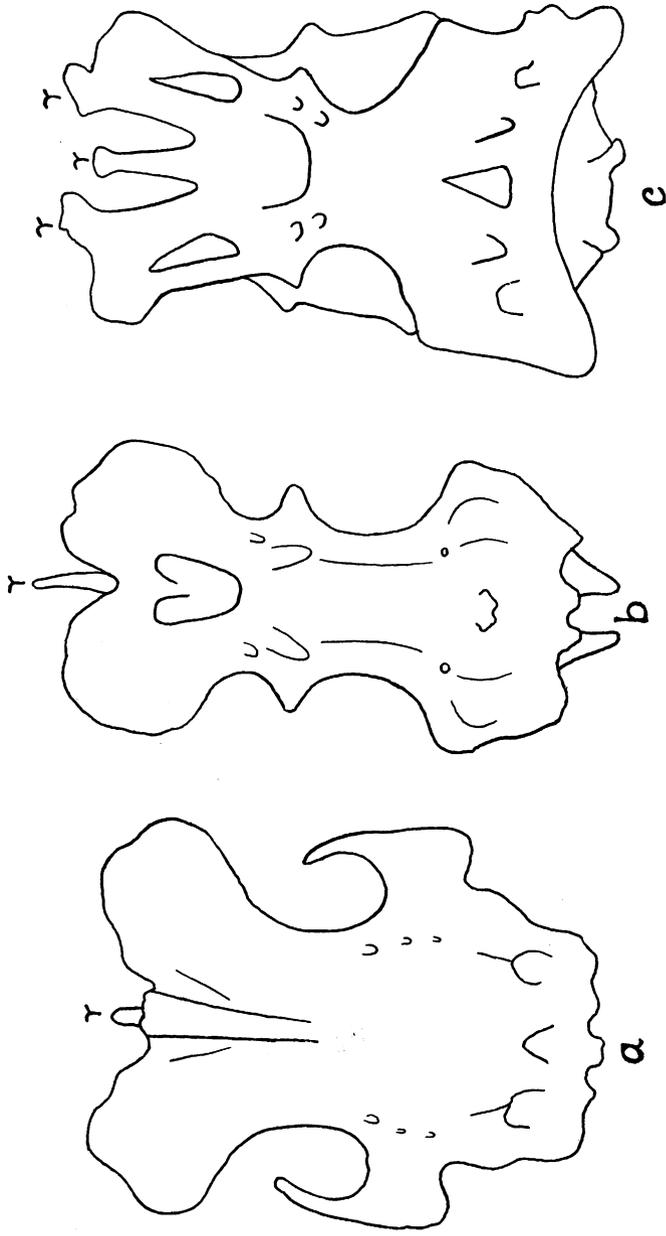
Skulls, to show rostrum. Dorsal view.

a, *Heterodontus japonicus*, with no rostrum; b, *Squalus misukurii*, showing trough-like rostrum; c, *Somniosus microcephalus*, showing a single rostral knob, after P. J. White; d, *Pristiophorus japonicus*, showing rod-like rostral cartilage fused to preoral bar, after Jaekel.



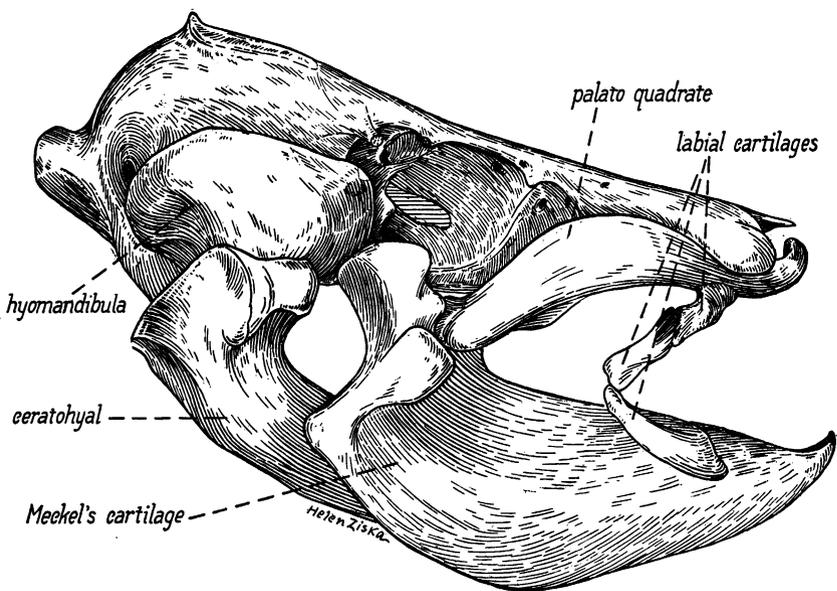
Skulls. Dorsal view.

a, *Galeus glauca* (note the triradiate rostral cartilages, typical of the Galea); b, *Rhinobatus granulatus*; c, *Chimaera monstrosa*, side view of skull of embryo, showing two rostral bars, r2 and r3, after Schauinsland; d, *Chimaera monstrosa*, side view of younger embryo, showing the origin of the rostral bar, r2 as a paired cartilage (=r1 and r2), after Schauinsland. The rostral bars of the Chismopnea arc not homologous with the rostral cartilages of the Plagiostomia; e, *Hepranchias perlo*.

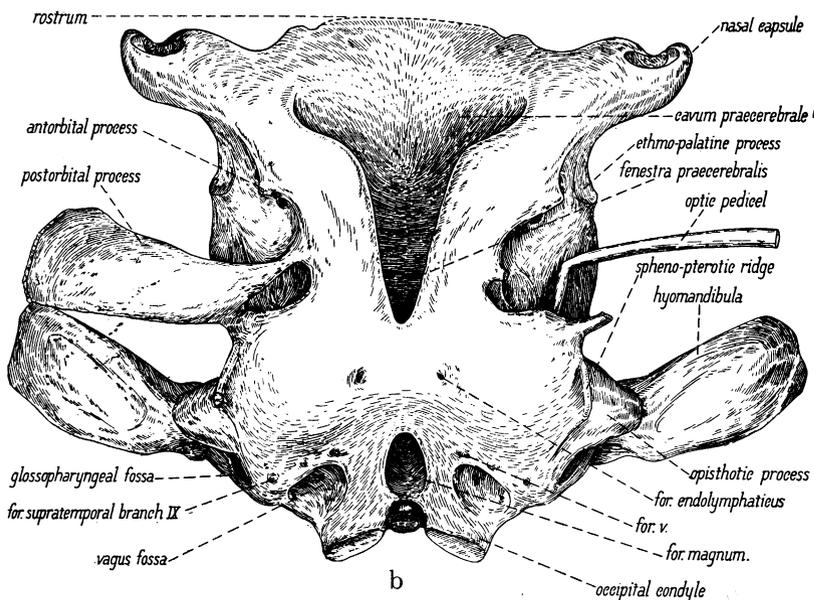


Skulls. Dorsal view.

a, *Stegostoma tigrinum*, showing extreme reduction of the ventral bar; b, *Chiloscyllium griseum*, showing the rostrum still further reduced to a single ventral bar; c, *Orectolobus*, showing the triradiate rostrum reduced to three knobs, after Haswell.



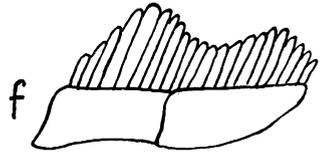
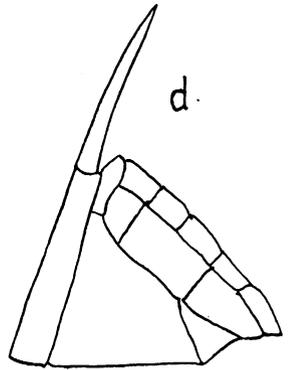
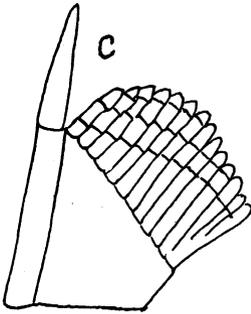
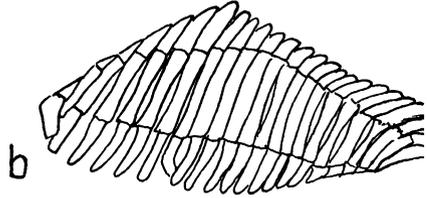
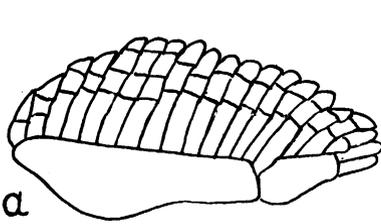
a



b

Skull of *Rhineodon typus*. After Denison.

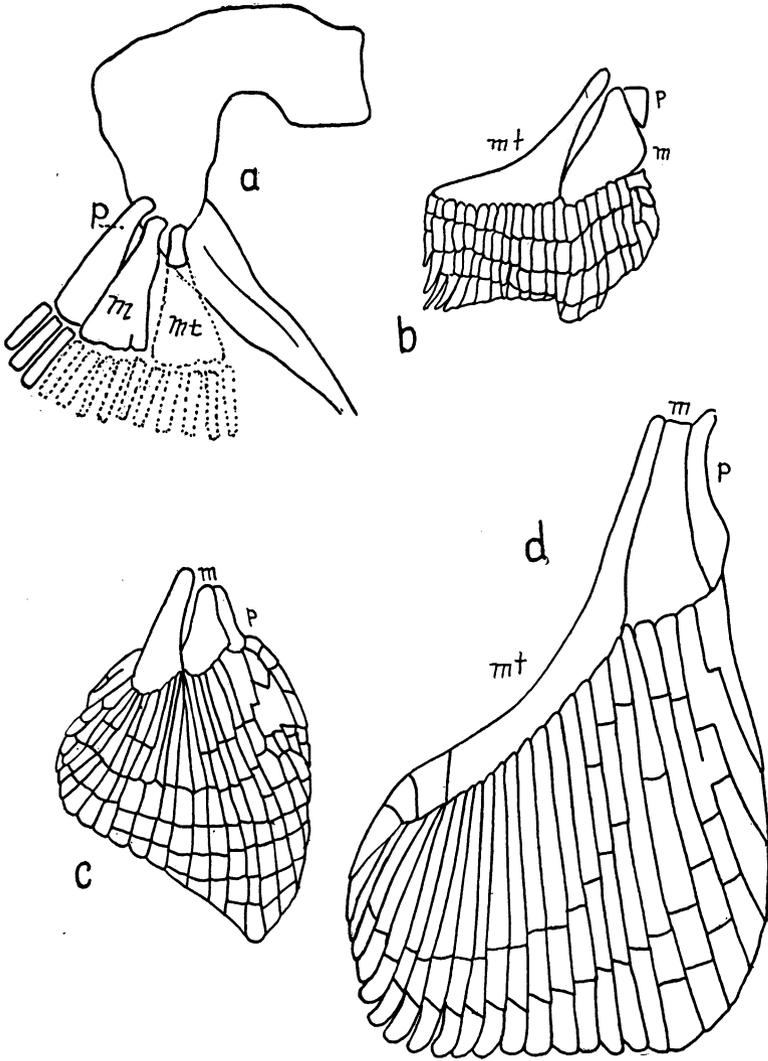
a, side view, $\times \frac{1}{8}$; b, top view, $\times \frac{2}{40}$.



