1. INTRODUCTION

This is the second volume of an extensively rewritten, revised, and updated version of the original FAO Catalogue of Sharks of the World (Compagno, 1984). It covers all the described species of living sharks of the orders Heterodontiformes, Lamniformes, and Orectolobiformes, including their synonyms as well as certain well-established but currently undescribed species (primarily Australian species mentioned by Last and Stevens, 1994). It includes species of major, moderate, minor, and minimal importance to fisheries (Compagno, 1990c) as well as those of doubtful or potential use to fisheries. It also covers those species that have a research, recreational, educational, and aesthetic importance, as well as those species that occasionally bite and threaten people in the water and the far more numerous species that are 'bitten' and threatened by people through exploitation and habitat modification. The Catalogue is intended to form part of a comprehensive review of shark-like fishes of the world in a form accessible to fisheries workers as well as researchers on shark systematics, biodiversity, distribution, and general biology. It also caters to other researchers that need comparative information on sharks, people who encounter sharks during the course of work or play in the sea or in fresh water, and the general public. This Catalogue builds on a progressive increase in our knowledge of shark biology over the past two decades, and addresses an exponential increase in popular interest in sharks and a growing concern over their burgeoning conservation problems.

The term *Shark* is used here in the broad sense of the FAO International Plan of Action for the Conservation and Management of Sharks (FAO 1999). Sharks include rays or batoids and chimaeroids as well as 'nonbatoid' or 'typical' sharks, which are the subject of the original shark catalogue and of the present volume. A problem with sharks is that most researchers, much less the general public, are unaware of their diversity and tend to focus on the larger, toothy, nonbatoids. There are approximately 1 200 *known* living and valid species of shark-like fishes, cartilaginous fishes, or chondrichthyans, which form the class Chondrichthyes. These include at least 50 species of ghost sharks, silver sharks, elephant fish, chimaeras or ratfish (order Chimaeriformes), over 600 species of batoids, flat sharks, or winged sharks (order Rajiformes), and nearly 500 species of nonbatoid, ordinary or traditional sharks. The living shark-like fishes are included in 10 orders, 60 families, and 186 genera. Diversity of all cartilaginous fishes, living and extinct, is far greater, with at least 140 valid families, 600 valid genera, and at least 3 700 valid species (from databases prepared by the writer).

The living cartilaginous fishes are divided into two sister-groups with a long separate, pre-Devonian history, the chimaeroids, Holocephali (with a single living order Chimaeriformes), and the sharks and rays proper or Elasmobranchii, with the surviving group subcohort Neoselachii or modern sharks including all of the living species. There is a traditional concept in the taxonomic literature that divides the living Neoselachii into sharks, Selachii or Pleurotremata, and rays or batoids, Batoidea or Hypotremata. Modern cladistic classifications rank the batoids as an order Rajiformes of the squalomorph sharks (superorder Squalomorphii), and a sister-group of the sawsharks (order Pristiophoriformes) (Fig.1). Hence the batoids are highly modified, highly diverse, and extremely successful sharks that outnumber all other cartilaginous fishes in species. Chimaeroids are the closest evolutionary cousins to elasmobranchs within the Chondrichthyes, and may find a higher profile as silver sharks or ghost sharks. Considering them as 'sharks' brings batoids and chimaeroids out of the perceptual dark. The batoids and chimaeras tend to receive far less attention than nonbatoid sharks in most places. Some of the batoids currently are as important for fisheries or more so than nonbatoid sharks or chimaeroids, and some are under severe threat from overexploitation and habitat modification (i.e. sawfishes, freshwater stingrays). The batoid sharks will hopefully be the subject of a forthcoming and much overdue FAO Catalogue of Batoids of the World; likewise for the chimaeroids.

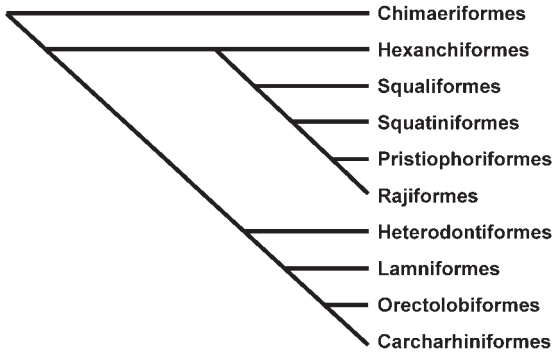

Fig. 1 Cladogram showing interrelationships of the orders of living cartilaginous fishes

The original 1984 FAO Shark Catalogue was in one volume in two parts, with pagination across both parts and with a single bibliography. As the new Catalogue has grown apace with new information and revisions, it is being published as three free-standing volumes, each with separate pagination, introduction, terminology, systematic sections, glossary, list of species by FAO Statistical Areas, and a dedicated bibliography. This will allow readers to independently use each volume without having to consult the other volumes for technical terms and measurements or bibliographic purposes, as was the case in the old catalogue. We hope that this added flexibility will be received as an improvement. A larger general introduction to the whole catalogue appears on the first volume and appendices on shark encounters and shark conservation are confined to the third volume. Readers are also encouraged to consult the addenda section included in the last volume of the catalogue. The present and second volume reviews all the species of living bullhead, mackerel and carpet sharks (orders Heterodontiformes, Lamniformes and Orectolobiformes), that is, the noncarcharhinoid galeomorph sharks (see Plan of the Catalogue below). The first volume covers the nonbatoid squalomorph sharks (orders Hexanchiformes, Squaliformes, Squatiniformes and Pristiophoriformes), and the third volume reviews the carcharhinoid galeomorphs (order Carcharhiniformes).

Apparently sharks are extremely popular at present with conservationists, fisheries managers, the news and entertainment media, and the general public, and are likely to stay that way for the foreseeable future. Negative concepts of sharks were reflected in the 1984 catalogue, sometimes embarrassingly so in hindsight, and partially due to the negative shark milieu of the times. Hopefully the present version departs from this perspective and portrays sharks as a major group of biologically interesting, poorly

known vertebrates with over 400 million years of unqualified success as predators and survivors of mass extinctions. Sharks were then and are now challenged by the ultimate and most terrible of predators, *Homo sapiens* ('man, prudent or wise' as optimistically named by Linnaeus, 1758); but unlike former times the human superpredator is apparently aware of the problems and is taking some steps (at last!) to solve it. One can hope that those efforts are successful.

1.1 Plan of the Catalogue

This Catalogue is based on original work on various groups of sharks as well as my interpretation of data in the literature. Original descriptions of shark species and other taxa were consulted if at all possible; when not, various authoritative works were consulted for consensus on citations. Some of the arrangements of families, genera and species used here disagree with those of previous workers including those in my own papers, but in such cases the disagreements are discussed or reference is made to discussions of such problems in the literature. Nonsystematists may not appreciate changes to classification and nomenclature wrought by systematic studies, and often consider them as annoyances, but shark systematics evolves as does any other science and changes are inevitable. Hopefully they are producing increased stability as knowledge improves in a former backwater of systematic ichthyology.

Classification and systematic arrangement used here. The present arrangement has evolved from my earlier works (Compagno, 1973, 1977, 1979, 1982, 1984, 1988, 1999), which initially divided the nonbatoid sharks into eight major groups or orders and the batoids into four or five orders. The relationships of the nonbatoid shark orders to one another other and to the batoids (order Rajiformes) is approaching a tentative consensus following the work of Compagno (1977, 1988, 1999 and unpublished), Shirai (1996), and de Carvalho (1996). The following classification of shark-like fishes to order is used in this work and reflects a tentative cladogram based on a summary of previous work and analysis in progress (* starred orders are covered in this volume):

Class Chondrichthyes (cartilaginous fishes)
- Subclass Holocephali (chimaeras and fossil relatives)
  - Order Chimaeriformes (chimaeras or silver sharks)
- Subclass Elasmobranchii (sharks)
  - Cohort Euselachii (modern sharks and fossil relatives)
    - Subcohort Neoselachii (modern sharks)
      - Superorder Squalomorphi (squalomorph sharks)
        - Order Hexanchiformes (cow and frilled sharks)
        - Order Squaliformes (dogfish sharks)
        - Order Squatiniformes (angel sharks)
        - Order Pristiophoriformes (sawsharks)
        - Order Rajiformes (batoids)
      - Superorder Galeomorphi (galeomorph sharks)
        - Order Heterodontiformes (bullhead sharks)*
        - Order Lamniformes (mackerel sharks)*
        - Order Orectolobiformes (carpet sharks)*
        - Order Carcharhiniformes (ground sharks)

Orders are the highest taxonomic groups dealt with here, and many of their synonyms are listed even though the present International Code of Zoological Nomenclature does not treat groups higher than the family-group level (superfamilies, families, subfamilies, tribes, etc.). The nomenclature for orders is modified from that of Compagno (1973, 1984, 1999), with synonyms listed from oldest to newest. The orders are suffixed with *-iformes* following common ichthyological practice at present. Families are suffixed with *-idae*, the universal ending for zoological families. Other levels between orders, families, genera and species are mostly not covered here. Subgenera are discussed under their appropriate genera but species are not grouped under subgenera and given parenthetical subgeneric names such as ***Somniosus (Rhinoscymnus) rostratus***, even where subgenera are considered valid, so as not to eliminate the utility of listing species alphabetically within genera. Subspecies are listed in the synonymies of their species but are not given separate coverage.

Valid families, genera and species are provided with citations for their author or authors, year of publication, reference and pagination (illustrations also included for species), while synonyms are similarly cited except for their references (which are listed in the bibliography). Other combinations of genera and species that have been used in the literature but are at variance with valid names are cited with author and date only. The bibliography covers a wide selection of references used in writing the catalogue, but is not intended to be all-inclusive.

The information pertaining to each family, genus and species is arranged in the form used in the first edition of this Catalogue (Compagno, 1984), with some modifications:

Family accounts include the valid modern form of the family name with author and year; the original citation of the family name with its author, year, reference and pagination; the valid type genus with author and date; the number of recognized genera in the family; the FAO family vernacular names in English, French and Spanish; family Synonyms with name, author, year, and pagination; Field Marks and Diagnostic Features of members of the family; an account of the natural history of the family under separate sections covering Distribution, Habitat and Biology; a section on Interest to Fisheries and Human Impact, a synopsis of the human issues affecting shark families; Local Names when available; a Literature section covering references to the entire family; a Remarks section mostly with systematic comments; and a Key to Genera, when families have more than one genus.

Generic accounts include the valid modern form of the genus name with author and year; the original citation of the genus or subgenus, with its author, year, reference and pagination, and, if a subgenus, the original genus name with author and year that the subgenus was originally placed in; the type species and means of designating it (for example, by original designation, monotypy, absolute tautonymy, or subsequent designation); the number of recognized species in the genus; the synonyms of genera, with their rank (genus, subgenus, or other genus-group ranking such as W.H. Leigh-Sharpe's 'pseudogenera'), author, year, pagination, and genus they were described in if originally ranked as subgenera or equivalents; FAO Names if they exist; sometimes Field Marks if genera are large and distinctive; Diagnostic Features of the genus; a Key to Species if the genus has more than one species (is not monotypic); and a Remarks section where necessary.

Species accounts include the valid modern names of the species, with author and date; the original citation of the species (or subspecies), with its author, year, reference

pagination; the holotype, syntypes, lectotype or neotype of each species (paratypes are not listed in the present account), including the total length and sex of the specimen, its institutional deposition, and its catalogue number; the type locality including the location, coordinates and depth if available, where the holotype, syntypes, lectotype or neotype were caught; Synonyms of the species, including their names, authors and dates; a section listing other scientific names recently in use; the English, French, and Spanish FAO Names for the species; a lateral view illustration, and often other useful illustrations (lateral view drawings are given of each shark species, usually ventral views of heads, and often teeth and denticles of the shark in question); Field Marks; Diagnostic features (except in monotypic genera); Distribution, including a map; Habitat; Biology; Size; Interest to Fisheries and Human Impact; Local Names when available; a Remarks section when necessary; and Literature.

Synonyms include only true taxonomic synonyms of the valid family, genus and species given. For species, another category, **Other Combinations**, is provided for common misidentifications of a given species with another, valid species (for example, ***Carcharhinus brachyurus*** was often termed ***C. remotus***, but the latter is a junior synonym of ***C. acronotus***) as well as commonly used combinations that place a valid species in different genera (for example, ***Odontaspis taurus*** or ***Eugomphodus taurus*** for ***Carcharias taurus***).

FAO Family and Species Names. English, French and Spanish names for each family and species, primarily for use within FAO, were selected by the following criteria: (a) each name applies to a single family or species worldwide; (b) the name conforms with FAO spelling nomenclature; (c) the name conforms to prior usage when possible. FAO names are not intended to replace local species names, but are necessary to overcome the confusion caused by the use of a single name for more than one species or several names for one species. The FAO names used here conform with prior FAO usage and when possible and appropriate national and international checklists and reviews of species such as Whitley (1940), Fowler (1966-1970), Shiino (1972, 1976), Hureau and Monod (1973), Smith (1975), Robins et al. (1980, 1991a, b), and Lindberg, Heard and Rass (1980). The French names were selected jointly with Dr J.C. Quéro, Institut Scientifique et Technique de Pêches Maritimes, Ministère de la Marine Marchande, La Rochelle, France, and for recently discovered species with Dr B. Seret, Museum National d'Histoire Naturelle, Paris. When possible, the names selected correspond to official French species nomenclature established by the Direction des Pêches Maritimes. The selection of Spanish names presented considerable difficulties due to the lack of denominations for many species. Wherever possible, the "official" Spanish names adopted by F. Lozano in his book "Nomenclature ictiologica", Madrid, 1963, were used, along with names for additional species coined by Dr R. Bonfil, Fisheries Centre, University of British Columbia, Vancouver.

The broader use of 'shark' here for all living cartilaginous fishes is noted above. The term 'shark' is broadly and popularly used as a catchall term in English for all living members of the Class Chondrichthyes that are not batoids or chimaeras, although guitarfishes (Rhinobatidae) are also termed 'sand sharks', chimaeras are termed 'ghost sharks' or 'silver sharks', and even certain aquarium teleosts (some loaches, Cobitidae) are termed 'sharks'. The French 'requin' and Spanish 'tiburón' are comparable general terms to 'shark'. Several names not incorporating 'shark' or its French or Spanish equivalents are mostly used only for sharks and not for other fishes; these include the English 'dogfish', 'smoothhound', 'tope', 'porbeagle' and 'hammerhead'. However, 'freshwater dogfish' is a regional name for the bowfin, ***Amia calva***, in the USA. 'Wobbegong' is adapted from an Australian Aboriginal term for sharks of the genera ***Eucrossorhinus***, ***Orectolobus*** and ***Sutorectus***). French 'roussette', 'emissole', 'renard', 'milandre', 'marteau', and 'griset', and Spanish 'gato', 'cazón', 'tollo', 'pintarroja', 'tintorera', and 'cornuda', are similar terms for certain kinds of sharks.

Usage of local names for different kinds of sharks varies from country to country. 'Catshark' is used for members of the Scyliorhinidae and sometimes related families (such as Proscylliidae) in the United States, but also for various orectoloboids in Australia. 'Dogfish' is variably used for members of the families Squalidae ('spiny dogfishes'), Scyliorhinidae (especially ***Scyliorhinus***), and Triakidae ('smooth dogfishes', ***Mustelus* spp.**). 'Sand shark' may refer to Odontaspididae (especially ***Carcharias taurus***, the 'sand tiger shark' of the eastern USA, called 'ragged-tooth shark' in South Africa and 'grey nurse shark' in Australia), to Triakidae (especially to ***Mustelus* spp.**) off the western USA, or guitarfishes off South Africa. In the present Catalogue 'catshark' is restricted to members of the Scyliorhinidae and Proscylliidae ('false catsharks' are members of the Pseudotriakidae), 'dogfish' to the Squaliformes, and 'sand sharks' in the form of 'sand tiger shark' to the Odontaspididae. Orectoloboid 'catsharks' are termed 'carpet sharks', and 'sand sharks' and 'smooth dogfishes' of the triakid genus ***Mustelus*** are termed 'smoothhounds' (except for ***M. antarcticus***, the Australian 'gummy shark').