Dorsal fin skeletons.

All after Tate Regan.

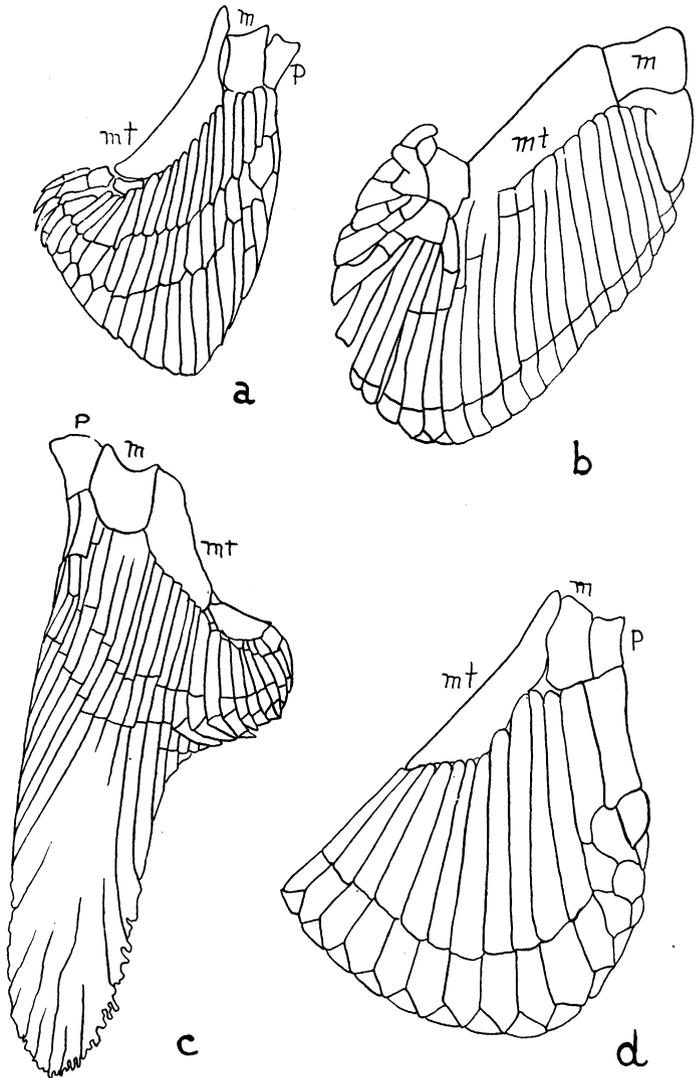
a, *Hexancha* (*Heptanchias*); b, *Galea* (*Galeorhinus*); c, *Heterodontea* (*Heterodontus*); d, *Squala* (*Squalus*); e, *Squala* (*Rhina*); f, *Platosomeae* (*Rhinobatus*).



Pectoral fins.

p, propterygium; *m*, mesopterygium; *mt*, metapterygium.

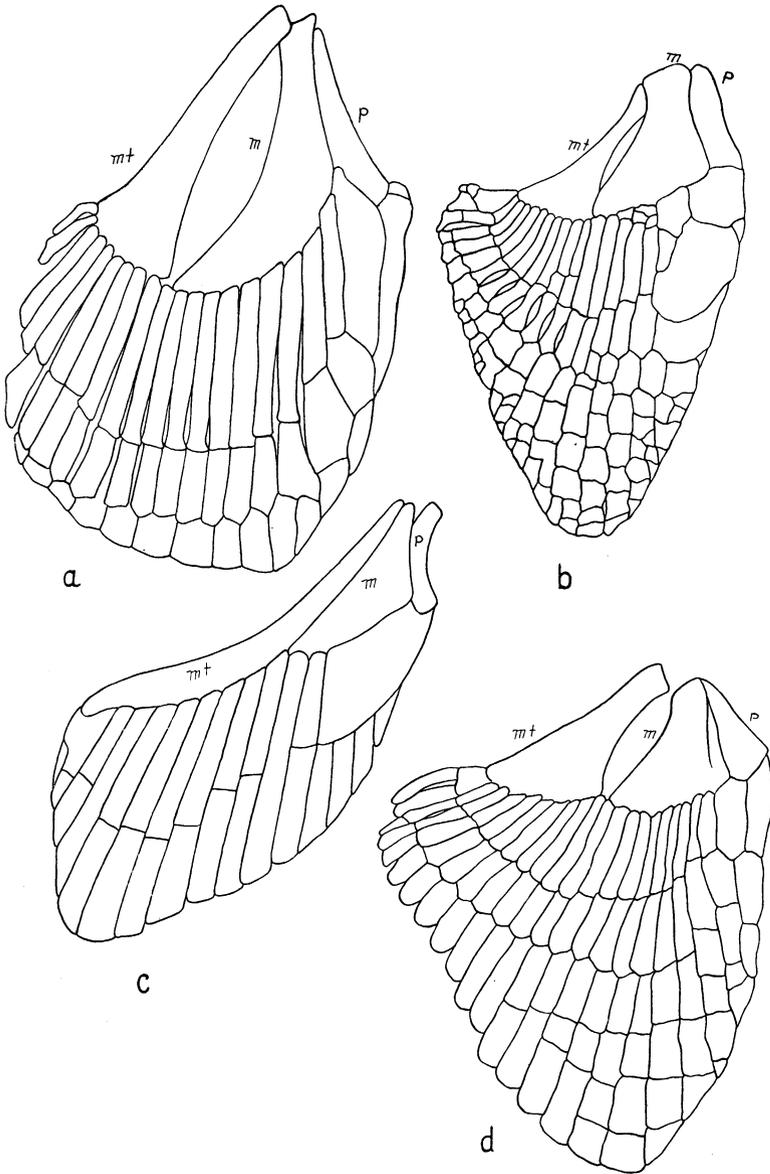
a, *Macropetalichthys prümiansis* E. Kayser, Devonian (restored), right pectoral fin, after F. Broili; *b*, *Heptanchias perlo*, left pectoral; *c*, *Ginglymostoma*, left pectoral, after Wesley; *d*, *Carcharias taurus*, left pectoral.



Pectoral fins.

p, propterygium; *m*, mesopterygium; *mt*, metapterygium.

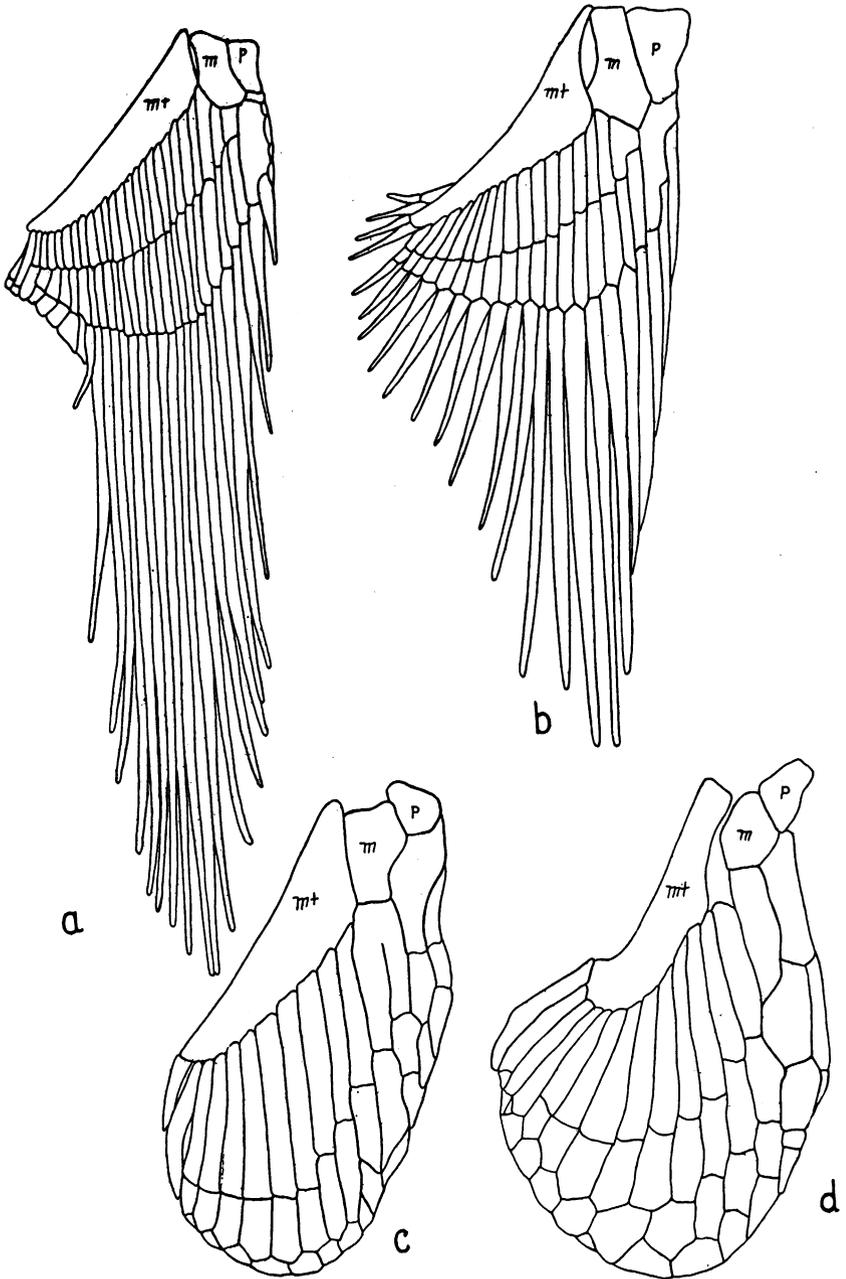
a, *Triakis scyllium*, left pectoral fin; b, *Callorhynchus callorhynchus*, left pectoral, after Wesley; c, *Isurus punctatus*, right pectoral, after Garman; d, *Catulus torazame*, left pectoral.



Left pectoral fins.

p, propterygium; m, mesopterygium; mt, metapterygium.

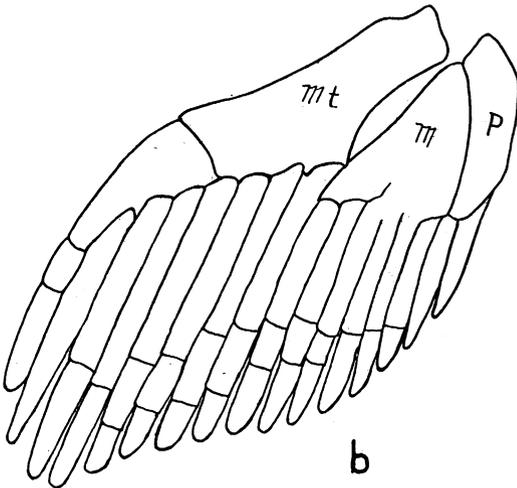
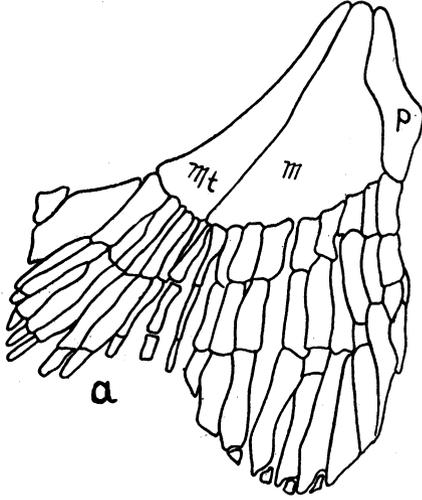
a, *Chiloscyllium griseum*; b, *Heterodontus japonicus*; c, *Scapanorhynchus owstoni*; d, *Stegostoma tigrinum*.