Keys, Field Marks and Diagnostic Features. These sections include identification data in different forms. Keys to orders, families, genera and species are standard dichotomous biological keys that are followed in steps of alternate choices to single out the taxa covered. Diagnostic Features are comprehensive lists of characters at the ordinal, familial, generic, and species level, with the character choice generally limited to external characters, particularly at the species level, because of space considerations and their primary purpose of identification rather than indication of relationships. Some exceptions are taken with higher taxonomic levels, to support a solid, sound higher classification. The Diagnostic Features sections are hierarchical, with characters at the ordinal level not duplicated at the family, genus and species levels. Monotypic orders with one family (such as Pristiophoriformes), monotypic families with one genus (Chlamydoselachidae) or monotypic genera with one species (***Carcharodon***) all have the Diagnostic Features section present only in the highest taxon covered. In a monotypic order, Diagnostic Features are omitted in the account of its single family; in a monotypic family, they are omitted from its single genus; and in a monotypic genus, they are omitted from its single species.

Field Marks generally include a few obvious characters of use in field identification, extracted from Diagnostic Features at various levels, but included in a separate section. Field Marks are listed at the ordinal, familial and species levels, and occasionally the generic level in cases of large genera with many species. The arrangement of Field Mark characters is semihierarchical and pragmatic and may include characters from a higher level such as an order in lower level taxonomic accounts such as those of species.

An example of the different application of Diagnostic Features and Field Marks is indicated with the sevengill shark, ***Heptranchias perlo***. Starting with the order Hexanchiformes, Diagnostic Features applicable to it are given at decreasing hierarchical levels through the family Hexanchidae and genus ***Heptranchias*** (a monotypic genus). However, the species account of ***H. perlo*** also has a short Field Marks section, "A narrow-headed, big-eyed, small seven-gilled shark with one dorsal fin, no dark spots, and a black blotch on the dorsal fin (inconspicuous in large individuals)", that can suffice to identify it without additional information, although this is available in the Diagnostic Features sections as needed. In some large families such as the Carcharhinidae the Field Marks for an easily recognized species such as ***Carcharhinus longimanus*** may not repeat familial and ordinal characters but merely indicates its family and unique characters.

Distribution and Maps. Geographic distributions for nearly all species of sharks are given by listing the countries off the coasts of which the sharks occur, and, in some instances with large countries (Australia) or those with coasts fronting more than one ocean (e.g. Mexico, South Africa), more detailed data are given when available. In compiling distributional data and preparing maps it was noted that the distributions of many wide-ranging coastal species are very spottily known as present, especially with species occurring in the Indian and western Pacific Oceans. In many cases gaps in distribution may not indicate absence of a given species but absence of knowledge. Continental slope shark faunas are poorly known for much of the world, and a number of deepwater species probably have wider ranges than are currently known. A recent example of this is the capture of the Australian and New Zealand sharks ***Proscymnodon plunketi*** and ***Parmaturus macmillani*** on submarine ridges south of Madagascar and east of South Africa by a commercial bottom trawler in 1999. The locality data in the literature and on specimen labels is often very general and imprecise; and even with bottom or pelagic trawl hauls with detailed oceanographic data and accurate coordinates, hauls may be of such long duration that locations are approximate. Longline locality data can be more accurate than trawls thanks to GPS or other navigation systems, but often is not accurate because detail data were not collected when specimens were landed. Hence distributional data and maps presented here are to be considered as rough approximations of distribution. Some of the data comes from a database (approximately 14 000 records) of shark distribution compiled by the writer and plotted with commercial digital mapping programmes and a spreadsheet-based programme for southern Africa developed by the writer. Much effort was made to screen out errors of shark distribution, based on misidentifications of species, at a cost of presenting distributional lists and maps that are spotty if more accurate. An extreme example is discussed in detail under ***Glyphis gangeticus*** (Carcharhinidae; see volume 3).

Elasmobranchs are primarily marine organisms, but a number of species readily enter brackish to almost freshwater estuaries, river mouths, lagoons and bays; a few species of the family Carcharhinidae and many batoids occur far up rivers and in freshwater lakes with connections to the sea. Records of elasmobranchs in fresh water were reviewed by Compagno and Cook (1995), who classified species as *euryhaline* (occurring in fresh, brackish and salt water, and found far from the sea), *marginal* (peripheral species penetrating fresh water in estuaries or the lower reaches of rivers, but not extending far up river), *brackish* (found in water of reduced salinity, but not in fresh or salt water), and *obligate* (found in fresh water only, and not in salt water).

In the case of certain carcharhinid sharks (the bull shark, ***Carcharhinus leucas*** and the river sharks, ***Glyphis* spp.**) that are known from verifiable records from entirely freshwater parts of rivers and freshwater lakes, the names of major river systems and lakes where they occur are noted. There are various freshwater records of other members of the family Carcharhinidae and several other families of nonbatoid sharks (including the zebra shark family, Stegostomatidae), but some of these records may be of marginal species from semi-brackish lower reaches of rivers and estuaries and may indicate that the species involved are tolerant of reduced salinities but are not truly euryhaline. Some of these carcharhinid freshwater records may be based on ***C. leucas*** or ***Glyphis*** species rather than the species indicated (such as ***C. melanopterus*** or ***C. hemiodon***). Batoids are more numerous than nonbatoid sharks in fresh water, including several sawfish (Pristidae), potamotrygonid stingrays, and several dasyatid stingrays. Many stingrays are obligate freshwater species.

For the compilation of maps of distribution in the present catalogue, a new approach has been undertaken to better represent the real distribution of each species. The main source of information for building the maps was that given in each species' account under **Habitat** and **Distribution**. It was possible to use this information using a modern GIS approach after standardizing all the terminology provided in the species accounts following the method briefly explained below.

For those species that show some type of relationship with the ocean bottom, the depth information given under **Habitat** has been translated into pre-chosen depth ranges using the tables shown below. These depth ranges were extracted from a single data set, i.e. GEBCO Digital Atlas (Natural Environment Research Council. 1994. Digital version of the IOC/IHO General Bathymetric Chart of the Oceans) and transferred to a GIS. Then, geographic distribution information on localities and oceanographic provinces were extracted from WVS (World Vector Shoreline, at scale 1:43.000.000) and ArcWorld (distributed by ESRI (Environmental Systems Research Institute), 380 New York St., Redlands, California, 92373-8100, USA) and overlaid with the previous information to produce the final output. With this methodology, the maps for bottom-dwelling or coastal species give a better idea of the spatial coverage of their distribution as inferred from our current knowledge. This can give an approximate idea of the relative size of different stocks among and between species.

Criteria used to define upper and lower limits of habitat when compiling maps of distribution.

Table 1
Lower limits (m) used for different marine habitats

Coast-line	Coastal area	Upper continental shelf	Deep shelf	Upper slope	Maximum limit of the slope
0	50	100	200	500	1 000

If specific depth ranges were given under **Habitat**, such values were used after rounding them according to Table 2 below, using the closest values found. In cases of values larger than 1 000 m, the 1 000 m isobath was used.

Table 2
Limits used to convert upper and lower limits of depth ranges (m)

For original depth data in the interval	Limit used
0-30	0
31-75	50
76-150	100
151-250	200
251-751	500
751 and below	1 000

If more than one bathymetric range of distribution was mentioned (e.g. different ranges for adults and juveniles), the widest range given was used. However, when different depth ranges existed for different regions or areas, each was chosen and plotted independently.

If no depth data was mentioned in the original account, textual descriptions have been translated using the criteria in Table 3 below.

Table 3
Upper and lower limits of depth ranges (m) used for textual descriptions of habitat

Fot text indicating	Upper limit	Lower limit
Shelf or continental shelf	0	200
Shallow waters, inshore waters, coastal	0	50
Continental shelf, neritic	0	200
Upper shelf	0	100
Deep shelf	100	200
Slope	200	1 000
Upper slope	200	500
Deep slope	500	1 000

Terms like benthic, pelagic, surface, bottom deeper water, deepish, great depths included under **Habitat** were not used. If more than one type of habitat was given, the one corresponding to the widest possible range of distribution was used.

For species with an oceanic habitat, the main source of information was their known geographic distribution irrespective of depth. Thus, the maps of oceanic species give only information on distribution.

All data were transferred to hand drawn maps which were directly digitized and georeferenced using WVS and ArcWorld for the exact plotting of localities and oceanic provinces.

Where necessary, maps show two different kinds of distribution for a given species. Dark red is used to show the **known** and certain distribution of a species from reliable records, whilst light red or orange is used to show the suspected or **uncertain** distribution of a species.

Maps presented in the Catalogue can be largely divided into two categories, Global (or world maps) and Regional maps. For better visualization, global maps include the species distribution and the land masses especially generalized and prepared from the WVS data set. The regional maps, in addition to the above, include the 200 m depth isobath as a reference of their depth distribution.

Note: Whenever the narrowness of the continental or insular shelves and the scale of the maps have caused parts of the distribution of a species to be undistinguishable, coloured arrows have been used on the map to point to such distribution areas.

Habitat. Habitat covers information on physical conditions where various sharks are found. The known depth range of the species (in metres), position in the water column, type of substrate occupied, and preferences relative to coasts are noted when available. In most cases data on salinity, oxygen content, and specific temperature of the water in which they occur was not available or was not in an easily usable form and has not been regularly compiled here.

Biology. Includes data on population structure and dynamics, reproduction, behaviour, sociobiology, age and growth, and feeding. Compilation of these data suggests that very few species of sharks are biologically well known, and even in the piked dogfish (***Squalus acanthias***), perhaps the best-known of living cartilaginous fishes, there are areas of its biology that are very poorly known (such as its behaviour and sociobiology). There is a bias in available natural history data towards reproductive biology, feeding, and fisheries-related subjects such as age and growth, and correspondingly little on ecology, behaviour and sociobiology.

Size. All size data are given as total lengths; this is the measurement most often used as an independent variable and standard measurement in the shark literature, although particularly in fisheries papers precaudal lengths, fork lengths, and other measurements have been used from choice or necessity. Unfortunately shark workers have not agreed on a standard method of measuring total length, so total lengths from different sources in the literature may not be strictly comparable. I prefer and advocate as a standard method a direct measurement, in which the shark is held belly down with its dorsal caudal-fin lobe depressed into line with its body axis and total length measured as a point to point distance (not over the curve of the body) from the snout tip to the tip of the dorsal caudal-fin lobe (see also Compagno, 1988). This method lends itself readily to quick use of a fishboard with a perpendicular front bar or plate to index the shark's snout against, a one metre or two metre ruler or folding rule slipped under the shark, or even a steel or cloth tape, and avoids the trouble of computation and possible errors and loss of data.

A comparable computational method adding the precaudal length and dorsal caudal-fin margin is advocated by Sadowsky (1968). Bigelow and Schroeder (1948) and Springer (1964) measured total length from the snout tip along the body axis to a vertical projection from the tip of the dorsal caudal-fin lobe with the caudal fin in a 'natural position'. Bass (1973) advocated a computational method which adds the precaudal length to a number computed by multiplying the length of the dorsal caudal-fin margin by a constant (1.0 or less, 0.97 and 0.80 were the numbers) that corrects for the different 'natural angles' of the caudal axis to the body axis in different species. The method advocated

here and in Compagno (1984, 1988) dispenses with all computation and avoids arbitrary constants to correct for supposed 'natural positions' of the caudal axis as well as the difficulties in obtaining accurate vertical projections from the caudal tips held in 'natural positions'. Also, with the present method a comparable measurement can be obtained for all or most sharks, rays and chimaeras, although there are problems with species that have greatly elongated filamentous snouts or tails. In contrast methods using 'natural positions' arbitrarily generate incompatible total lengths for different groups of sharks, and also do not take into account changes in the angle of the caudal axis when sharks swim or as they grow (Compagno, 1988).

Total length data presented includes maximum size, size at maturity (in some cases, a size range at maturity, when abundant data were available) and maximum size for both sexes (as sexual dimorphism in size is nearly universal among sharks, with females usually attaining larger sizes than males, except for some scyliorhinid catsharks where the reverse occurs), and size at birth or hatching. Sometimes size at sexual maturity for either or both sexes is not known, in which cases reported minimum and maximum sizes of adult individuals are given. In some cases maximum size exceeds that recorded for either sex, in which case the sex of the outsized individual or individuals representing the maximum size measurements was not indicated. In some poorly known species only immature individuals are known, in which case the hypothetical maximum adult size is almost certainly larger than the known immature maximum (no cases are known of adult sharks that are considerably smaller than large immature individuals of the same sex, unlike some other vertebrates). The writer tends to discount old, unverifiable size records of some well-known species, but mentions them as such.

Some fisheries biologists and shark researchers use precaudal length (PCL) or fork length (FL) as standard lengths instead of total length. The first eliminates problems with sharks having damaged caudal fins but is difficult to determine on some sharks with weakly defined upper caudal-fin origins. The second is only applicable to species with notched caudal fins and defined upper and lower postcaudal-fin margins.

In some species length-weight equations are presented, usually of the form $W = a + TL^b$, where W is weight, a and b are constants, and TL is total length.

Interest to Fisheries and Human Impact. This section is expanded in scope from the 1984 catalogue, and in addition to fisheries information includes many other aspects of human interaction with sharks. In this section data on localities of fisheries, gear used, and uses of the particular species are noted when available. National fisheries data for sharks is often sketchy and combined for a number of species. Thus, catch statistics were available for relatively few species of sharks but are noted when available, with particular emphasis on data from those species reported to FAO. Additional data for sharks are increasingly available from national and regional fisheries bodies, but were used in a very limited way here due to time and literature constraints.

Initially data from the hard-copy FAO species yearbooks were used for compiling shark fisheries data on spreadsheets, as in Compagno (1990c), but this has been greatly facilitated by the advent of FAO FishStat, a data-handling and analytical software package which can be downloaded free from the FAO Fisheries website (http://www.fao.org/fi). FishStat handles a variety of annually revised FAO fisheries statistics databases and can export files into other programmes such as spreadsheets and databases.

Conservation and management issues and importance of sharks to human recreation including ecotouristic diving and visits to public aquaria are covered in this section. It also includes aspects of shark behaviour that were formerly placed in the biology section, that is, shark encounters with people. The 1984 Catalogue used the universal term 'shark attack' for encounters when sharks bite or otherwise injure people. I have tried to avoid this term in this Catalogue because of its extremely negative, subjective, and misleading connotations, along with a few other hyperbolic terms such as 'maneater'. I realize that the general public and especially the news and entertainment media will continue to use these emotive terms for a long time despite the limited realities. It is challenging to think of ways of discussing the subject without the dreadful, gory 'shark attack' image being brought forth, but it does help to build alternate and more realistic images of a minuscule objective phenomenon. This is discussed in more detail under Shark Encounters in the third volume of the Catalogue.