Left pectoral fins.

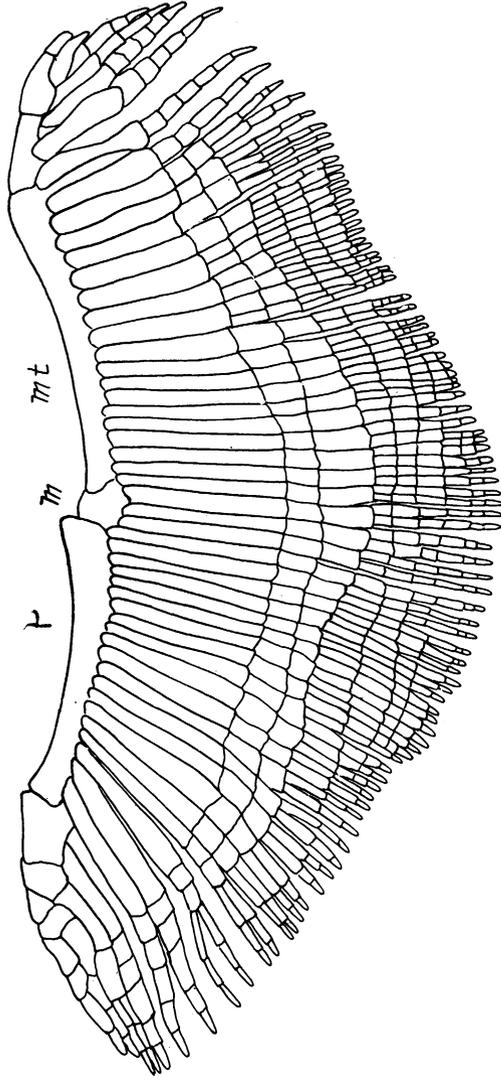
p, propterygium; m, mesopterygium; mt, metapterygium.

a, *Galeus glauca*; b, *Carcharinus japonicus*; c, *Halaelurus burgeri*; d, *Atelomycterus marmoratus*.

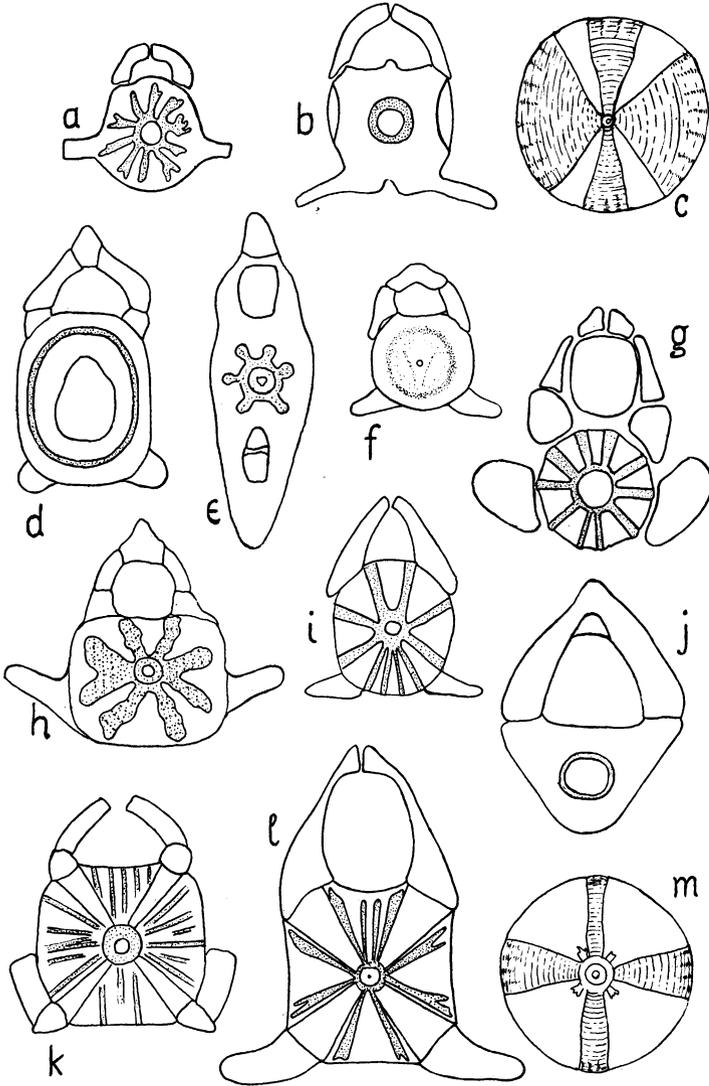


Left pectoral fins.

p, propterygium; *m*, mesopterygium; *mt*, metapterygium
a, *Squalus mitsukurii*; b, *Etmopterus lucifer*.



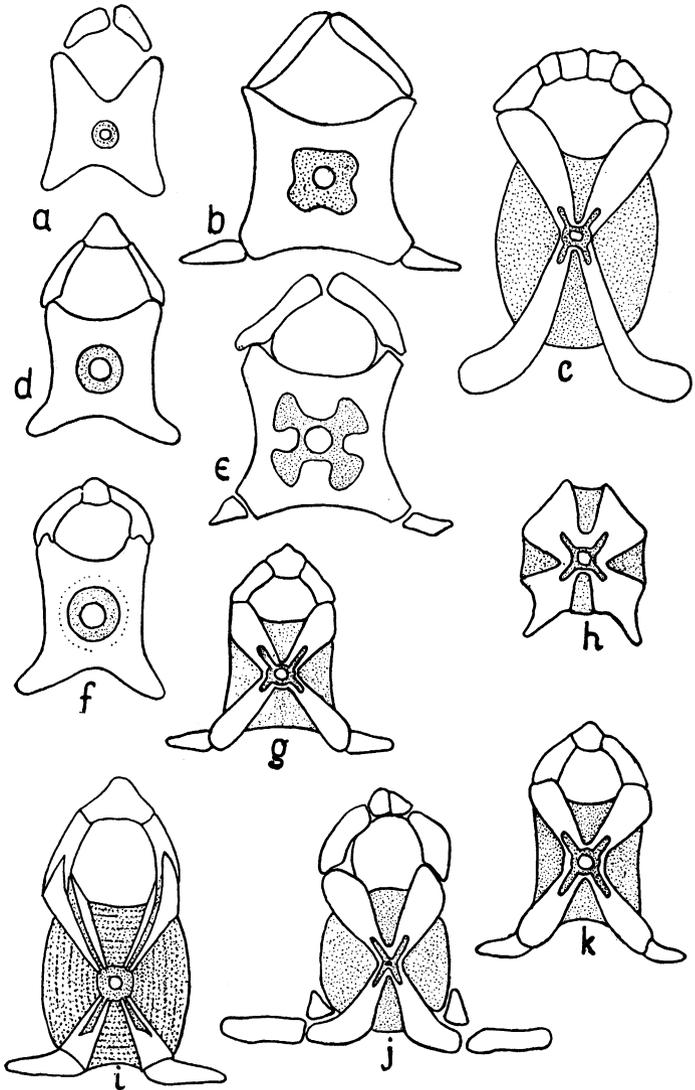
Left pectoral fin of *Rhinobatus granulatus*, showing the reduction of the mesopterygium, and lengthening of the propterygium in the expanded fin of the rays.



Vertebral centra from the thoracic region just over the heart (except e, caudal).

Calcified areas are stippled.

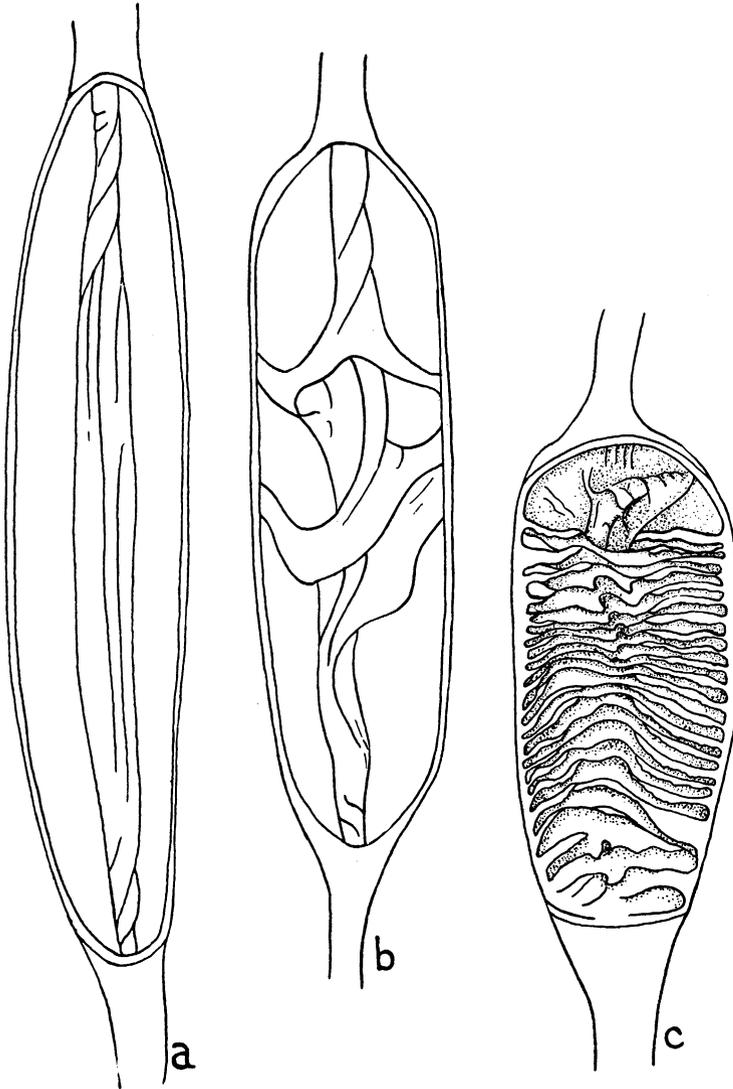
a, *Heterodontus japonicus*, tectospondylic; b, *Squalus mitsukurii*, cyclospondylic; c, *Cetorhinus maximus*, modified asterospondylic, after E. G. White; d, *Chimaera monstrosa*, uncalcified, after Hasse; e, *Heptranchias perlo*, caudal vertebra, tectospondylic; f, *Heptranchias perlo*, thoracic vertebra, uncalcified; g, *Stegostoma tigrinum*, radial asterospondylic; h, *Torpedo marmoratum*, tectospondylic, after Hasse; i, *Chiloscyllium griseum*, radial asterospondylic; j, *Etmopterus lucifer*, cyclospondylic; k, *Carcharias taurus*, radial asterospondylic; l, *Scapanorhynchus owstoni*, radial asterospondylic; m, *Rhineodon typus*, modified asterospondylic, after E. G. White.



Vertebrae from the thoracic region just over the heart. Note variations within the suborder Carcharinoidea. These are of the Maltese cross type.