Local Names. A change from the 1984 Catalogue is that local or regional family and species names in various languages are generally listed when available under a separate local names heading. These were compiled from the same sources used for FAO names (see above), but what is presented here is not comprehensive and represents what was readily available to the writer. Many species have no vernacular names whatsoever or are lumped under catchall names, while some sharks such as the white and basking sharks have dozens of names. Obviously some sharks have more of an impact or are much more familiar than others, and these get more names (some of which seem like curses or jokes). Wherever possible local names are presented for important wide-ranging sharks, including fisheries species such as ***Galeorhinus galeus*** ('school shark' in Australia, 'tiburón vitaminico' or 'vitamin shark' in Uruguay and Argentina, 'soupfin' or 'oil shark' off the Pacific USA and Canada, and 'vaalhai' in South Africa) and ***Carcharias taurus***, the very popular shark for fisheries, public aquaria, ecotourism, and conservation (termed 'ragged-tooth shark' in South Africa, 'grey nurse shark' in Australia, 'requin sable' in West Africa, and 'sand tiger shark' or 'sand shark' off the east coast of the United States). The broadening interest in sharks and urgent need to acquire species-specific data for their management and conservation should encourage fisheries biologists and other researchers to compile local names for their own countries or regions, and add to our sketchy knowledge of local names worldwide.

Remarks. Important information, especially on systematics and nomenclature are given in the remarks section.

Literature. References cited here include specific works with important information for each species and family as well as comprehensive accounts, but are not intended as a comprehensive bibliography. Reference sections have been updated and given more extensive coverage than the 1984 Catalogue.

1.2 Technical Terms and Measurements

1.2.1 Picture Guide to External Terminology of Sharks

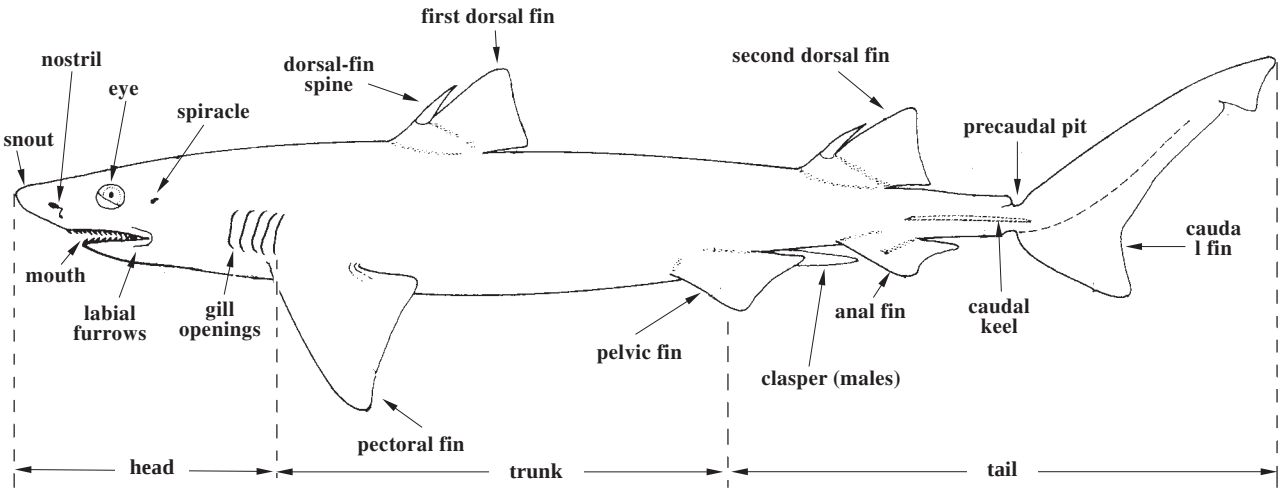

Fig. 2 Lateral view

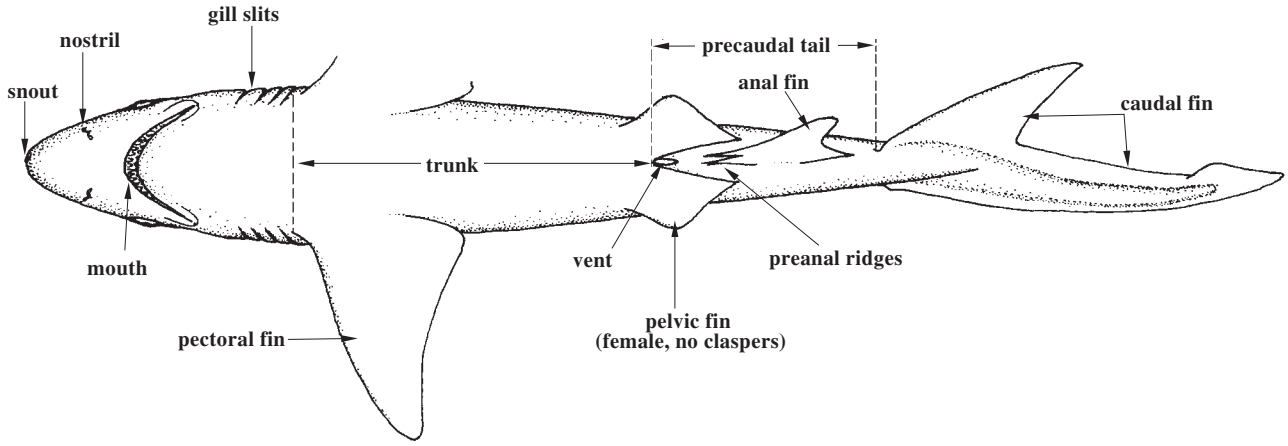

Fig. 3 Ventral view

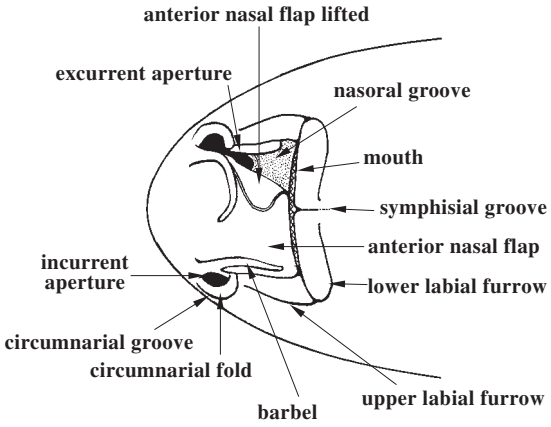

Fig. 4 Head of an orectoloboid shark (ventral view)

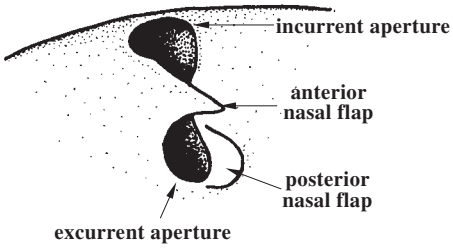

Fig. 5 Nostril

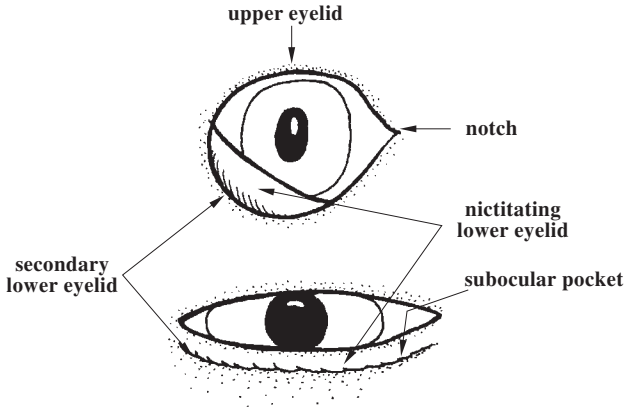

Fig. 6 Eyes

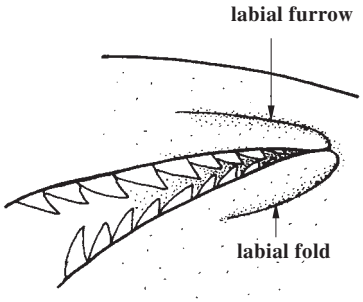

Fig. 7 Mouth corner

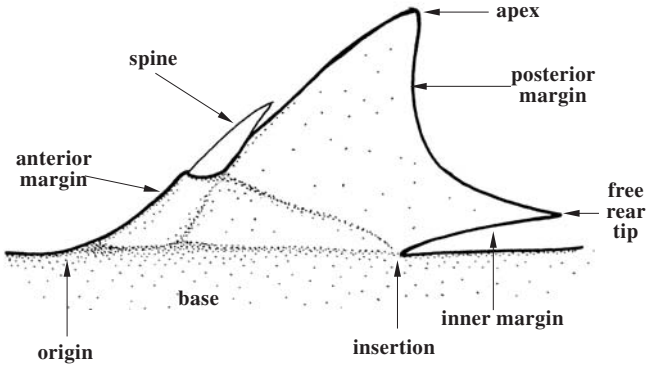

Fig. 8 Dorsal fin

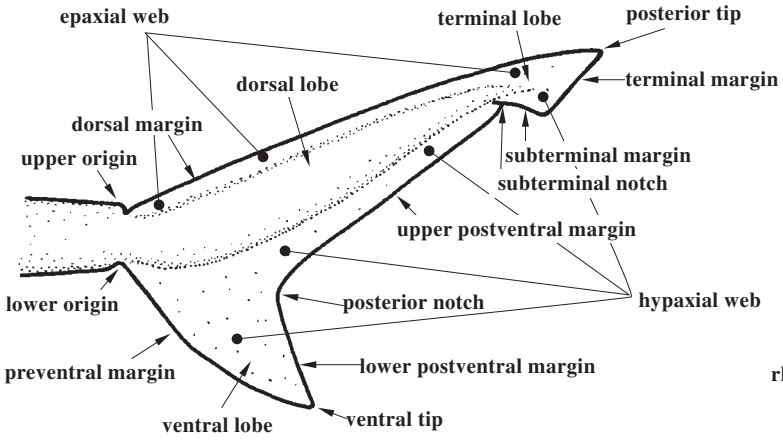

Fig. 9 Caudal fin

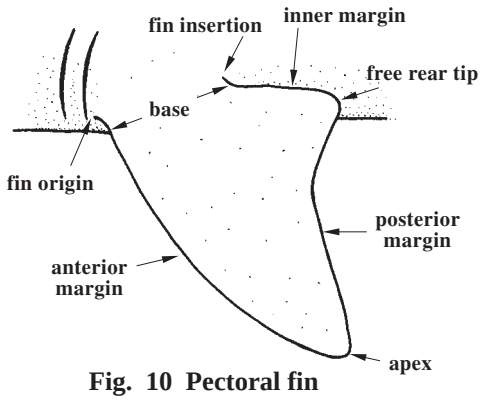

Fig. 10 Pectoral fin

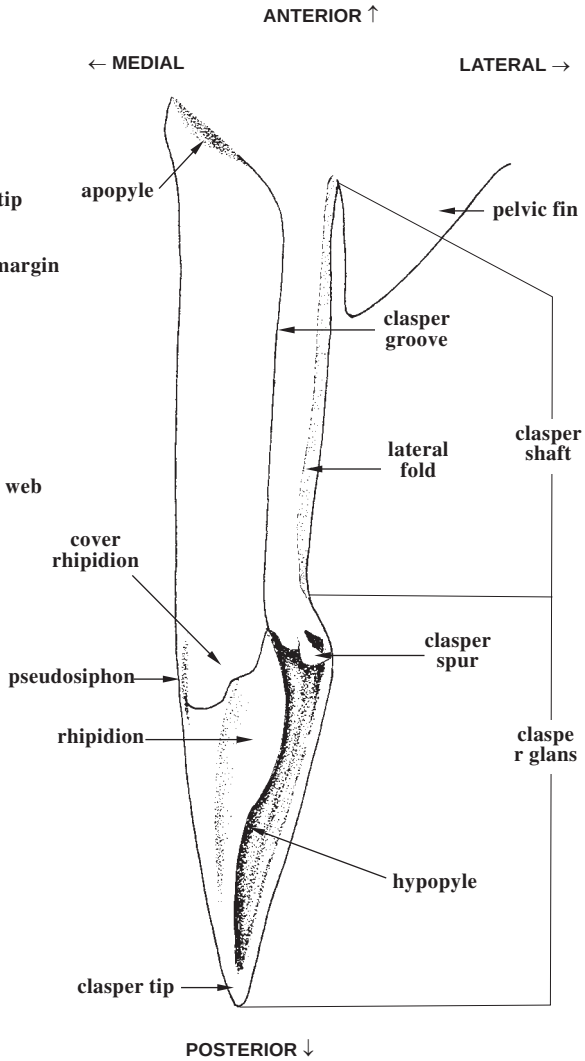

Fig. 11 Dorsal view of clasper (lamnid shark)

1.2.2 Picture Guide to Skeletal Terminology of Sharks

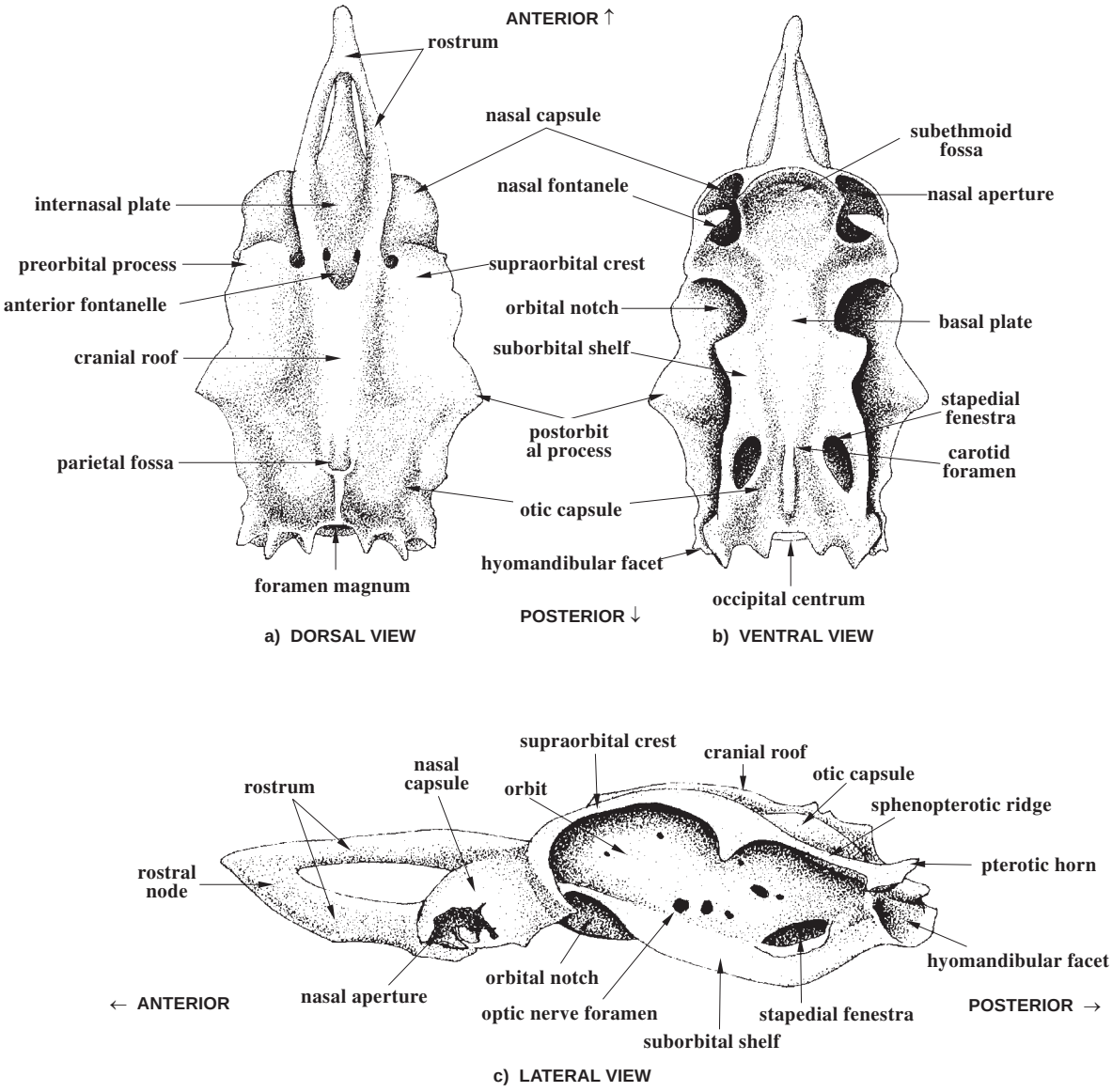

Fig. 12 Chondrocranium

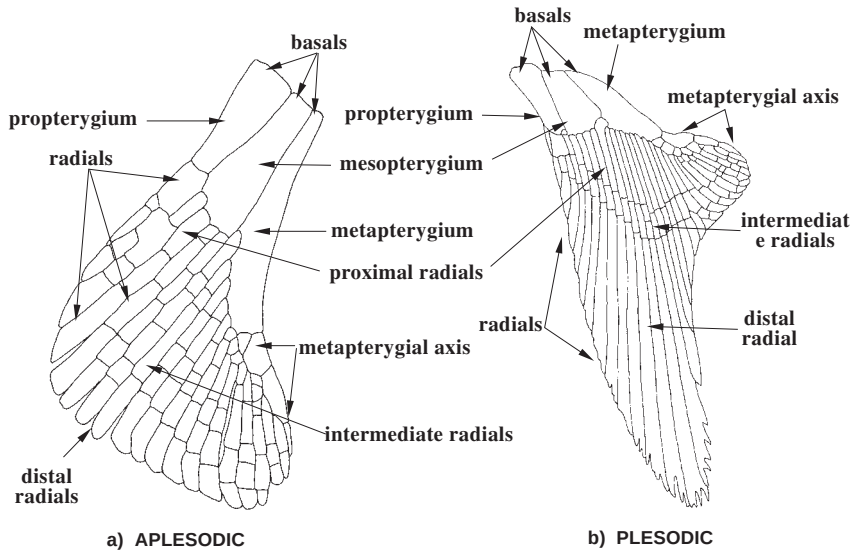

Fig. 13 Aplesodic and plesodic pectoral fins

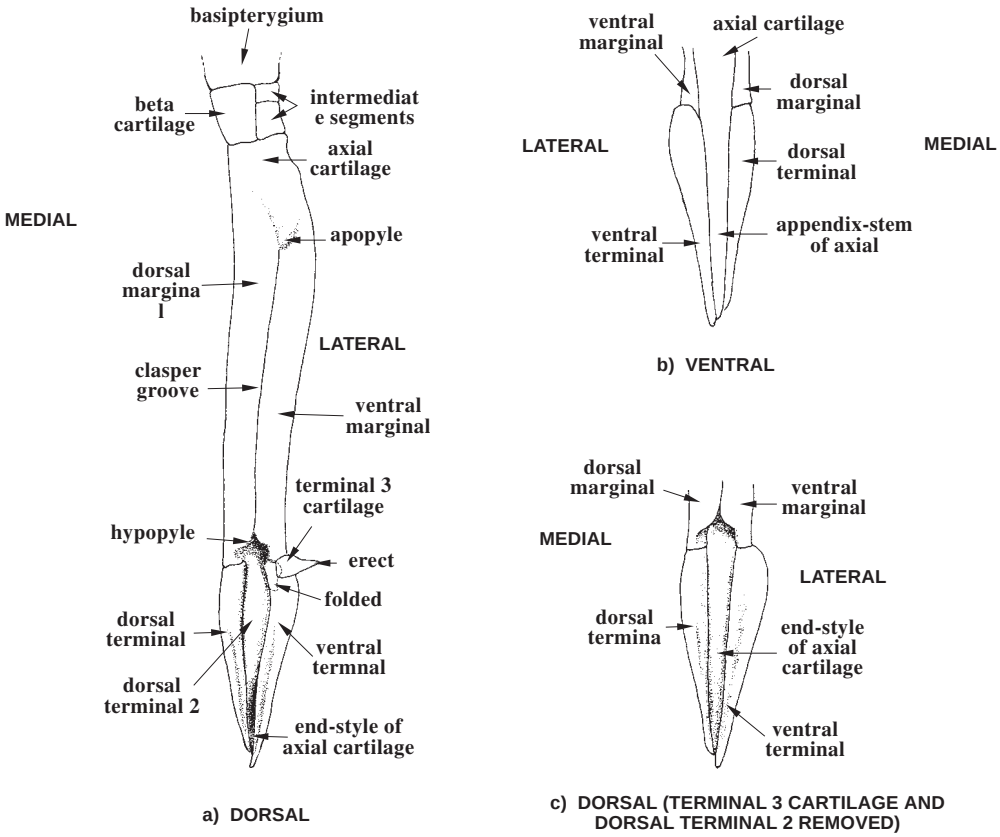

Fig. 14 Clasper skeleton of lamnid shark (right side)

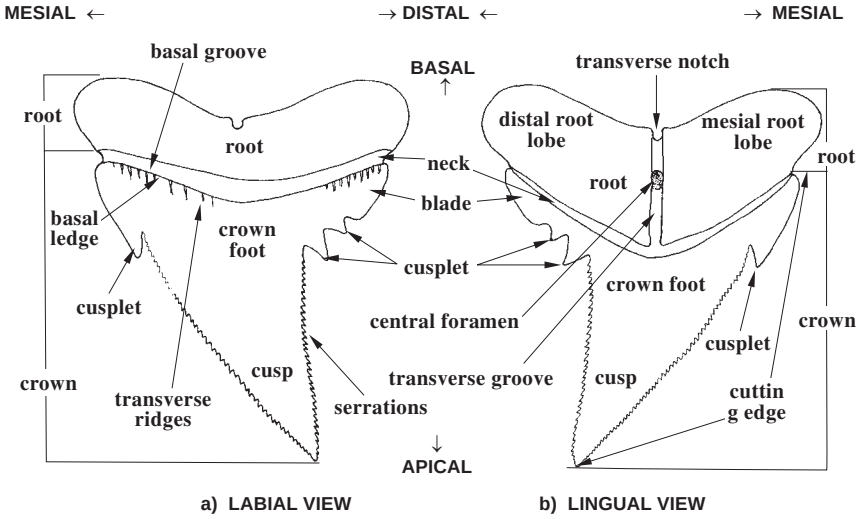

Fig. 15 Tooth terminology (left upper anterolateral tooth)

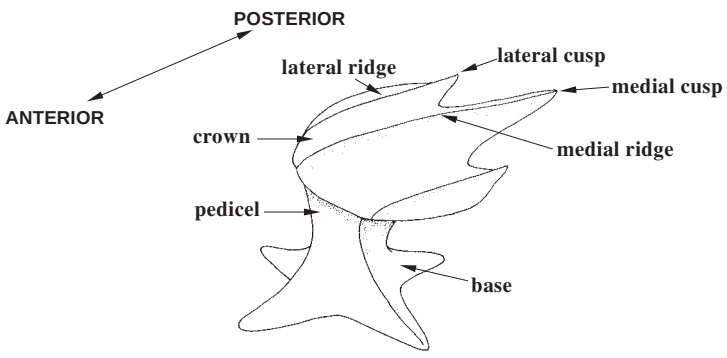

Fig. 16 Oblique anterolateral view of lateral trunk dermal denticle

1.2.3 Measurements Used for Sharks

TL = TOTAL LENGTH
FL = FORK LENGTH
PCL = PRECAUDAL-FIN LENGTH
PD2 = PRE-SECOND DORSAL-FIN LENGTH
PD1 = PRE-FIRST DORSAL-FIN LENGTH
HDL = HEAD LENGTH
PG1 = PREBRANCHIAL LENGTH
PSP = PRESPIRACULAR LENGTH
POB = PREORBITAL LENGTH
PP1 = PREPECTORAL-FIN LENGTH
PP2 = PREPELVIC-FIN LENGTH
SVL = SNOUT-VENT LENGTH
PAL = PREANAL-FIN LENGTH
IDS = INTERDORSAL SPACE
DCS = DORSAL CAUDAL-FIN SPACE
PPS = PECTORAL-FIN PELVIC-FIN SPACE
PAS = PELVIC-FIN ANAL-FIN SPACE
ACS = ANAL-FIN CAUDAL-FIN SPACE
PCA = PELVIC-FIN CAUDAL-FIN SPACE
VCL = VENT CAUDAL-FIN LENGTH

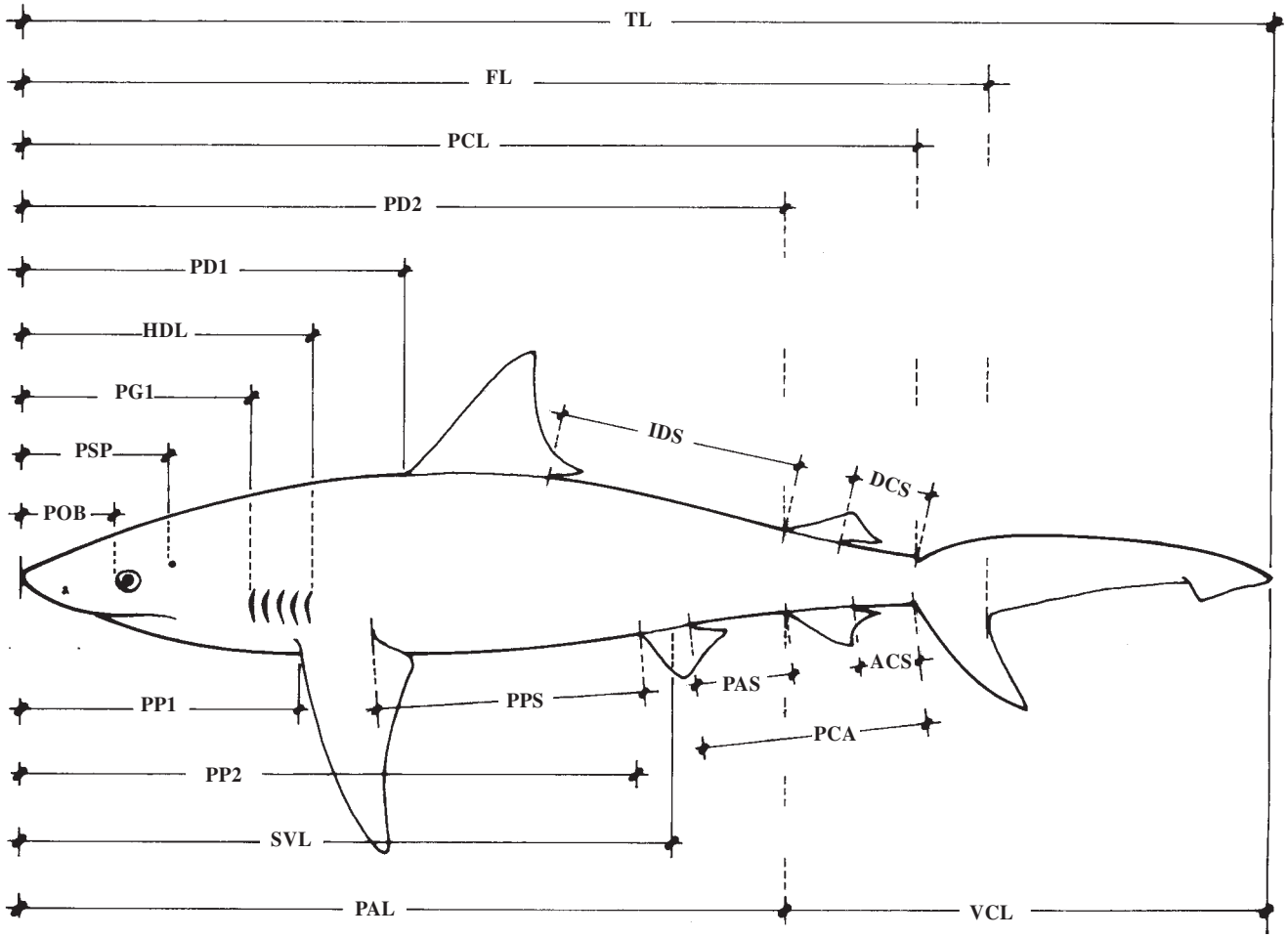

Fig. 17 Main longitudinal measures

PRN = PRENARIAL LENGTH
POR = PREORAL LENGTH
EYL = EYE LENGTH
EYH = EYE HEIGHT
ING = INTERGILL LENGTH
GS1 = FIRST GILL SLIT HEIGHT
GS2 = SECOND GILL SLIT HEIGHT
GS3 = THIRD GILL SLIT HEIGHT
GS4 = FOURTH GILL SLIT HEIGHT
GS5 = FIFTH GILL SLIT HEIGHT
GS6 = SIXTH GILL SLIT HEIGHT
GS7 = SEVENTH GILL SLIT HEIGHT
P1A = PECTORAL-FIN ANTERIOR MARGIN
P1R = PECTORAL-FIN RADIAL LENGTH
P1B = PECTORAL-FIN BASE
P1I = PECTORAL-FIN INNER MARGIN
P1P = PECTORAL-FIN POSTERIOR MARGIN
P1H = PECTORAL-FIN HEIGHT
P1L = PECTORAL-FIN LENGTH
SOD = SUBOCULAR POCKET DEPTH

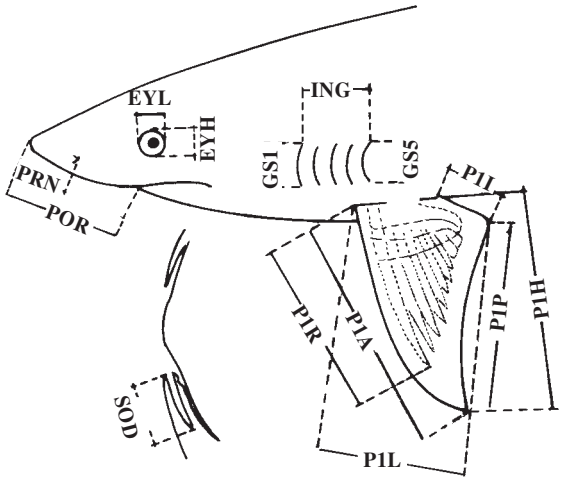

Fig. 18

CDM = DORSAL CAUDAL-FIN MARGIN
CPV = PREVENTRAL CAUDAL-FIN MARGIN
CPU = UPPER POSTVENTRAL CAUDAL-FIN MARGIN
CPL = LOWER POSTVENTRAL CAUDAL-FIN MARGIN
CFW = CAUDAL-FIN FORK WIDTH
CFL = CAUDAL-FIN FORK LENGTH
CST = SUBTERMINAL CAUDAL-FIN MARGIN
CSW = SUBTERMINAL CAUDAL-FIN WIDTH
CTR = TERMINAL CAUDAL-FIN MARGIN
CTL = TERMINAL CAUDAL-FIN LOBE

D1L = FIRST DORSAL-FIN LENGTH
D1A = FIRST DORSAL-FIN ANTERIOR MARGIN
D1B = FIRST DORSAL-FIN BASE
D1H = FIRST DORSAL-FIN HEIGHT
D1I = FIRST DORSAL-FIN INNER MARGIN
D1P = FIRST DORSAL-FIN POSTERIOR MARGIN

D2L = SECOND DORSAL-FIN LENGTH
D2A = SECOND DORSAL-FIN ANTERIOR MARGIN
D2B = SECOND DORSAL-FIN BASE
D2H = SECOND DORSAL-FIN HEIGHT
D2I = SECOND DORSAL-FIN INNER MARGIN
D2P = SECOND DORSAL-FIN POSTERIOR MARGIN