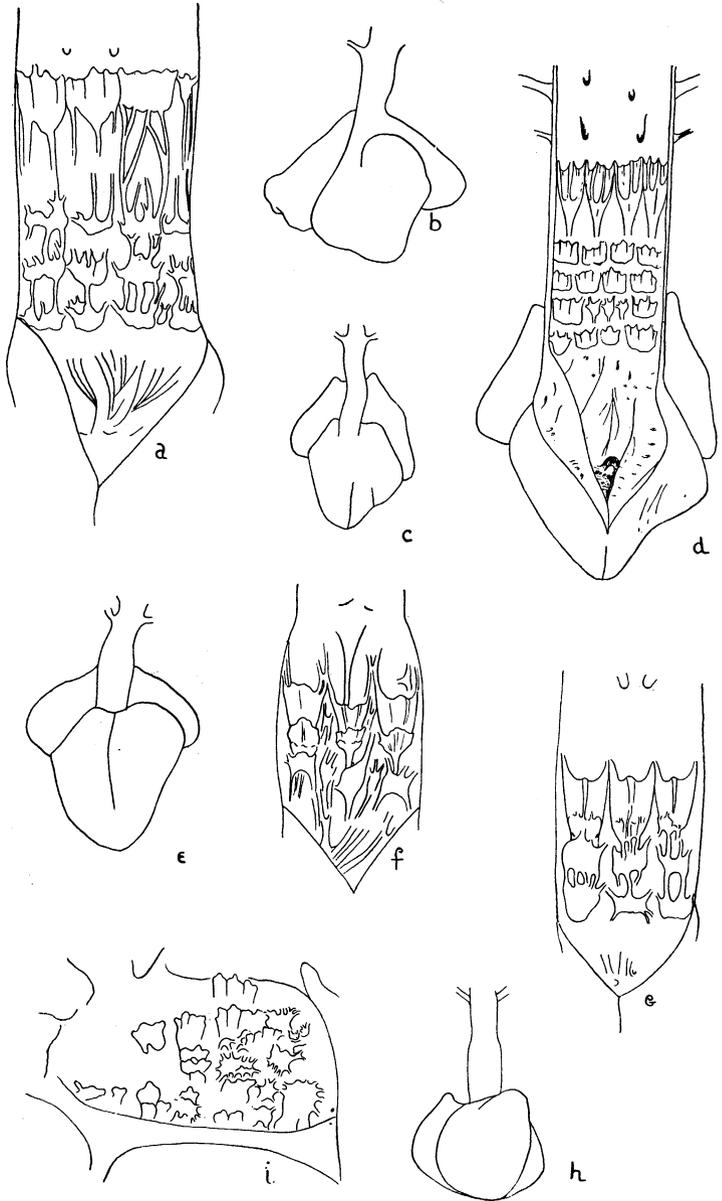
Calcified areas are stippled.

a, *Catulus torazame*; b, *Halaelurus burgeri*; c, *Galeus glauca*; d, *Catulus retifer*; e, *Calliscyllium venustum*; f, *Parmaturus xaniurus*; g, *Triakis scyllium*; h, *Galeorhinus manazo*; i, *Sphyrna zygaena*; j, *Carcharinus japonicus*; k, *Atelomycterus marmoratus*.



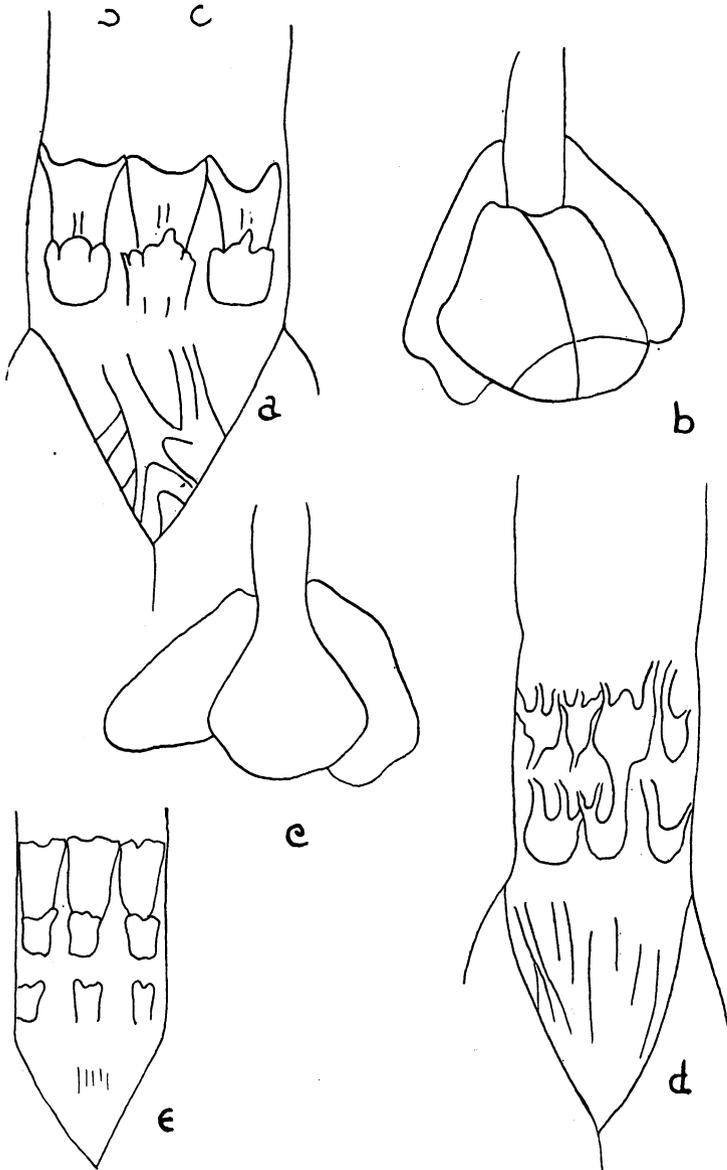
Spiral valves of three types.

a, Scroll type in *Carcharinus milberti*; b, spiral type in *Triakis scyllium*; c, ring type in *Chiloscyllium griseum*.



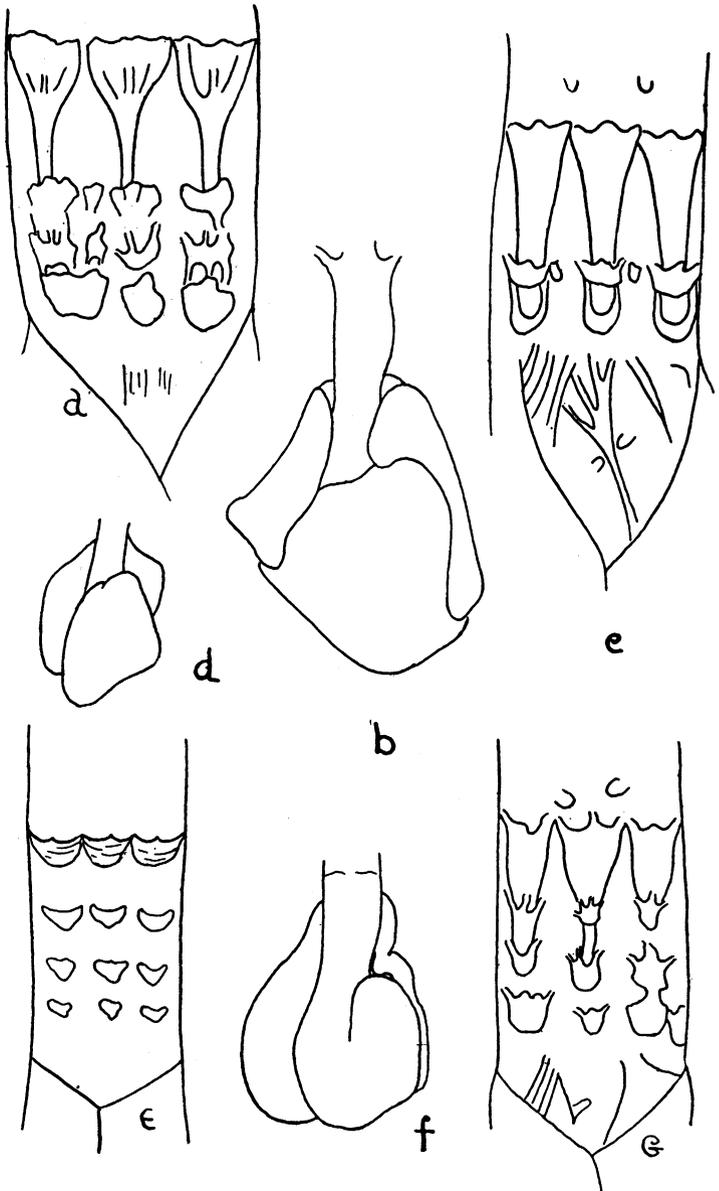
Hearts and heart valves in the open conus. Note transverse duplication in f, g, and i; and longitudinal duplication in a and d.

a and b, *Notorhynchus pectorosus*; c and d, *Chlamydoselachus anguineus*; e and f, *Carcharias taurus*; g and h, *Scapanorhynchus owstoni*; i, *Ceratodus forsteri*, after Lankester.



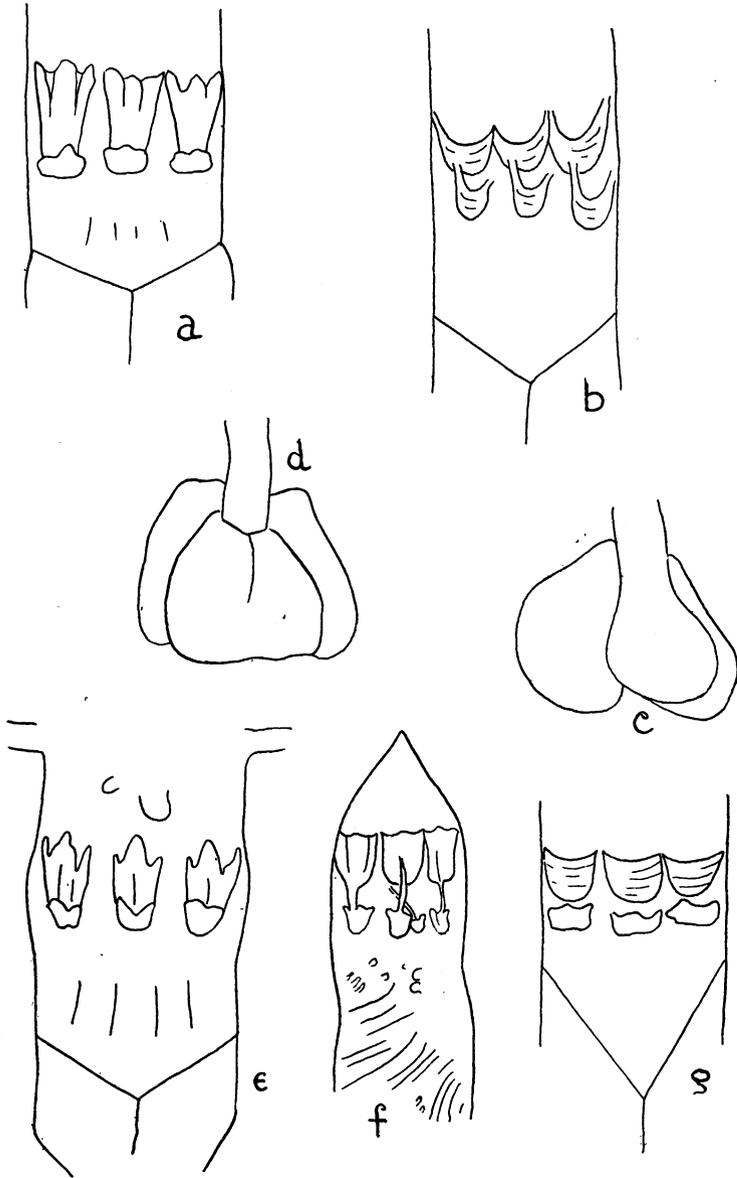
Hearts and heart valves in the open conus. Note longitudinal duplication in the upper row of d.

a and b, *Heterodontus japonicus*; c and d, *Callorhynchus callorhynchus*; e, *Chimaera monstrosa*, after Lankester.