P2L = PELVIC-FIN LENGTH
P2A = PELVIC-FIN ANTERIOR MARGIN
P2B = PELVIC-FIN BASE
P2H = PELVIC-FIN HEIGHT
P2I = PELVIC-FIN INNER MARGIN [LENGTH]
P2P = PELVIC-FIN POSTERIOR MARGIN [LENGTH]

ANL = ANAL-FIN LENGTH
ANA = ANAL-FIN ANTERIOR MARGIN
ANB = ANAL-FIN BASE
ANH = ANAL-FIN HEIGHT
ANI = ANAL-FIN INNER MARGIN
ANP = ANAL-FIN POSTERIOR MARGIN

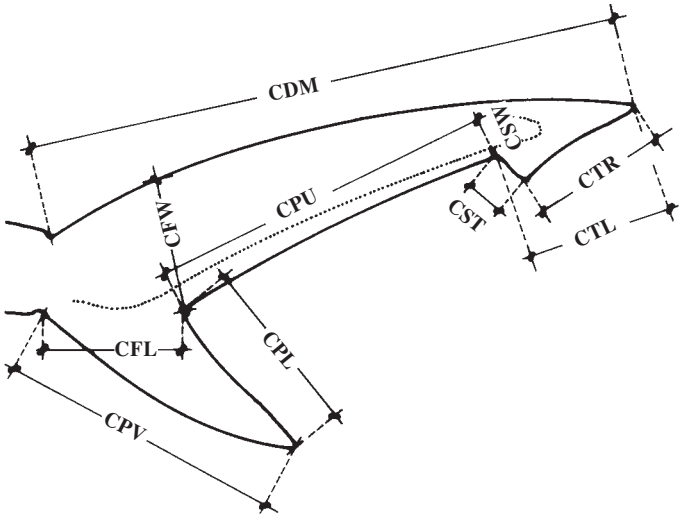

Fig. 19 Measurements of caudal fin

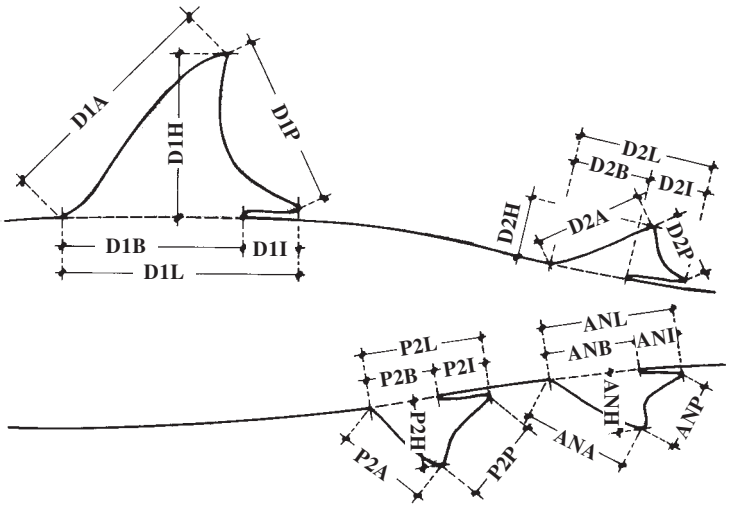

Fig. 20 Measurements of dorsal, pelvic and anal fins

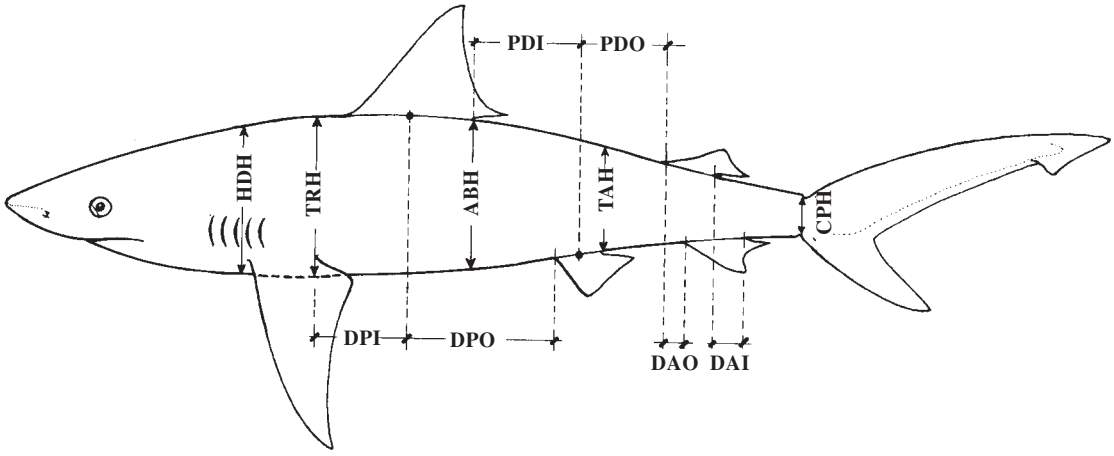

Fig. 21 Other common measurements

HDH = HEAD HEIGHT
TRH = TRUNK HEIGHT
ABH = ABDOMEN HEIGHT
TAH = TAIL HEIGHT
CPH = CAUDAL-FIN PEDUNCLE HEIGHT
DAI = SECOND DORSAL-FIN INSERTION ANAL-FIN INSERTION
DAO = SECOND DORSAL-FIN ORIGIN ANAL-FIN ORIGIN

DPI = FIRST DORSAL-FIN MIDPOINT PECTORAL-FIN INSERTION
DPO = FIRST DORSAL-FIN MIDPOINT PELVIC-FIN ORIGIN
PDI = PELVIC-FIN MIDPOINT FIRST DORSAL-FIN INSERTION
PDO = PELVIC-FIN MIDPOINT SECOND DORSAL-FIN ORIGIN

MOL = MOUTH LENGTH
MOW = MOUTH WIDTH
ULA = UPPER LABIAL-FURROW LENGTH
LLA = LOWER LABIAL-FURROW LENGTH
NOW = NOSTRIL WIDTH
INW = INTERNARIAL SPACE
ANF = ANTERIOR NASAL-FLAP LENGTH

CLO = CLASPER OUTER LENGTH
CLI = CLASPER INNER LENGTH
CLB = CLASPER BASE WIDTH

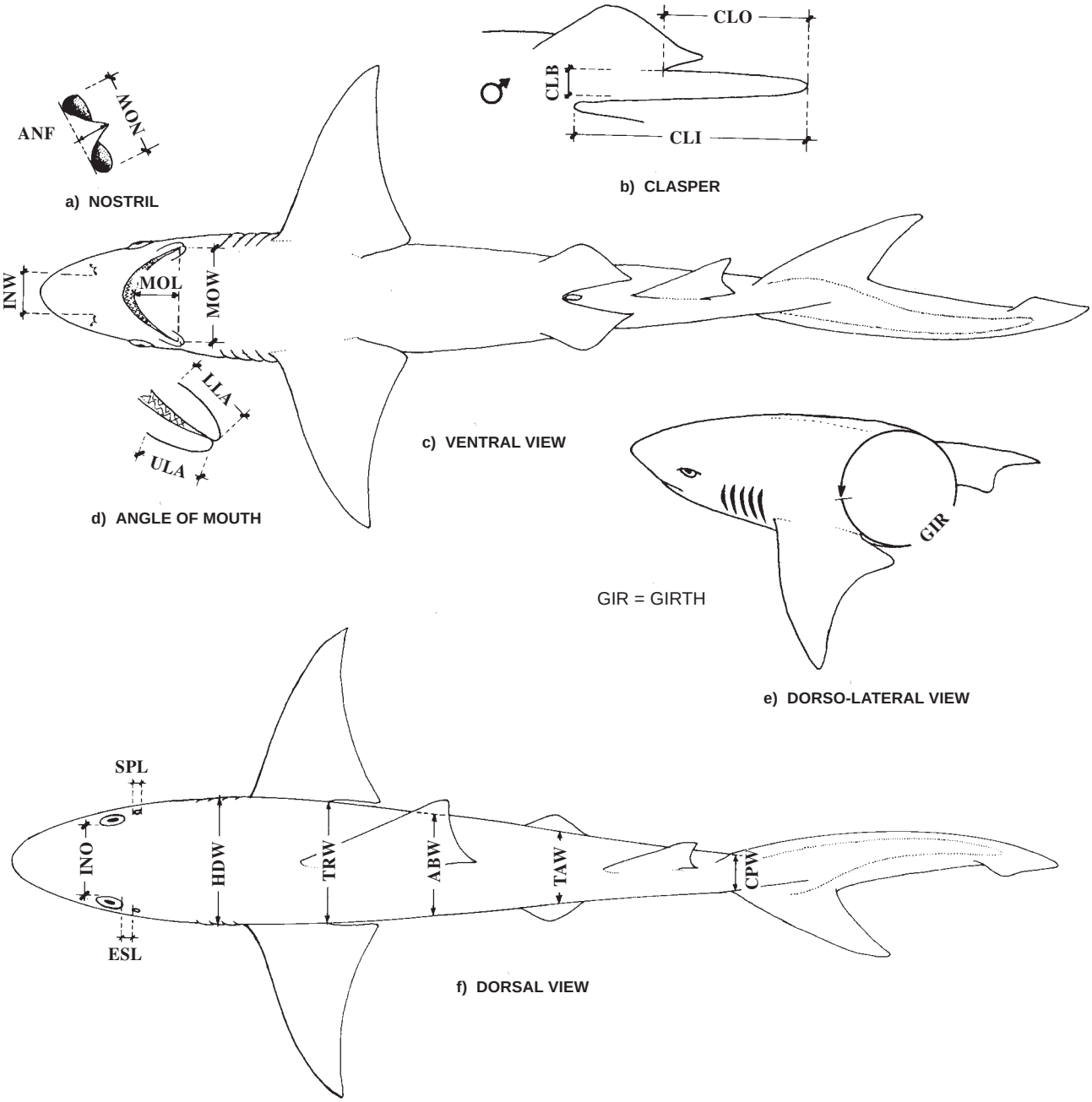

Fig. 22

INO = INTERORBITAL SPACE
SPL = SPIRACLE LENGTH
ESL = EYE SPIRACLE SPACE
HDW = HEAD WIDTH
TRW = TRUNK WIDTH
ABW = ABDOMEN WIDTH
TAW = TAIL WIDTH
CPW = CAUDAL-FIN PEDUNCLE WIDTH

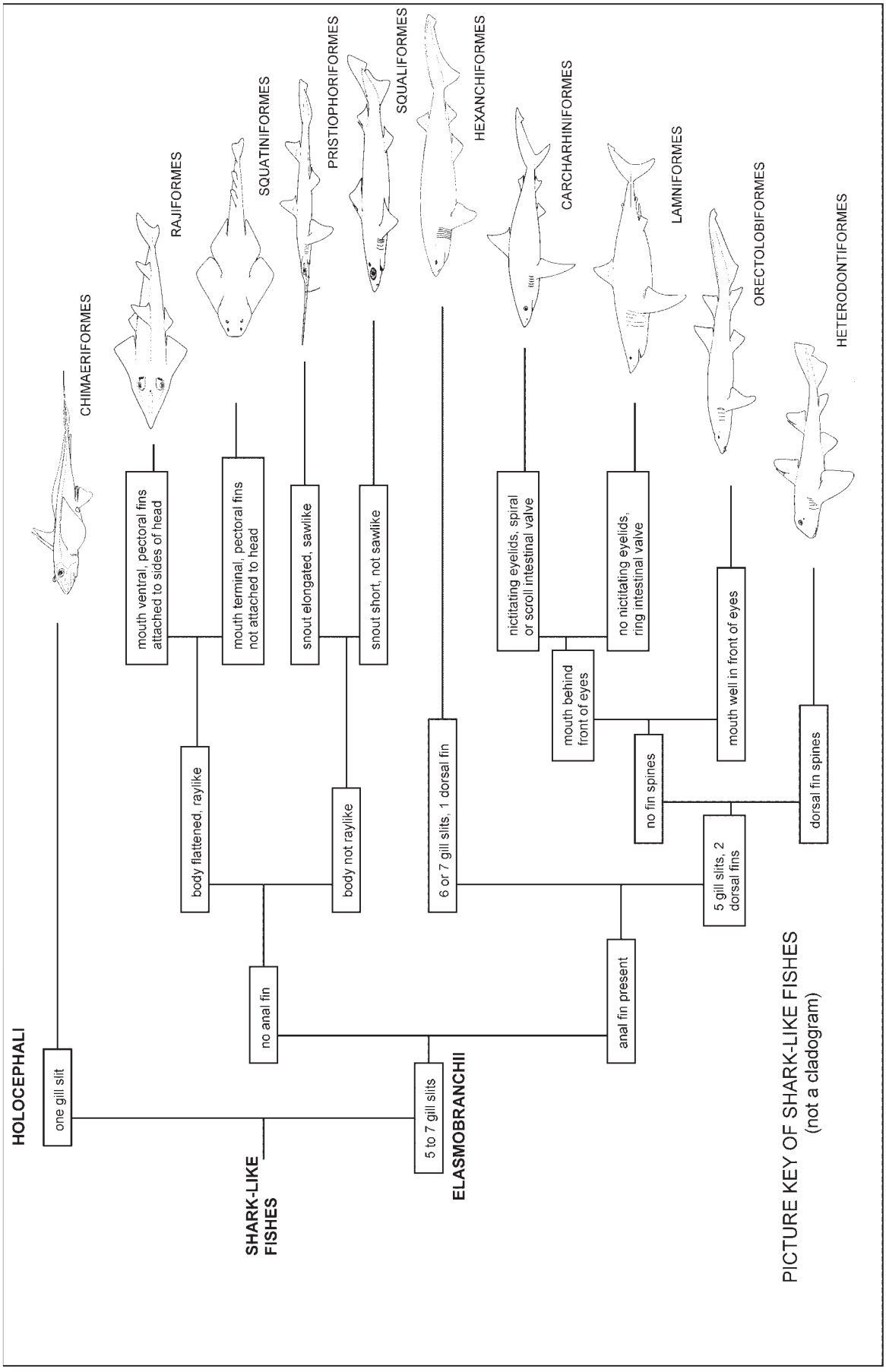

Fig. 23 Higher classification of sharks (Orders)

1.2.4 Glossary of Technical Terms

The following glossary of terms used for the anatomy and biology of shark-like fishes is modified from terms in Compagno (1984, 1988, 1999) and a short glossary in Compagno, Ebert and Smale (1989).

Abdominal ridges or keels: In some sharks, paired longitudinal dermal ridges that extend from the bases of the pectoral fins to the pelvic-fin bases.

Accessory dorsal marginal: In the clasper skeleton, a flat cartilage on the posterior end of the dorsal marginal cartilage that supports the cover rhipidion.

Adductor mandibulae muscles: Paired head muscles originating on the lateral faces of the quadrate process of the palatoquadrates and inserting on the lateral surface of the Meckel's cartilages; the primary jaw-closing muscles of sharks.

Adelphophagy: Foetus-eating, a mode of live-bearing reproduction employing uterine cannibalism; early foetuses deplete their yolk-sacks early and subsist by first eating their smaller siblings and then eating nutritive eggs produced by the mother. At present only known for certain in the sand tiger shark (***Carcharias taurus***), but suspected in a few other lamnoids.

Alternate teeth: Small oral teeth with asymmetrical crowns that form two interdigitated rows on the symphysis, with the cusps of each row hooked mesially towards the opposite row. Additional paired rows of alternates may be present distal to the symphysial rows.

Amphitemperate: Referring to a species that occurs in temperate water in the northern and southern hemispheres, but is absent from the tropics.

Anal fin: A single fin on the ventral surface of the tail between the pelvic fins and caudal fin of some sharks, absent in batoids, dogfish, sawsharks, angel sharks, and some chimaeras.

Annular rings or **annuli:** In a vertebral centrum in cross section, rings of calcified cartilage separated by uncalcified cartilage that occupy the intermedialia only, or concentric rings that cross both the intermedialia and basalia.

Anterior: Forward, in the longitudinal direction of the snout tip. Also, **cranial**.

Anterior fontanelle: On the elasmobranch neurocranium, an aperture on the anterodorsomedial surface, usually at the rear of the ethmoid region and forming a passage into the internal cranial cavity. It is closed by a tough membrane, varies tremendously in shape, and may be pinched off by the medially expanded orbits in a few sharks.

Anterior margin: In precaudal fins, the margin from the fin origin to its apex.

Anterior nasal flap: A flap on the front edges of the nostrils, that serves to partially divide the nostril into incurrent and excurrent apertures or openings.

Anterior teeth: Enlarged, tall, narrow-rooted oral teeth near the symphysis, often with lingually curved cusps.

Anterodorsal palpebral depressor muscle: In the orectoloboid family Parascylliidae, paired head muscles that originate at the insertions of the preorbitalis muscles on the anterolateroventral face of the Meckel's cartilage, and insert on the skin of the upper eyelid anterior to the eye. These are possibly for depressing the upper eyelids and closing the eyes, and are not found in any other sharks.

Antorbital cartilages: On the neurocranium of sawsharks and batoids, separate cartilages attached to the sides of the nasal capsules that support the sides or front of the head.

Apex: In precaudal fins, the distal tip, which can be acutely pointed to broadly rounded.

Apical: In oral teeth, towards the tip of the crown or cusp. Can also be used as indicating direction towards the apex or tip of a fin, fin-spine, etc.

Aplacental viviparity: Live-bearing in which the young do not have a yolk-sac placenta. Found in all groups of live-bearing sharks.

Aplesodic fin: A pectoral, pelvic, dorsal, or anal fin in which the fin radial cartilages do not extend into the distal fin web and between the supporting ceratotrichia of the fin web. Modern sharks always have aplesodic caudal fins, in which the haemal arches of the caudal vertebrae do not support the ventral caudal lobe.

Apopyle: The anterior opening of the clasper, on the anteromesial surface of the clasper and close to the vent. The apopyle receives sperm from the cloaca and fluid from the siphons, which enter the clasper groove and are discharged through the hypopyle. Apopyle is also used for clasper skeletons for the anterior opening of the tubular shafts formed by enlarged marginal and axial cartilages.

Axial cartilage: In the clasper skeleton, the elongated ventral rod or plate-shaped cartilage that forms the main support of the clasper. Also termed **appendix-stem**.

Barbels: Long conical paired dermal lobes on the snouts of sharks, that may serve to locate prey. Sawsharks have barbels on the underside of the snout in front of the nostrils as in sturgeon, but most barbelled sharks have them associated with the nostrils, either as an extension of the anterior nasal flaps or as separate structures medial to the nasal apertures.

Basal: In oral teeth, a proximal direction towards the crown foot and roots.

Basal cartilages or **basals:** In precaudal fins the large cartilages of the fin bases, immediately distal to the pectoral and pelvic fin girdles or the vertebral column (dorsal and anal fins), on which the radials articulate distally. The paired pectoral fins of living sharks primitively have a tribasal pectoral fin, with a propterygium, mesopterygium, and metapterygium as basals, although these may be fused; in batoids, additional neopterygial basals may be added between the mesopterygium and metapterygium and the propterygium is variably expanded anterior with a propterygial basal and axis. The pelvic fins have a basipterygium that supports the pelvic radials and, in males, the claspers. The caudal fin has no basals, but these are

functionally replaced by expanded neural and haemal arches of the vertebral column.

Basal communicating canals: See **subnasal fenestrae.**

Basal groove: In oral teeth, a deep groove proximal to the basal ledge on the labial surface of the crown neck and apical root margin.

Basal ledge: In oral teeth, a shelf-like projection on the labial surface of the crown foot.

Basal plate: The floor of the cranial cavity of the neurocranium, a ventral, medial plate extending from the ethmoid region between the orbits and otic capsules and below the cranial cavity to the occipital condyles, occipital centrum and foramen magnum.

Basals or **basalia:** In a vertebral centrum, the diagonal spaces below the attachment surfaces of the basidorsal cartilages, above the basiventral cartilages, and between the two halves of the double cone. Basalia may be filled with uncalcified cartilage, may have diagonal calcifications penetrating the uncalcified cartilage, or may have calcified annuli or solid calcified cartilage that are continuous with calcification of the intermedialia. See diagonal calcifications and intermedialia.

Base: In precaudal fins, the proximal part of the fin between the origin and insertion, extending distally, and supported by the cartilaginous fin skeleton. In the caudal fin, that thickened longitudinal part of the fin enclosing the vertebral column and between the epaxial and hypaxial lobes or webs of the fin. In oral teeth, the proximal root and crown foot, in apposition to the distal cusp. In denticles, the proximal anchoring structures, often with four or more lobes, holding the denticles in the skin.

Basidorsal cartilages: A pair of wedge-shaped arched, thin cartilages articulating with the dorsolateral surfaces of a vertebral centrum and forming a continuous neural arch with the interdorsal cartilages to protect the spinal cord.

Basipterygium: The large elongate longitudinal cartilage at the fin base of the pelvic fin, attached to the posterolateral ends of the pelvic girdle or puboischiadic bar. The basipterygium has pelvic radials attached along its distal edge and has the clasper skeleton attached posteriorly in males.

Basiventral cartilages: A pair of rounded or wedge-shaped cartilages on the ventrolateral surfaces of a vertebral centrum that form the bases for attachment of ribs in monospondylous precaudal vertebrae. In diplospondylous precaudal and caudal vertebrae the basiventrals form haemal arches along with the interventral cartilages for protecting the caudal artery and vein.

Batoid: A ray or flat or winged shark, a neoselachian of the superorder Squalomorphii, order Rajiformes: a sawfish, sharkray, wedgefish, guitarfish, thornray, panray, electric ray, skate, stingray, butterfly ray, eagle ray, cownose ray, devil ray or manta. Rays are closely allied to the sawsharks (Pristiophoriformes) and angel sharks (Squatiniformes), but differ from them in having the pectoral fins fused to the sides of the head over the gill openings, which are ventral rather than laterally or ventrolaterally placed.

Beta cartilage: In the clasper skeleton, a single, dorsolateral flattened, wedge-shaped or cylindrical cartilage connecting the pelvic basipterygium and axial cartilage and reinforcing the intermediate segments, possibly derived from a pelvic radial.

Blade: In oral teeth, an arcuate, convex-edged section of the cutting edge of the crown foot, without cusplets.

Body ridges: Elongated longitudinal dermal ridges on the sides of the trunk and precaudal tail in certain carpet sharks (Orectolobiformes), in the whale, zebra and some bamboo sharks.

Body: Can refer to an entire shark, sometimes restricted to the trunk and precaudal tail.

Branchial arches: The paired visceral arches behind the hyoid arch and just in front of the scapulocoracoid that support the gills. In elasmobranchs the five to seven branchial arches primitively consist of a pair of dorsomedial and wedge-shaped cartilages, the **pharyngobranchials,** closely situated against the roof of the pharynx, a pair of dorsolateral and more cylindrical **epibranchials** that are connected dorsomedially to the pharyngobranchials, a pair of ventrolateral cylindrical **ceratobranchials** that are connected ventrolaterally to the epibranchials, a pair of ventromedial **hypobranchials** that are connected ventrolaterally to the ceratobranchials, and unpaired ventromedial **basibranchials** that are connected ventrolaterally to the hypobranchials. The hypobranchials and basibranchials along with the expanded ventral ends of the ceratobranchials form the **basibranchial skeleton** of the floor of the branchial pharynx. The branchial skeleton is variably modified in elasmobranchs, with basibranchials and sometimes hypobranchials often lost, the last two pharyngobranchials and the last epibranchial often fused together, and the last basibranchial often expanded into a long, broad **copula** with which the anterior hypobranchials and posterior ceratobranchials articulate.

Calcified cartilage: Shark skeletons are formed of hyaline cartilage or gristle, but this is often reinforced with layers of calcified cartilage, cartilage impregnated with a mineral, hydroxyapatite, similar to that of bone but organized differently, in a hard, tile-like pavement of tiny **tesserae**, or more compactly as in the calcified structures of vertebral centra.

Calcified double cones: In vertebrae, the primary calcifications of the notochordal sheath, in lateral view resembling two hollow, horizontal cones with their apices merged, or an hourglass.

Cannibal viviparity: See **uterine cannibalism**.

Carcharhinoid: A ground shark, a member of the order Carcharhiniformes, and including the catsharks, false catsharks, finbacked catsharks, barbeled houndsharks, houndsharks, weasel sharks, requiem sharks and hammerheads.

Carina: On the crowns of oral teeth, a low blunt mesodistal ridge replacing the cusp and cutting edge, in sharks that eat hard-shelled invertebrate prey.

Carotid foramen: A single foramen or one of a pair of foramina that penetrate the basal plate usually near its midlength and allow passage of the internal carotid arteries into the cranial cavity. In some advanced elasmobranchs the carotid foramina shift through the stapedial foramina and onto the medial wall of the orbit.

Cartilaginous fishes: Members of the class Chondrichthyes.

Caudal crest: A prominent saw-like row of enlarged pointed denticles along the dorsal caudal margin and sometimes along the ventral caudal margin of the caudal fin. Found in certain sharks including hexanchoids and some carcharhinoids.

Caudal fin: The fin on the end of the tail in shark-like fishes, lost in some batoids.

Caudal keels: A dermal keel on each side of the caudal peduncle that may extend onto the base of the caudal fin, and may, in a few sharks, extend forward as a body keel to the side of the trunk.

Caudal peduncle: That part of the precaudal tail extending from the insertions of the dorsal and anal fins to the front of the caudal fin.

Central foramen: In oral teeth, a nutrient foramen on the midline of the lingual surface of the root, in the transverse groove.

Centrum (plural, Centra): A spool-shaped, partially or usually fully calcified structure that forms as a segmental constriction in the notochordal sheath of neoselachians, and which as an articulated string forms the principal structural units of the vertebral column. Centra are primarily formed by the calcified double cones in the notochordal sheath, which may be their only calcification, but additional secondary calcification may occur in the centrum between the outer surfaces of the calcified double cones, including calcified intermedialia, radii, annuli, and diagonal calcifications.

Ceratotrichia: Slender soft or stiff filaments of an elastic protein, superficially resembling keratin or horn, from the Greek *keratos*, horn, and *trichos*, hair. Ceratotrichia run in parallel and radial to the fin base and support the fin webs. The prime ingredient of shark-fin soup.

Chimaera: A member of the order Chimaeriformes, subclass Holocephali, see also **Chimaeroid**, **Holocephali**.

Chimaeroid: A chimaera, ratfish, silver shark, ghost shark, spookfish or elephant fish, a member of the order Chimaeriformes.

Chondrichthyan: Referring to the class Chondrichthyes.

Chondrichthyes: The class Chondrichthyes, from Greek *chondros*, cartilage, and *ichthos*, fish, a major taxonomic group of aquatic, gill-breathing, jawed, finned vertebrates with primarily cartilaginous skeletons, 1 to 7 external gill openings, oral teeth in transverse rows on their jaws, and mostly small, tooth-like scales or dermal denticles. Chondrichthyes include the living elasmobranchs and holocephalans and their numerous fossil relatives, and also can be termed shark-like fishes or simply sharks.

Chondrocranium: See **neurocranium**.

Circumnarial fold: A raised semicircular, lateral flap of skin around the incurrent aperture of a nostril, in heterodontoids, orectoloboids, and a few batoids, defined by a circumnarial groove.

Circumnarial groove: A shallow groove defining the lateral bases of the circumnarial folds.

Clasper claws: In parascylliid orectoloboids, a longitudinal row of large anterolaterally directed claw-like denticles on the dorsolateral surface of the clasper glans, supported by the terminal ventral.

Clasper dactyl: In parascylliid orectoloboids, a large finger-like process on the medial face of the clasper, supported by the dorsal terminal and having a **mesospur**, an analogue to the lateral spur or spine of the terminal 3 cartilage of other orectoloboids and other sharks.

Clasper gaff or **hook:** In the external clasper glans, a posterior hook-like structure, like a clasper spur but formed from the dorsal terminal cartilage, found in squaloids of the family Squalidae.

Clasper glans: The distal and dorsal part of the external clasper from the hypopyle to its tip, and including various movable terminal structures; also, the same area of the clasper skeleton.

Clasper groove: The longitudinal groove through the clasper, surrounded by the axial and marginal cartilages, and connecting the apopyle and hypopyle.

Clasper hooks: In the clasper glans of some carcharhinoid sharks, small claw-like dermal denticles arranged in a row along the ventral surface of the free edge of the exorhipidion.

Clasper sacs: Dermal sacs with longitudinally ribbed walls on the ventral and medial surfaces of the claspers of hexanchoids.

Clasper shaft: That part of the clasper skeleton from its origin on the pelvic fin basipterygium to the hypopyle; also, that part of the external clasper from its base to the hypopyle.

Clasper spine: In the external clasper, a projection of the terminal 3 cartilage on the lateral surface of the clasper glans, which forms a short to long, acutely pointed, spine that is covered with shiny hard tissue, possibly enameloid, dentine or both. In some squaloids other terminal cartilages may have spines.

Clasper spur: In the external clasper, a projection of the terminal 3 cartilage on the lateral surface of the clasper glans, which may be pointed but is not covered with shiny hard tissue.

Clasper tip: The posterior end of a clasper.

Claspers: The paired copulatory organs present on the pelvic fins of male cartilaginous fishes, for internal fertilization of eggs, also termed **mixopterygia**.

Classification: The ordering of organisms into groups on the basis of their relationships, which may be by similarity or common ancestry.

Cloaca: The common chamber at the rear of the body cavity of elasmobranchs through which body wastes and reproductive products including sperm, eggs, and young pass, to be expelled to the outside through a common opening or **vent**.

Cover rhipidion: On the external clasper glans, an elongated, longitudinal blade or flap on its dorsomedial

external edge, often supported by an accessory dorsal marginal cartilage.

Cranial cavity: The central cavity of the neurocranium, containing the brain, pituitary gland, and roots of the cranial nerves. It extends posteriorly between the orbits and otic capsules to the foramen magnum.

Cranial roof: The anterior roof of the cranial cavity of the neurocranium, a dorsomedial, arched or flattened plate extending from the anterior fontanelle and between the orbits to the parietal fossa of the otic capsule. Sometimes perforated by a frontal or parietal foramen or fenestra, which may be continuous with the anterior fontanelle and can occupy most of the cranial roof.

Craniomandibular muscles: Paired head muscles in heterodontoid sharks that originate from long tendons on the medial walls of the orbits that extend below and transverse to the levator palatoquadrati and spiracular constrictor muscles and behind the spiracles to insert on the posterodorsolateral face of the Meckel's cartilages. They are found in no other sharks and may serve to retract or elevate the jaws.

Crown: The distal part of the oral tooth, almost entirely covered with shiny enameloid except for the neck. In denticles, a flat dorsal plate-like or thorn-like structure, elevated above the denticle base on a stalk or pedicle or confluent with the base.

Crown foot: The expanded, proximal, basal part of the crown, often bearing cusplets or blades.

Cusp: A usually pointed large distal projection of the crown. A **primary cusp** is situated on the midline of the crown foot. **Multicuspid** refers to oral teeth or denticles with more than one cusp. In lateral trunk denticles, the posterior ends of the crown may have **medial** and **lateral cusps**, sharp or blunt projections associated with the medial and lateral ridges.