Hearts and heart valves in the open conus. Note variation in *Squalus acanthias*, and longitudinal duplication in a, c, and g.

a, *Squalus acanthias*, north Atlantic specimen; b, *Squalus fernandinus*; c, *Squalus acanthias*, South American specimen; d and e, *Etmopterus lucifer*; f, *Squalus acanthias*, north Atlantic specimen; g, *Squalus fernandinus*.



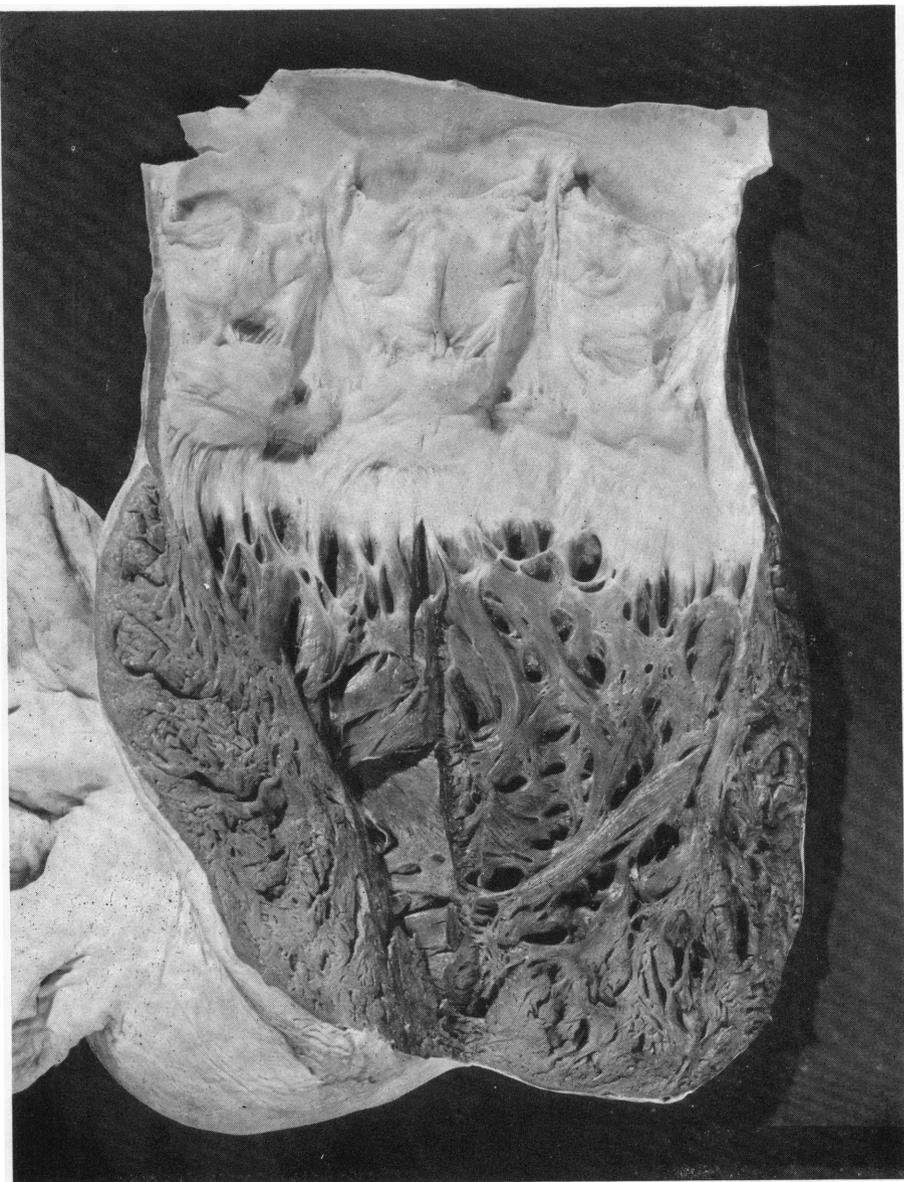
Hearts and heart valves in the open conus.

a, *Chiloscyllium plagiosum*; b and c, *Stegostoma tigrinum*; d and e, *Chiloscyllium griseum*; f, *Orectolobus japonicus*, after Garman; g, *Chiloscyllium indicum*.



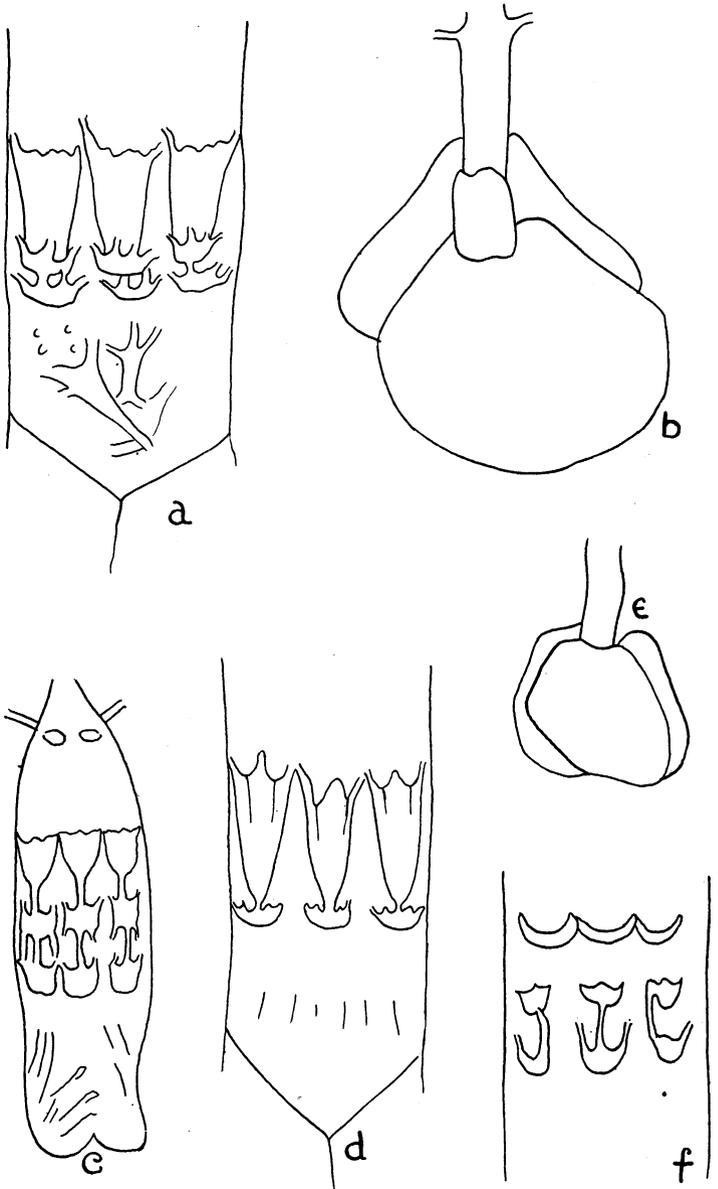
Conus of heart of *Rhineodon typus*, drawn from fresh specimen. Width of conus opened, 16 inches.

u, upper row of valves; *l*, lower row of valves; *a*, accessory valve.



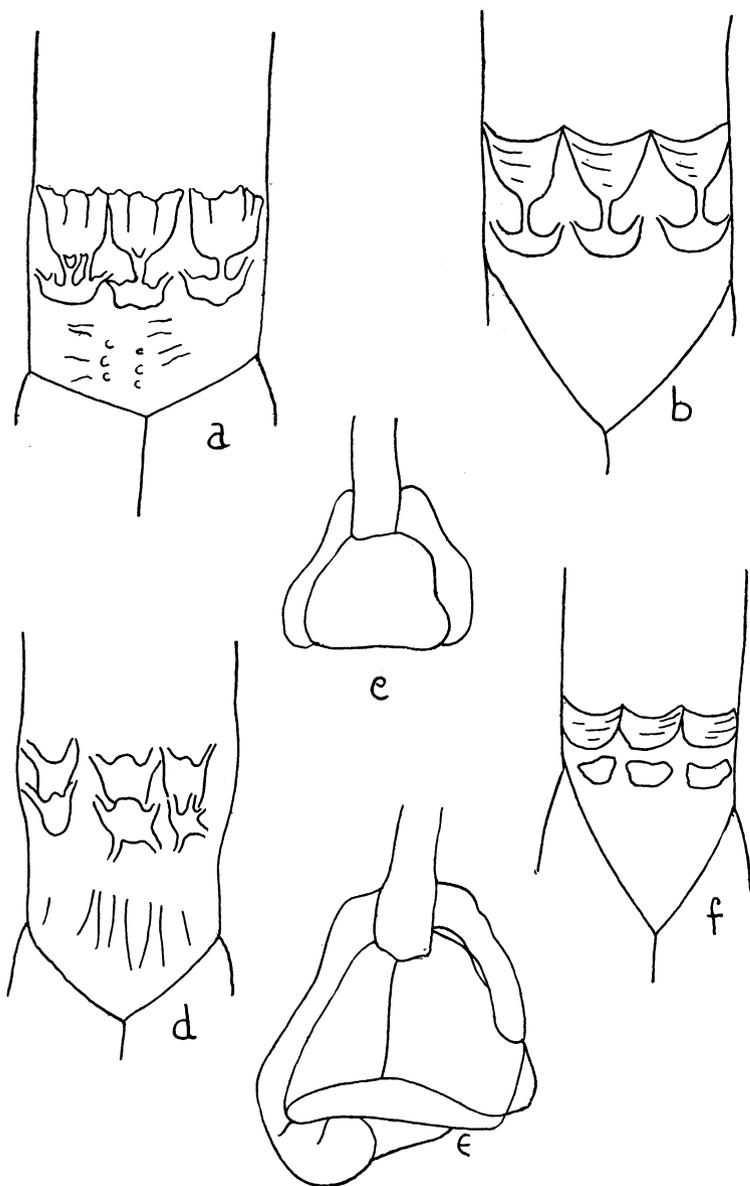
Photograph of heart of *Rhineodon typus*, open to show valves.

Photograph by A. M. N. H.