Cusplet: As with a cusp, but a small projection in association with a cusp, and usually mesial and distal but not medial on the crown foot.

Cutting edge: In oral teeth, the compressed sharp longitudinal ridge on the mesodistal edges of the crown.

Dentine: The primary material of shark oral teeth, a hard tissue with numerous vascular and nonvascular canals.

Dermal denticle or **placoid scale:** A small tooth-like scale found in cartilaginous fishes, covered with enameloid, with a core and base of dentine and usually small and often close-set to one another and covering the body. A few nonbatoid sharks, many batoids, and chimaeroids generally have them enlarged and sparse or reduced in numbers.

Dermal lobes: In wobbegongs, family Orectolobidae, narrow or broad-based, simple or branched projections of skin along the horizontal head rim and on the chin.

Diagonal calcifications: In a vertebral centrum in cross-section, plate-like (**diagonal calcified lamellae**) or knob-like (**diagonal calcified lobes**) structures of calcified cartilage that partially fills the uncalcified basalia. These have a radial orientation from the centre of the centrum.

Diphycercal: A caudal fin with the vertebral axis running horizontally into the fin base, which is not elevated.

Diplospondylous vertebrae: Vertebrae of the tail with two centra and two basidorsal and basiventral elements per segment, and mostly with a haemal arch formed by the basiventral and interventral elements. These include diplospondylous precaudal vertebrae between the monospondylous vertebrae and the base of the caudal fin, and diplospondylous caudal vertebrae in the caudal fin.

Distal: In any direction, at the far end of a structure. In oral teeth, used in a special sense for structures on the teeth towards the posterolateral mouth corners or rictuses. See **apical** and **basal**.

Dorsal: Upwards, in the vertical direction of the back. See **ventral**.

Dorsal fin: A fin located on the trunk or precaudal tail or both, and between the head and caudal fin. Most sharks have two dorsal fins, some batoids one or none.

Dorsal fin spine: A small to large enameloid-covered, dentine-cored spine located on the anterior margins of one or both of the dorsal fins, found on bullhead sharks (Heterodontiformes), many dogfish sharks, fossil (but not living) batoids, chimaeroids, but lost entirely or buried in the fin bases of other shark-like fishes.

Dorsal lobe: In the caudal fin, the entire fin including its base, epaxial and hypaxial webs but excepting the ventral lobe.

Dorsal margin: In the caudal fin, the margin from the upper origin to its posterior tip. Usually continuous, but in angel sharks (Squatiniformes) with their hypocercal, superficially inverted caudal fins, it is subdivided. See **squatinoid caudal fin**.

Dorsal marginal: In the clasper skeleton, a flat semicylindrical cartilage that is partially fused to the medial edge of the axial cartilage, and forms the medial wall of the clasper groove.

Dorsal terminal: On the skeleton of the clasper glans, an often triangular, elongated, curved, plate-like cartilage that articulates or is attached to the medial or dorsomedial edge of the end-style and anteriorly to the dorsal marginal.

Dorsal terminal 2: A flat elongated cartilage with its mesial edge attached to the floor of the glans, and supporting the rhipidion.

Ectethmoid chambers: On the neurocranium, cavities in the nasal capsule that drain the nasal sinuses through the orbitonasal canals into the orbital sinuses.

Ectethmoid processes: On the neurocranium of hexanchoid and some squaloid sharks, posteroventrolateral angular or lobular projections of the nasal capsules and the preorbital walls.

Egg case: A stiff-walled elongate-oval, rounded rectangular, conical, or dart-shaped capsule that surrounds the eggs of oviparous sharks, and is deposited by the female shark on the substrate. It is analogous to the shell of a bird's egg and is made of protein, which is a type of collagen that superficially resembles horn or keratin. Egg cases often

have pairs of tendrils or horn-like structures on their ends, or flat flanges on their sides or spiral flanges around their lengths, which anchor the cases to the bottom. As the egg travels from the ovaries into the oviducts and through the nidamental glands, the egg case is secreted around it and the egg is fertilized. Live-bearing sharks may retain egg cases, and these vary from being rigid and similar to those of oviparous sharks to soft, bag-like, degenerate and membranous. Soft egg cases may disintegrate during the birth cycle.

Elasmobranch: Referring to the subclass Elasmobranchii.

Elasmobranchii: The subclass Elasmobranchii, (from Greek *elasmos*, plate, and *branchos*, gills, in allusion to their plate-like gill septa), the shark-like fishes other than the Holocephali or chimaeras, and including the living nonbatoid sharks, batoids, and a host of fossil species. They differ from holocephalans in having 5 to 7 pairs of gill openings open to the exterior and not covered by a soft gill cover, oral teeth separate and not formed as tooth plates, a fixed first dorsal fin with or without a fin spine, and a short spined or spineless second dorsal.

Embryo: An earlier development stage of the young of a live-bearing shark, ranging from nearly microscopic to moderate-sized but not like a miniature adult. See **foetus**.

Enameloid: The shiny hard external coating of the crowns of shark oral teeth, superficially similar to enamel in land vertebrates.

End-style: In the clasper skeleton, the posterior end of the axial cartilage, between the dorsal and ventral terminal cartilages.

Endemic: A species or higher taxonomic group of organisms that is only found in a given area. It can include national endemics found in a river system or along part or all of the coast of a given country, but also regional endemics, found off or in adjacent countries with similar habitat, but not elsewhere.

Epaxial lobe or **web:** In the caudal fin, that part of the caudal fin between the base and dorsal margin, supported by ceratotrichia.

Epaxial web: The entire fin web above the vertebral column and caudal base.

Epiphysial foramen or **notch:** On the neurocranium, a foramen or notch in the cranial roof at the dorsomedial edge of the anterior fontanelle, that houses the pineal body.

Ethmoid region: That anteriormost sector of the neurocranium including the nasal capsules, internasal plate between them, and the rostrum.

Ethmonuchal muscles: In the orectoloboid family Parascylliidae, paired head muscles that originate on the dorsal myomeres of the nape, and insert via long tendons on the nasal capsules. These are possibly for elevating the snout. Not found in any other sharks, though analogous muscles exist in batoids.

Euselachian: Referring to the Euselachii.

Euselachii: The cohort Euselachii (Greek *Eu*, true, good or original, and *selachos*, shark or cartilaginous fish), the spined or 'phalacanthous' sharks, including the modern sharks or Neoselachii, and fossil shark groups including the hybodonts, the ctenacanths, and the xenacanths, all primitively with anal fins and having two dorsal fins with fin spines.

Excurrent apertures: The posterior and ventrally facing openings of the nostrils, which direct water out of the nasal cavities and which are often partially covered by the anterior nasal flaps. These are usually medial on the nostrils and posteromedial to the incurrent apertures, but may be posterior to the incurrent apertures only.

Exorhipidion: In claspers, a longitudinally elongated, external blade or flap with its base attached to the dorsolateral edge of the clasper glans, and with its free edge directed medially. It is supported by the **ventral terminal 2 cartilage**.

Eye notch: A sharp anterior or posterior indentation in the eyelid, where present cleanly dividing the upper and lower eyelids.

Filter screens: In the whale shark (Rhincodontidae) and devil rays (Mobulidae), transverse bars with lateral dermal lobes on the internal gill openings that form devices for screening out plankton.

Fin skeletons: In unpaired precaudal fins, the basal plates and radials; in the caudal fin, the vertebral column including expanded neural and haemal arches; and in the paired fins, the fin girdles, basals, and radials.

Fin web: The usually thin, compressed part of the fin, distal to the base, that is supported by ceratotrichia alone (in aplesodic fins) or by ceratotrichia surrounding expanded fin radials or by radials only (plesodic fin).

First dorsal constrictor muscles: Paired head muscles that are confluent and functionally part of the levator palatoquadrati muscles in most nonbatoid sharks, except in orectoloboids where they are discrete muscles with separate origins and insertions similar to but more lateral than the levators.

First dorsal fin: The anteriormost dorsal fin of two, ranging in position from over the pectoral fin bases to far posterior on the precaudal tail.

Foetus: A later development stage of the unborn young of a live-bearing shark, that essentially resembles a small adult. **Term foetuses** are ready to be born, and generally have oral teeth and denticles erupting, have a colour pattern (often more striking than adults), and, in ovoviviparous sharks, have their yolk-sacs reabsorbed.

Foramen magnum: On the neurocranium, the 'great hole' or posteromedial aperture through the occiput into the cranial cavity, above the occipital centrum and medial and usually dorsal to the occipital condyles. The spinal cord passes from the brain through the foramen magnum into the neural canal of the vertebral column.

Free rear tips: The pectoral, pelvic, dorsal, and anal fins all have a movable rear corner or flap, the free rear tip, that is separated from the trunk or tail by a notch and an inner margin. In some sharks the rear tips of some fins are very elongated.

Frontal and **parietal fenestrae:** On the neurocranium, medial apertures in the cranial roof between the anterior fontanelle and the parietal fossa, the frontal fenestra being closer to the anterior fontanelle and the parietal fenestra to the parietal fossa. Sometimes the two merge and become a **frontoparietal fenestra**, while in many batoids and in some orectoloboid sharks there is a merging of the anterior fontanelle with the frontoparietal fenestra so that it extends nearly to the parietal fossa. All of these fenestrae are closed by tough membranes.

Functional series: A series of oral teeth that are in functional position on the jaw.

Galeomorph: Referring to the Galeomorphii.

Galeomorphii: The neoselachian superorder Galeomorphii, including the heterodontoid, lamnoid, orectoloboid, and carcharhinoid sharks.

Gill openings or **slits:** In elasmobranchs, the paired rows of five to seven transverse openings on the sides or underside of the head for the discharge of water through the gills. Chimaeras have their four gill openings hidden by a soft gill cover and discharge water through a single external gill opening.

Gill-raker denticles: In the basking shark (Cetorhinidae), elongated denticles with hair-like cusps arranged in rows on the internal gill openings, which filter out planktonic organisms.

Gill-raker papillae: Sparse to dense dermal papillae on the gill arches of some sharks that serve as filters to collect small food organisms.

Girdle: A bar of cartilage buried in the body wall that supports the basals of the paired fins: the pectoral girdle (scapulocoracoid) and pelvic girdle (puboischiadic bar).

Haemal arch: The arch ventral to the notochord or vertebral centra on tail vertebrae that is formed by the basiventrals and interventrals and which houses the caudal artery and caudal vein in a **haemal canal**.

Haemal spines: On the haemal arches of the diplospondylous precaudal and caudal vertebrae, elongated ventral surfaces forming vertical plates, particularly well-developed on the caudal fin.

Head: That part of a cartilaginous fish from its snout tip to the last or (in chimaeras) only gill slits.

Heterocercal: A caudal fin with the vertebral axis slanted dorsally into the fin base, which is also dorsally elevated.

Heterodontoid: A bullhead shark, horn shark, or Port Jackson shark, a member of the order Heterodontiformes, family Heterodontidae.

Heterodonty: In oral teeth, structural differences between teeth in various positions on the jaws, between teeth in the same position during different life stages, or between teeth in the same positions in the two sexes.

Hexanchoid: A cowshark or frilled shark, members of the order Hexanchiformes, and including the sixgill sharks, sevengill sharks, and frilled sharks.

Holocephalan: Referring to the Holocephali.

Holocephali: The subclass Holocephali (from Greek *holos*, entire, and *kephalos*, head), the living chimaeras and their numerous fossil relatives, a major subdivision of the class Chondrichthyes. The name is in reference to the fusion of the upper jaws or palatoquadrates to the skull in all living species and in many but not all fossils. The living holocephalans include three families in the order Chimaeriformes. The living species differ from elasmobranchs in having four pairs of gill openings covered by a soft gill cover and with a single pair of external gill openings, oral teeth fused and reduced to three pairs of ever-growing tooth plates, an erectile first dorsal fin with a spine and a long, low spineless second dorsal.

Holotype: Either the only specimen used and mentioned in an original description of a species, with or without a designation of such, or one of two or more specimens used and mentioned in an original description of a species and designated as such. This becomes the 'name-bearer' of the species, and is used to validate the species or scientific name by anchoring it to a single specimen.

Homodonty: In oral teeth, structural similarity between teeth in various positions on the jaws, between teeth in the same position during different life stages, or between teeth in the same positions in the two sexes.

Hyoid arch: The visceral arch that supports the tongue and, in elasmobranchs, the rear of the upper jaws. The hyoid arch is between the mandibular arch and the first branchial arch, and has the spiracular pocket between it and the mandibular arch. The hyoid arch in elasmobranchs includes a medial **basihyoid** in the floor of the mouth and inside the tongue, a pair of elongated **ceratohyals** articulating with the basihyoid and the hyomandibulae, and a pair of **hyomandibulae** articulating with the ceratohyals and the hyomandibular facets of the neurocranium. Chimaeroids have a nonsuspensory hyoid arch similar to the gill arches, with a pair of **epihyals** and **pharyngohyals** equivalent to the hyomandibulae. Batoids have the ceratohyals reduced and separated from the hyomandibulars or absent, and functionally replaced by paired dorsal and ventral **pseudohyoids**.

Hyomandibular facet: On the neurocranium of elasmobranchs, a joint surface, socket or cotyle that is usually on the ventrolateral surfaces of each otic capsule but may be extended posteriorly or arched dorsally. The heads of the hyomandibulae articulate with these facets. Chimaeras lack hyomandibular facets and differentiated hyomandibulae.

Hyomandibular nerve foramina: Foramina for the roots of the hyomandibular nerves, behind the orbital fissures. These foramina are confluent with the orbital fissure in many sharks.

Hypaxial web: The entire fin web below the vertebral column (vertebral axis) and the caudal base.

Hypercalcified structures: Parts of the skeleton that have developed extremely dense calcified cartilage, primarily during growth and maturation, which sometimes swell to knobs that distort and engulf existing cartilaginous structures. The rostrum of the salmon shark (***Lamna ditropis***) is a particularly impressive hypercalcified structure.

Hypocercal: A caudal fin with the vertebral axis slanted ventrally into the fin base, which is also ventrally depressed. Found only in angel sharks (Squatiniformes) among living sharks.

Hypopyle: On the external clasper and clasper skeleton, the posterior opening of the clasper groove onto the clasper glans.

Incurrent apertures: The anterior and ventrally facing openings of the nostrils, which direct water into the nasal cavities. These are usually lateral on the nostrils and anterolateral to the excurrent apertures, but may be anterior to the excurrent apertures only.

Independent dentition: Teeth along a mesodistal series in which the roots do not overlap and are separated by a space. See **overlapping dentition**.

Inner margin: In precaudal fins including the pectoral, pelvic, dorsal and anal fins, the margin from the fin insertion to the rear tip.

Insertion: The posterior or rear end of the fin base in precaudal fins. The caudal fin lacks insertions except with many batoids and some chimaeroids that have a caudal filament that extends posterior to the fin. See **origin**.

Interdorsal cartilages: A pair of wedge-shaped arched thin cartilages fitting between the basidorsal cartilages of each vertebra to complete the neural arch.

Interdorsal ridge: A ridge of skin on the midback of sharks, in a line between the first and second dorsal fins; particularly important in identifying grey sharks (genus ***Carcharhinus***, family Carcharhinidae).

Intermedialia: In a vertebral centrum, dorsal, ventral and lateral spaces between the attachment surfaces of the basidorsal and basiventral cartilages and between the two halves of the double cone. These can be filled with uncalcified cartilage, with solid or hollow wedges of calcified cartilage, or with plate-like, branched calcified radii within uncalcified cartilage. See **basalia**.

Intermediate segments: In the clasper skeleton, one or more short cylindrical cartilages connecting the pelvic basipterygium to the axial cartilage of the clasper. Also termed **stem-joints**.

Intermediate teeth: Small oral teeth between the laterals and anteriors of the upper jaw, found in most lamnoids.