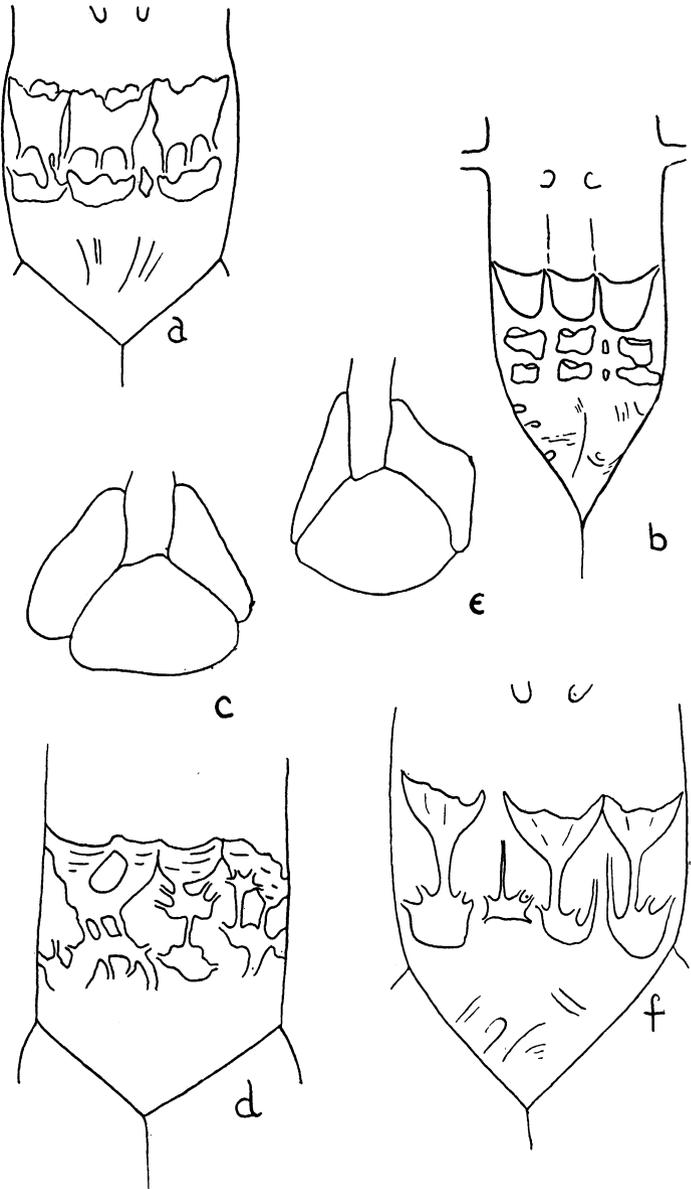
Hearts and heart valves in the open conus.

a and b, *Eugaleus galeus*; c, *Isurus punctatus*, after Garman; d and e, *Galeus glauca*; f, *Carcharodon carcharias*, after Parker.



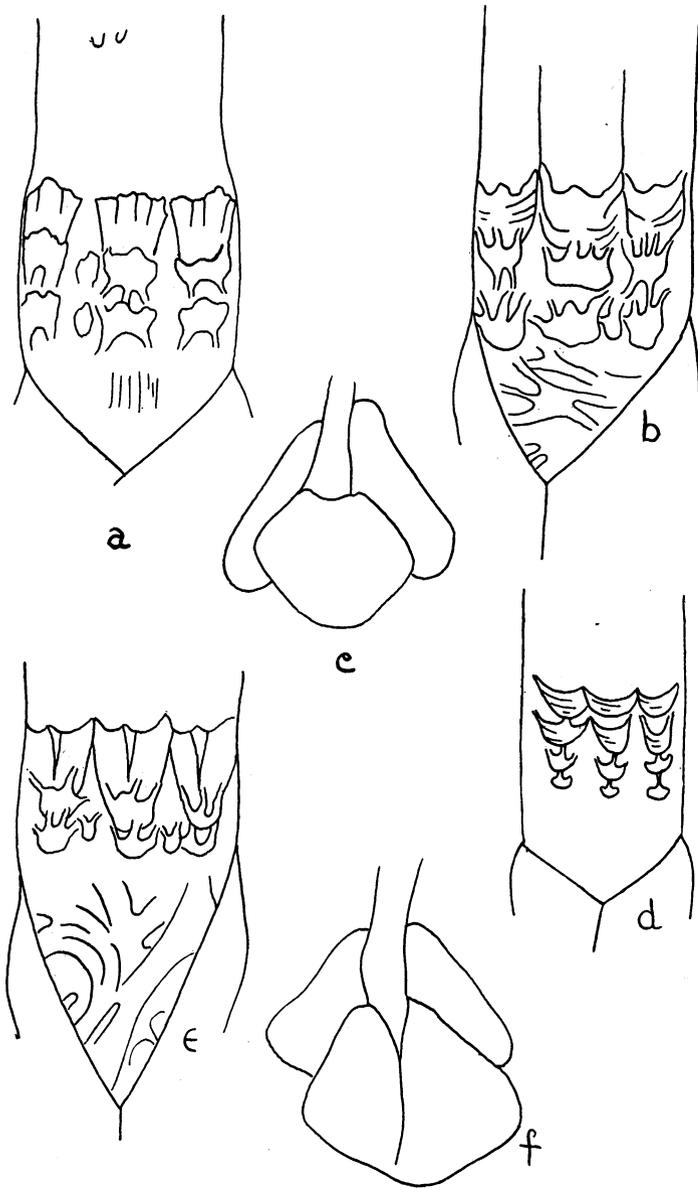
Hearts and heart valves in the open conus.

a, *Halaelurus bivius*; b and c, *Atelomycterus marmoratus*; d, *Pristiurus eastmani*;
e, *Halaelurus bivius*; f, *Halaelurus burgeri*.



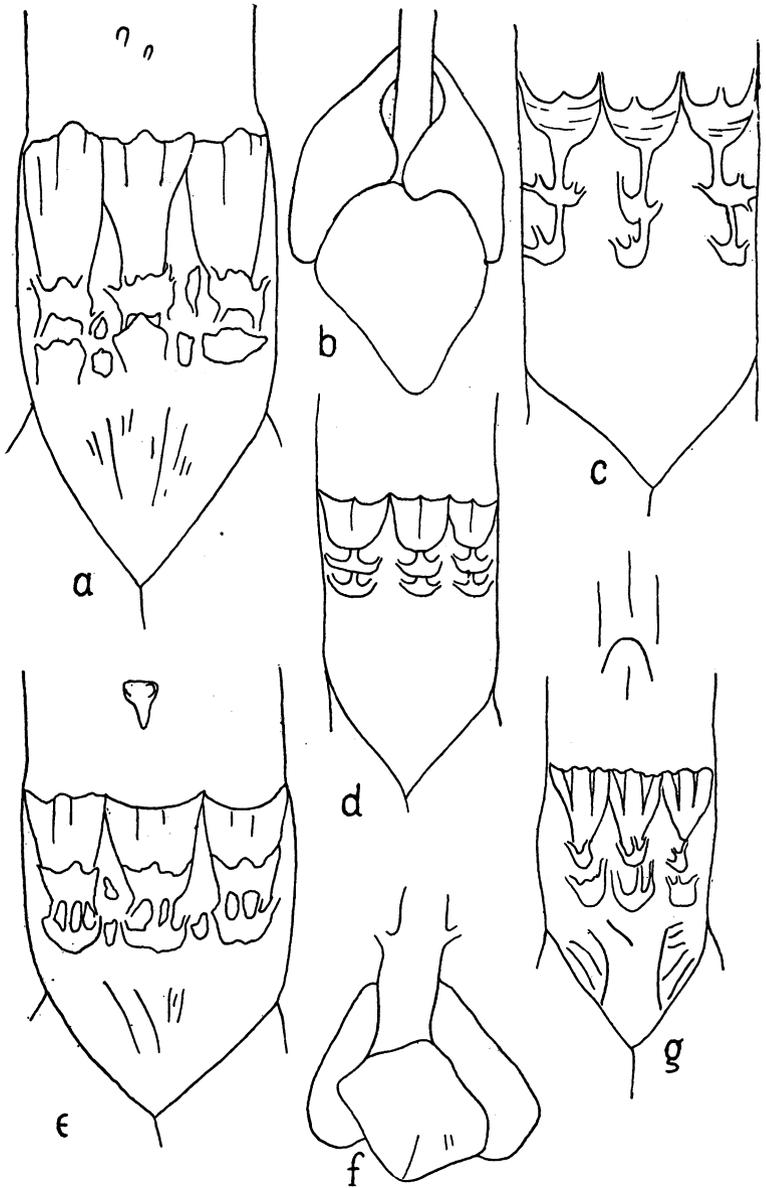
Hearts and heart valves in the open conus. Note transverse duplication in process in d, and variation of b from the other members of group.

a, *Catulus retifer*; b, *Calliscyllium venustum*; c and d, *Catulus torazame*; e and f, *Parmaturus xaniurus*.



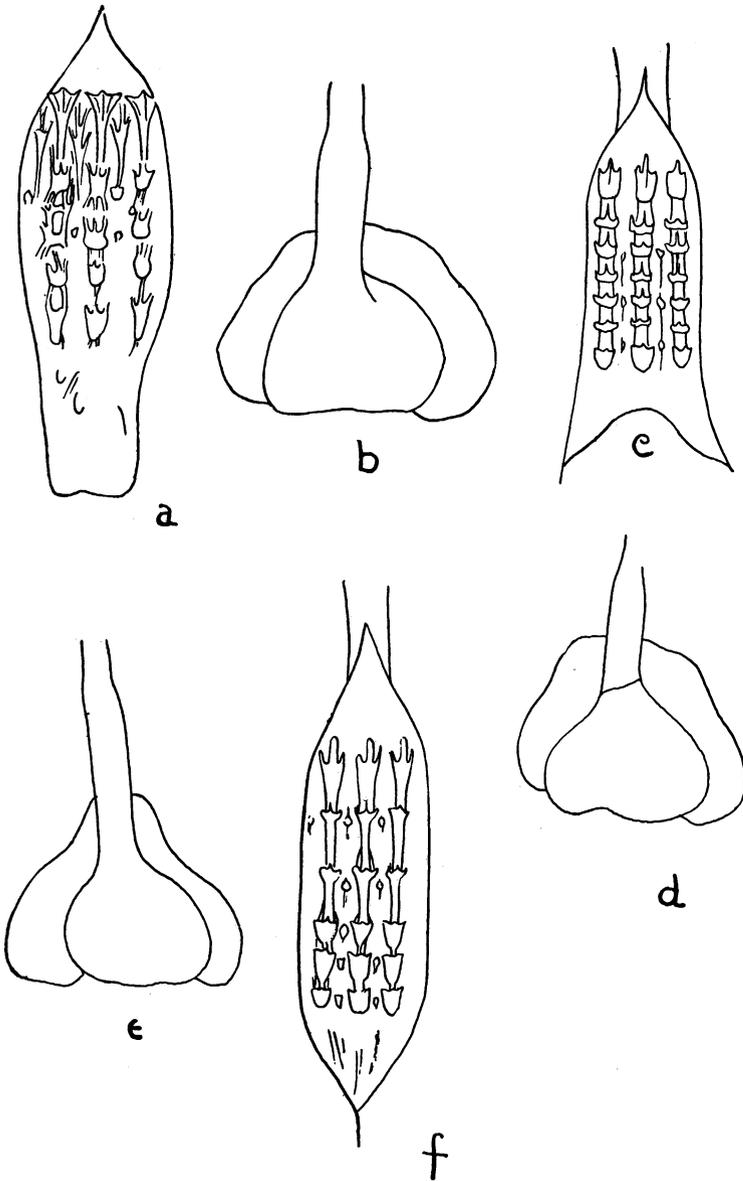
Hearts and heart valves in the open conus. Note variation in d, and the longitudinal duplication in the other species.

a, *Galeorhinus laevis*; b, *Galeorhinus mustelus*; c and d, *Galeorhinus manazo*; e, *Galeorhinus fasciatum*.



Hearts and heart valves in the open conus.

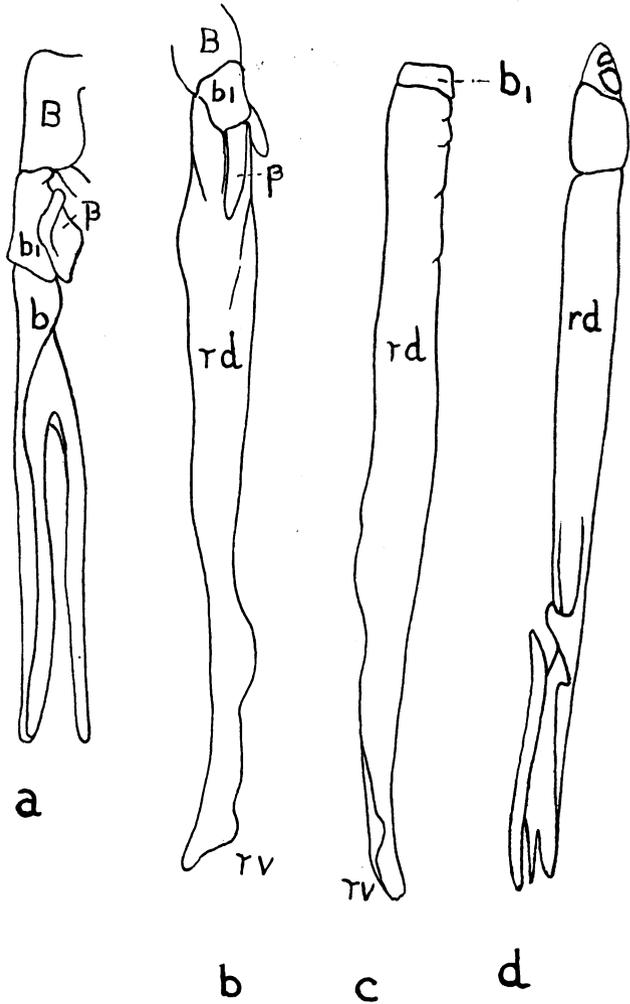
a, *Carcharinus milberti*; b and c, *Sphyrna zygaena*; d, *Carcharinus sorrah*; e, *Carcharinus commersonii*; f, *Carcharinus sorrah*; g, *Sphyrna blochii*.



Hearts and heart valves in the open conus. Note lengthening of the bulbus to accommodate the increased number of rows.

a and b, *Aetobatus*; c and d, *Rhinoptera jussieui*; e and f, *Mobula hypostoma*.

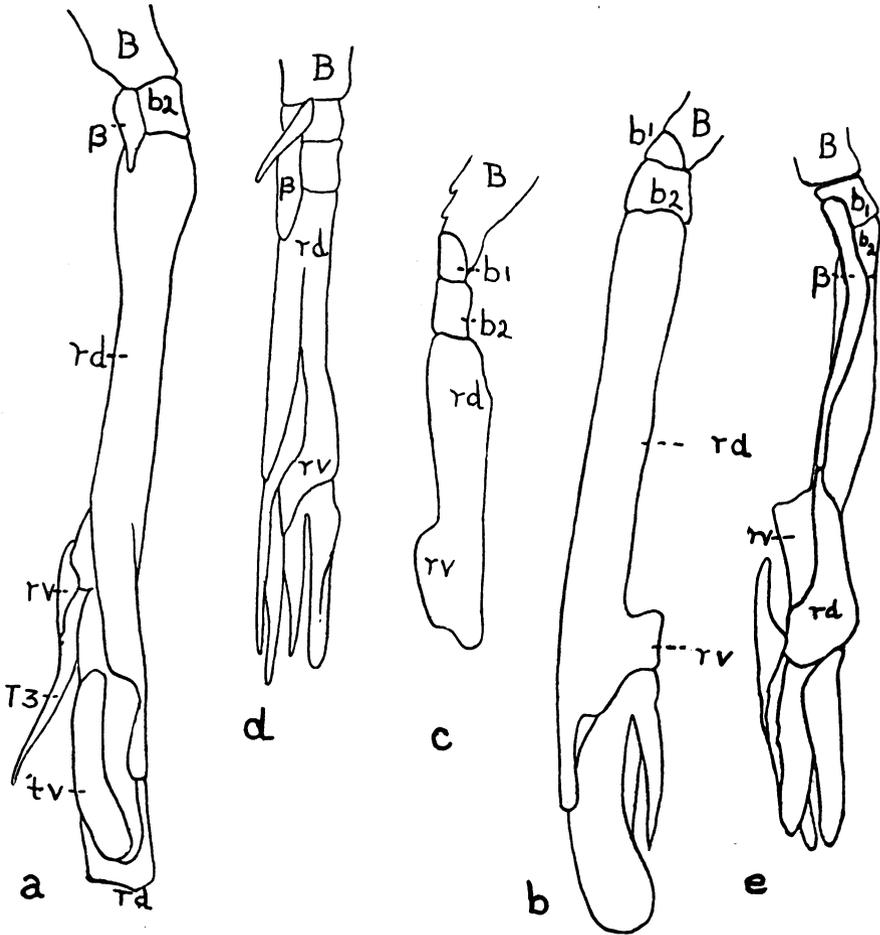
All after Garman.



Myxopterygia of mature males.

B, basale metapterygii; b_1 , stem joint; β , modified radial; rd, dorsal marginal cartilage; rv, ventral marginal cartilage.

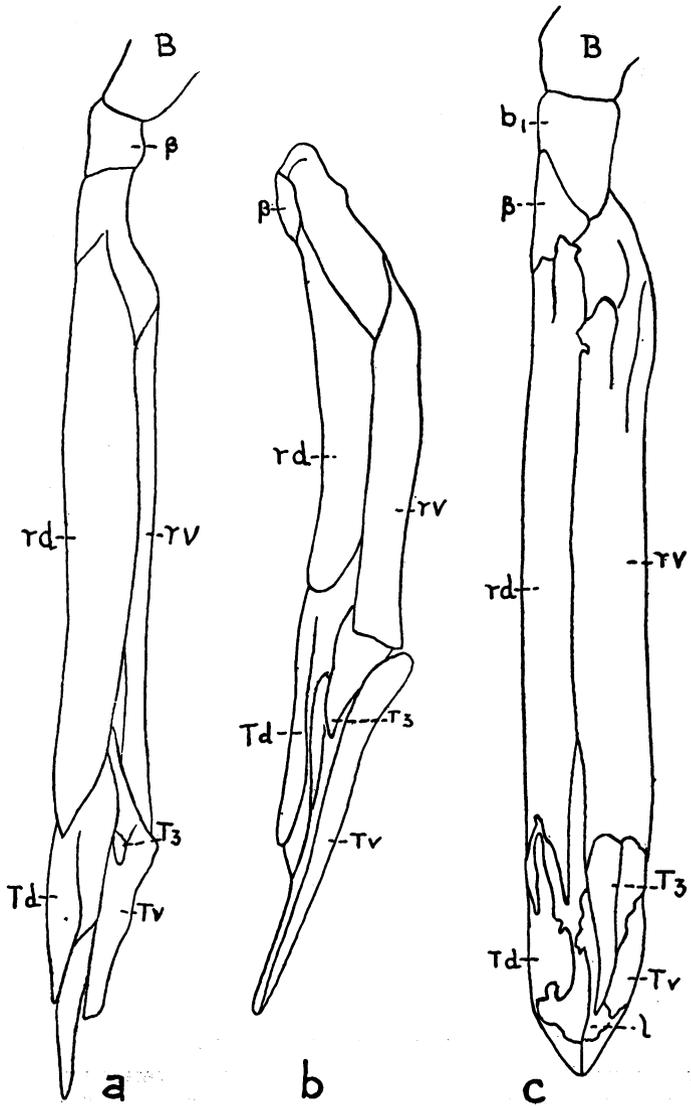
a, *Chimaera monstrosa*, dorsal view, after Jungersen; b, *Heptanchias perlo*, view of inner side; c, *Heptanchias perlo*, dorsal view; d, *Chlamydoselachus anguineus*, ventral view, after Günther.



Myxopterygia of mature males.

B, basale metapterygii; b₁, b₂, basal stem joints; β, beta piece; rd, dorsal marginal cartilage; rv, ventral marginal cartilage; t₃, spur; tv, ventral terminal piece; td, dorsal terminal piece.

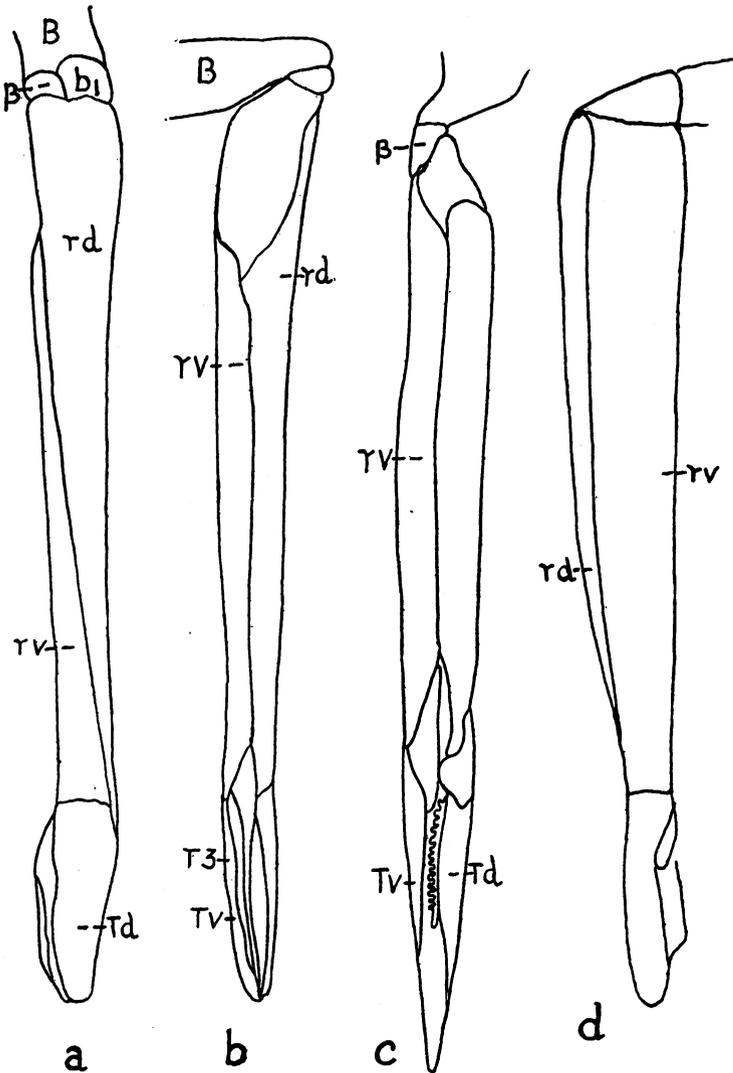
a and b, *Squalus mitsukurini*, showing the typical myxopterygium of the Squalea from two aspects: a, dorsal view; b, ventral view; c, *Elmopterus lucifer*, ventral view; d, *Heterodontus philippi*, lateral view, after Gegenbaur; e, *Trygon* sp., dorsal view, after Huber.



Myxopterygia of mature males.

B, basale metapterygii; b₁, stem joint; rd, dorsal marginal cartilage; rv, ventral marginal cartilage; td, dorsal terminal piece; tv, ventral terminal piece; t₃, spur; l, lamella; β, beta piece.

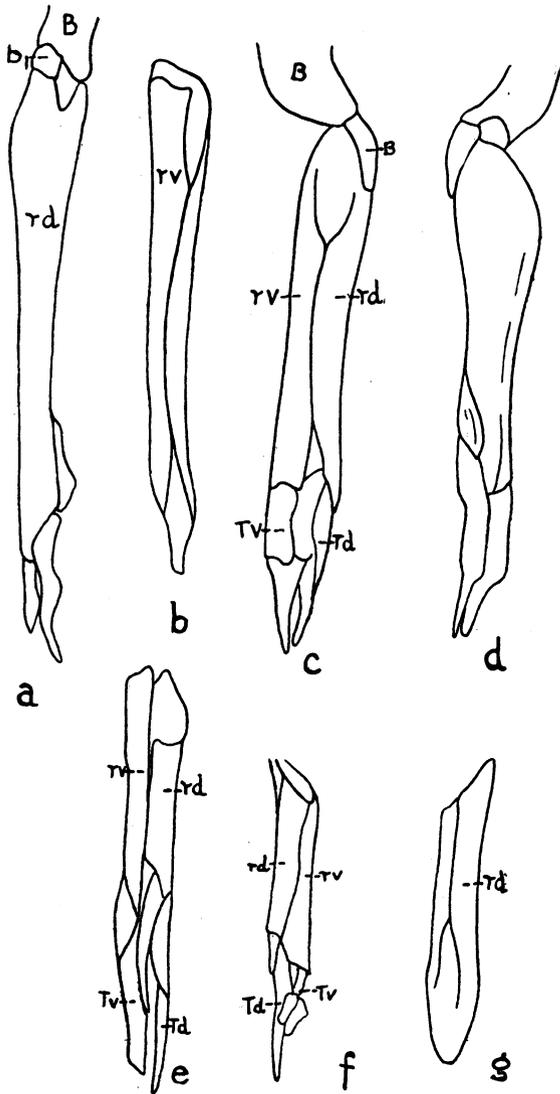
a, *Isurus punctatus*, dorsal view, after Jungersen; b, *Cetorhinus maximus*, dorsal view, after Jungersen; c, *Rhineodon typus*, dorsal view, after E. G. White, 1928.



Myxopterygia of mature males.

B, basale metapterygii; b_1 , basal joint; β , beta piece; rd, dorsal marginal cartilage; rv, ventral marginal cartilage; td, dorsal terminal piece; tv, ventral terminal piece; t3, spur.

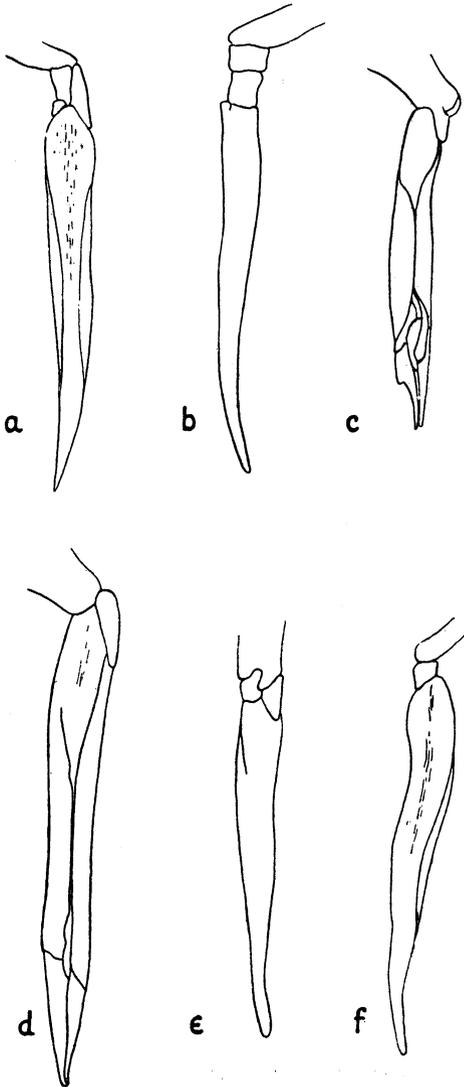
a, *Catulus torazame*, lateral view; b, *Catulus torazame*, dorsal view; c, *Halaelurus burgeri*, dorsal view; d, *Calliscyllium venustum*, dorsal view.



Male myxopterygia.

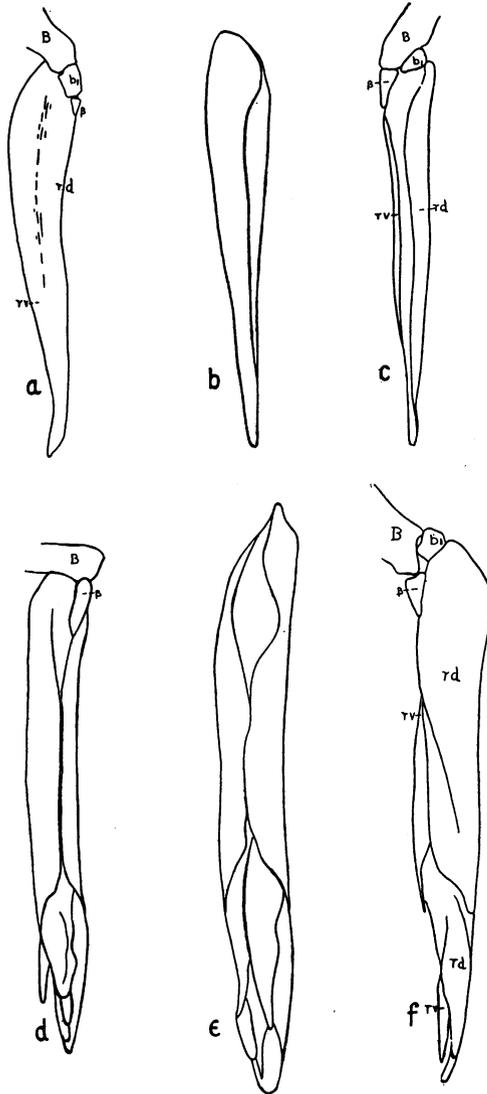
B, basale metapterygii; b₁, stem joint; β, beta piece; rd, dorsal marginal cartilage; rv, ventral marginal cartilage; td, dorsal terminal piece; tv, ventral terminal piece.

a, *Atelomycteris marmoratus*, lateral view; b, *Atelomycteris marmoratus*, dorsal view, terminal pieces omitted; c, *Parmaturus zaniurus*, dorsal view; d, *Parmaturus zaniurus*, ventral view; e, *Chiloscyllium griseum*, dorsal view; f, *Pristiurus melanostomus*, dorsal view, after Jungersen; g, axial cartilage of immature *Catulus retifer*, dorsal view. Note that cartilages are fully coiled in immature specimen. The terminal pieces were incompletely developed.



Myxopterygia of the Carcharinoidea, showing variation within the group.

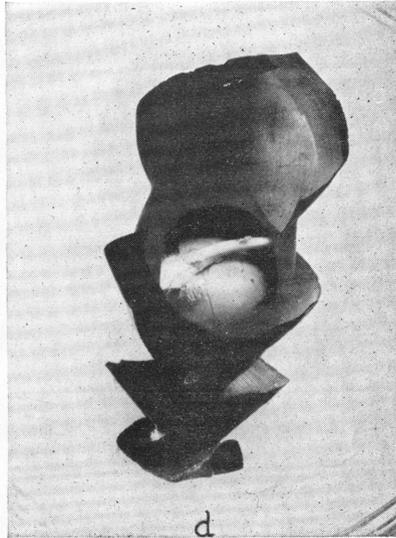
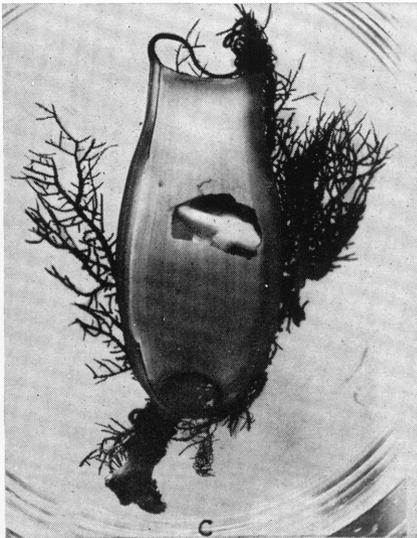
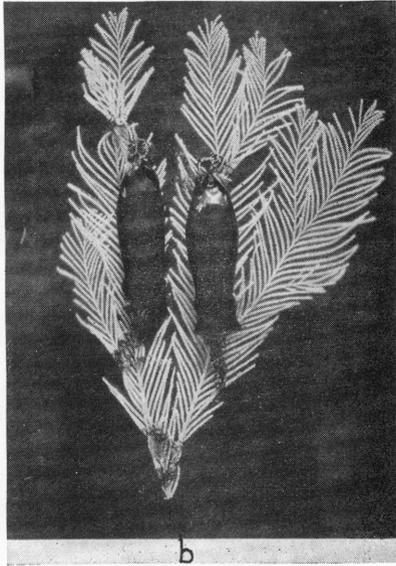
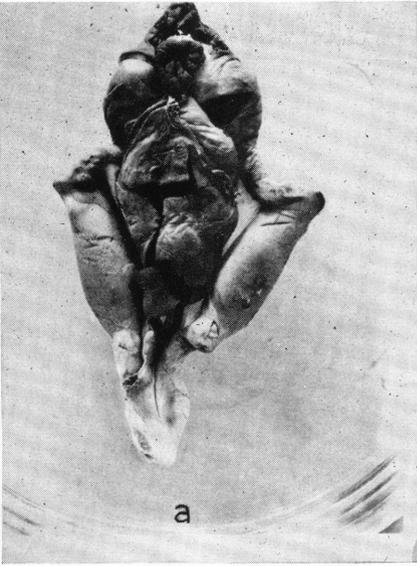
a, *Triakis scyllium*, dorsal view; b, *Triakis scyllium*, ventral view; c, *Galeorhinus laevis*, dorsal view, after Huber; d, *Galeorhinus mustelus*, dorsal view; e, *Galeorhinus manazo*, immature, ventral view; f, *Galeorhinus manazo*, dorsal view.



Myxopterygia of the Carcharinoidea, showing variation within the group.

B, basale metapterygii; b_1 , stem joint; β , beta piece; rd, dorsal marginal cartilage; rv, ventral marginal cartilage; td, dorsal terminal piece; tv, ventral terminal piece.

a, *Galeus glauca*, dorsal view; b, *Carcharinus milberti*, dorsal view; c, *Carcharinus japonicus*, dorsal view; d, *Carcharinus acronotus*, dorsal view; e, *Sphyrna zygaena*, dorsal view; f, *Sphyrna zygaena*, lateral view.



Egg cases of elasmobranchs from the Sagami Sea, Japan.

a, Reproductive organs of *Catulus torazame*, showing mature egg cases in the oviducts.

b, Egg cases of *Catulus torazame* attached by coiled thread-like extensions of the egg case to a branch of *Sertularia*.

c, Egg case of *Cephaloscyllium* opened to show the embryo in position.

d, Egg case of *Heterodontus japonicus* opened to show embryo in position.

Photographs original.