Internasal plate or septum: On the neurocranium, a plate or partition between the two nasal capsules. It ranges from a vertical plate to a broad horizontal plate.

Interventral cartilages: A pair of rounded or wedge-shaped cartilages fitting between the basiventral cartilages of each vertebra, that in diplospondylous precaudal and caudal vertebrae form the haemal arches with the basiventral cartilages.

Intestinal valve: A dermal flap inside the intestine, protruding into its cavity or lumen, and of various forms in different cartilaginous fishes. Often formed like a corkscrew or augur. See **spiral, ring** and **scroll valves**.

Jaws: See **mandibular arch**.

Labial cartilages: Paired cartilages that are internal and support the labial folds at the lateral angles of the mouth. Living neoselachians typically have two pairs of upper labial cartilages, the **anterodorsal** and **posterodorsal** labial cartilages, and one pair of **ventral labial cartilages**, but these are variably reduced and sometimes absent in many sharks. Chimaeras have more elaborate labial cartilages than living elasmobranchs.

Labial flange: On tooth crowns of many squaloids and some orectoloboids, a narrow, vertically elongated labial basal ledge.

Labial folds: Lobes of skin at the lateral angles of the mouth, usually with labial cartilages inside them, separated from the sides of the jaws by pockets of skin (labial grooves or furrows).

Labial furrows or **labial grooves:** Grooves around the mouth angles on the outer surface of the jaws of many cartilaginous fishes, isolating the labial folds. Primitively there is a distinct **upper labial furrow** above the mouth corner and a **lower labial furrow** below it.

Labial: In oral teeth, the outer face of the tooth that is directed outside the mouth and towards the lips. See **lingual**.

Lamnoid: A mackerel shark, a member of the order Lamniformes, and including the sand tiger sharks, goblin sharks, crocodile sharks, megamouth shark, thresher sharks, basking shark, and the makos, porbeagle, salmon shark and white shark.

Lateral clasper fold: In mackerel sharks (family Lamnidae), a unique longitudinal flap of skin along the lateral edge of the external clasper shaft.

Lateral commissures: On the neurocranium, tube-like or ring-like enclosed passages for the lateral head veins, which drain the orbital sinuses, through the postorbital walls of the orbits and below the sphenopterotic ridges and above the hyomandibular facets in neoselachians. The lateral commissures are reduced or absent in many living neoselachians.

Lateral or **laterad:** Outwards, in the transverse direction towards the periphery of the body. See **medial**.

Lateral orolabial grooves: Shallow longitudinal grooves on the lower jaw that connect the edge of the lip on each side with the medial ends of the lower labial furrows. Found in more advanced orectoloboids.

Lateral teeth: Large broad-rooted, compressed, high crowned oral teeth on the sides of the jaws between the anteriors and posteriors.

Lateral trunk denticle: A dermal denticle from the dorsolateral surface of the back below the first dorsal fin base.

Lectotype: One of two or more specimens that were syntypes in an original description, designated as a lectotype by a subsequent writer. It then becomes equivalent to a holotype, and anchors the name of the species to a specimen unless invalidated by a ruling of the International Commission on Zoological Nomenclature or a previous designation of a lectotype.

Levator palatoquadrati muscles: Paired head muscles that primitively originate on the underside of the postorbital processes and sphenopterotic ridges, extend vertically, and insert on the posteromedial surfaces of the quadrate processes of the palatoquadrates. In advanced carcharhinoids the origins of the levator palatoquadrati muscles are expanded far forwards and diagonally into the orbits. Primitively these muscles lift or retract the jaws upwards, but in advanced carcharhinoids may help rotate the jaws forwards and downwards in opposition to the levator hyomandibularis muscles, which retract the jaws.

Lingual: In oral teeth, the inner face of the tooth that is directed inside the mouth and towards the tongue. See **labial**.

Live-bearing: A mode of reproduction in which female sharks give birth to young sharks, which are miniatures of the adults. See **viviparity**.

Longitudinal ridges: In lateral trunk denticles, parallel ridges that extend anteroposteriorly on the distal surface of the crown. These may be in the form of a single **medial ridge** (sometimes paired), and paired **lateral ridges**, and may terminate in medial and lateral cusps.

Lower eyelid: The ventral half of the eyelid, separated by a deep pocket (conjunctival fornix) from the eyeball. In some derived batoids the pocket also fuses with the eyeball.

Lower origin: In the caudal fin, the anteroventral beginning of the hypaxial or lower web of the caudal fin, at the posterior end of the anal-caudal or pelvic-caudal space (see measurement illustrations).

Lower postventral margin: In the caudal fin, the lower part of the postventral margin of the hypaxial web, from the ventral tip to the posterior notch.

Mandibular arch: The paired primary jaw cartilages of sharks, including the dorsal palatoquadrates and the ventral Meckel's cartilages.

Mandibulocutaneous muscles: Paired head muscles in squaloid and hexanchoid sharks, that originate on the inside of the skin of the head behind the eyes and near the spiracles, and insert on the dorsoposterolateral face of the quadrate processes of the palatoquadrates.

Meckel's cartilages: The paired lower jaw cartilages, articulating mesially with each other at the midline or symphysis of the lower jaw, and articulating laterally with the distal ends of the palatoquadrates. The Meckel's cartilages are fused together at the symphysis in some shark-like fishes or are articulated to a symphysial cartilage in others.

Medial teeth: Small oral teeth, generally symmetrical and with narrow roots, in one row at the symphysis and often in additional paired rows on either side of the symphysial one.

Medial: Inwards, in the transverse direction towards the middle of the body. See **lateral**.

Mesial: In oral teeth, mesial structures are towards the midlines of the jaws, the symphyses. See **distal**.

Mesopterygium: In the pectoral fin skeleton of living neoselachians, the middle basal cartilage, between the propterygium and metapterygium. The mesopterygium is sometimes fused to the propterygium or metapterygium, or to both.

Mesorhipidion: A knife-like or blade-like structure on the lateral clasper glans of some carcharhinoid sharks, formed from the terminal 3 cartilage, and over and partially lateral to the ventral terminal and mesial to the pseudopera.

Metapterygial axis: In the pectoral fin skeleton of living neoselachians, the posterior extension of the mesopterygium as a flattened, elongated segmented series of cartilages that supports the distal bases and free rear tips of the pectoral fins; the axis has radials along its distal edge continuous with the radials on the metapterygial basal.

Metapterygial basal: In the pectoral fin skeleton of living neoselachians, the anteriormost, expanded cartilage of the metapterygium.

Metapterygial proximal segment: In the hexanchoid pectoral fin skeleton, a short jointed segment on the proximal end of the metapterygial basal, not found in other sharks.

Metapterygium: In the pectoral fin skeleton of living neoselachians, the rearmost basal cartilage, adjacent to the posterior edge of the mesopterygium and with several radials attached to its distal edge. It includes the **metapterygial basal** and the **metapterygial axis**.

Molariform: In oral teeth, referring to a tooth with a broad flat crown with low cusps or none, for crushing hard-shelled invertebrate prey.

Monospondylous precaudal vertebrae: Vertebrae with one centrum and one pair of basidorsals, basiventrals, and ribs per body segment (myotome), and generally extending from the occiput to the end of the body cavity and to over the pelvic girdle. However there is much variation in the position of the monospondylous-diplospondylous transition, which can range well in front or behind the pelvic girdle.

Monospondylous-diplospondylous transition: The position on the vertebral column where monospondylous centra end and diplospondylous centra begin. In lateral view the transition often appears as an abrupt decrease in length of the diplospondylous centrum compared to the last monospondylous centrum, but this can be obscure in various sharks with very numerous, very short centra. Often a centrum of intermediate length appears between a long monospondylous centrum and a short diplospondylous centrum. In a few sharks there is a **stutter zone** of alternating long and short centra that marks the transition. Also, the basidorsals and basiventrals have foramina for the spinal nerves on every other vertebra, rather than on each vertebra as in monospondylous vertebrae. The transition from long to short centra is generally coordinated with the transition of vertebrae with free ribs and no haemal arches to those without ribs and with haemal arches. However, in some sharks the two transitions can be anterior or posterior to each other.

Multiple oviparity: A mode of egg-laying or oviparity in which female sharks retain several pairs of cased eggs in the oviducts, in which embryos grow to advanced developmental stages. When deposited on the bottom (in captivity) the eggs may take less than a month to hatch. Found only in the scyliorhinid genus ***Halaelurus***, with some uncertainty as to whether the eggs are normally retained in

the oviducts until hatching. Eggs laid by these sharks may be abnormal, unusual, or an alternate to ovoviviparity. The whale shark (***Rhincodon typus***) may have multiple retention of egg cases; near-term foetuses have been found in their uteri and egg-cases with developing foetuses have been collected on the bottom.

Nasal aperture: On the neurocranium, an aperture in the anteroventral surface or floor of each nasal capsule, through which the nostril directs water into and out of the nasal organ.

Nasal capsules: On the neurocranium, a pair of spherical, oval or trumpet-shaped, thin-walled structures behind the rostrum (when present) and in front of the orbits, cranial roof and basal plate. They serve as containers for the nasal organs or organs of smell, and have passages into the cranial cavity to connect the nasal organs with the brain.

Nasal curtain: Anterior nasal flaps that are expanded medially and posteriorly and have fused with each other. Nasal curtains are found in some carcharhinoid sharks and in many batoids.

Nasal flap: One of a set of dermal flaps associated with the nostrils, and serving to direct water into and out of them, including the anterior, posterior, and mesonarial flaps.

Nasal fontanelle: On the neurocranium, an aperture in the posteroventral surface or floor of each nasal capsule, behind the nasal apertures and closed by a dermal membrane.

Nasoral grooves: Many bottom-dwelling, relatively inactive sharks have nasoral grooves, shallow or deep grooves on the ventral surface of the snout between the excurrent apertures and the mouth. The nasoral grooves are covered by expanded anterior nasal flaps that reach the mouth, and form water channels that allow the respiratory current to pull water by partial pressure into and out of the nostrils and into the mouth. This allows the shark to actively irrigate its nasal cavities while sitting still or when slowly moving. Nasoral grooves occur in heterodontoids, orectoloboids, chimaeroids, some carcharhinoids, and most batoids. Also termed **oronasal grooves**.

Neck: A narrow band of finely porous dull tissue (possibly orthodentine) encircling the proximal end of the crown of a tooth, and apparently covered with dental membrane.

Neoselachian: Referring to the Neoselachii.

Neoselachii: From Greek *neos*, new, and *selachos*, shark. The modern sharks, the subcohort Neoselachii, consisting of the living elasmobranchs and their immediate fossil relatives. See **Euselachii**.

Neotype: A specimen, not part of the original type series for a species, which is designated by a subsequent author, particularly if the holotype or other types have been destroyed, were never designated in the original description, or are presently useless.

Neural arch: In shark vertebrae, a dorsal arch formed by basidorsal and interdorsal cartilages above the centrum and forming a **neural canal** containing the spinal cord.

Neural spines: On the neural arches of shark vertebrae, elevated dorsal plate-like surfaces, particularly well-developed in many squalomorph sharks.

Neurocranium: In sharks, a box-shaped complex cartilaginous structure at the anterior end of the vertebral column, containing the brain, housing and supporting the nasal organs, eyes, ears, and other sense organs, and supporting the visceral arches or splanchnocranium. Also termed **chondrocranium**, **chondroneurocranium**, or **endocranium**.

Nictitating lower eyelid: In the ground sharks (order Carcharhiniformes), a movable lower eyelid that has special posterior eyelid muscles that lift it and, in some species, completely close the eye opening (or palpebral aperture). Often incorrectly termed **nictitating membrane**, a different, nonhomologous structure in terrestrial vertebrates.

Nictitating upper eyelid: In parascylliid orectoloboids, the upper eyelid has anterior eyelid muscles that pull it down and close the eye opening, analogous to the nictitating lower eyelids of carcharhinoids.

Nomenclature: In biology, the application of distinctive names to groups of organisms.

Nostrils: The external openings of the cavities of the nasal organs, or organs of smell.

Notochord: In embryonic sharks (and other chordates) the notochord is a fluid-filled tube below the spinal cord that has a connective-tissue notochordal sheath surrounding it. The notochord forms the primitive developmental base of the chondrichthyan vertebral column. Chimaeroids retain the notochord and its sheath without constriction (although some have ring-like centra in the sheath), but in neoselachians it is constricted by the development of double-cone calcifications of the centra within the sheath into biconical chambers between each centrum. The addition of centra to the notochordal sheath strengthens the vertebral column. Some deepwater squaloid, hexanchoid, and lamnoid sharks have the sheath constriction and calcified double cones variably reduced, sometimes to connective tissue septa only. Some of these taxa with a 'notochordal' vertebral column have been considered primitive but are apparently derived from ancestors with well-calcified, constricted vertebral centra.

Occipital centrum: On the occiput of the neurocranium, the posterior half of a calcified double cone of the vertebral column, imbedded in the basal plate and articulating with the anteriormost centrum of the vertebral column. Also termed **occipital hemicentrum**.

Occiput: The posteriormost sector of the neurocranium, behind and partially between the otic capsules, with its dorsal surface from the parietal fossa rearwards to the foramen magnum, and its posterior surface including the occipital condyles, the occipital centrum, the paired vagus nerve foramina, the paired glossopharyngial nerve foramina, and the rear surface of the hyomandibular facets.

Ocelli or **eyespots:** Large eye-like pigment spots located on the dorsal surface of the pectoral fins or bodies of some sharks including rays, angel sharks, and some bamboo sharks, possibly serving to frighten potential enemies.

Oophagy: From Greek *oön*, egg, and *phagos*, to eat. Egg-eating, a mode of live-bearing reproduction employing uterine cannibalism; early foetuses deplete their yolk-sacks early and subsist by eating nutritive eggs produced by the mother. Known in several lamnoid sharks, the carcharhinoid family Pseudotriakidae, and in the orectoloboid family Ginglymostomatidae (***Nebrius ferrugineus***).

Optic nerve foramen: A large foramen usually in the middle of the orbital wall, passing the optic nerve from the brain to the eye.

Optic pedicel: On the neurocranium, a slender cartilage that projects from the medial orbital wall and articulates with the eyeball; it serves as a pivot point for the eyeball and a spacer between the eyeball and the orbital wall.

Orbital fissures: The main foramina or fenestrae that pass the trigeminal and facial nerves from the brain to the orbits, located on the posteroventral ends of the medial walls of the orbits.

Orbital notches: On the neurocranium, the paired anterior notches in the suborbital shelves that articulate with the orbital processes of the palatoquadrates. In many squalomorph sharks these are enlarged, deepened, socket-like, and posteriorly situated in the orbits, with telescoping of the suborbital shelves, and are lost in batoids.

Orbits: Large, paired cavities on the sides of the neurocranium, behind the nasal capsules, mostly in front of the otic capsules, and separated medially by the cranial cavity. They are bounded anteriorly by the preorbital walls and processes, dorsally by the supraorbital crests, ventrally by the suborbital shelves (reduced or lost in various squalomorphs), and posteriorly by the postorbital processes and walls. The orbits contain the eyeballs and their muscles, venous sinuses, several arteries that connect to the cranial cavity, and most of the cranial nerves.

Orectoloboid: A carpet shark, a member of the order Orectolobiformes, including barbelthroat carpet sharks, blind sharks, wobbegong sharks, bamboo sharks, epaulette sharks, nurse sharks, zebra sharks, and whale sharks.

Origin: The anterior or front end of the fin base in all fins. The caudal fin has **upper** and **lower** origins but no insertion. See **insertion**.

Orthodentine: A primary hard tissue comprising the crown of oral teeth in sharks, with numerous fine mostly parallel nonvascular tubules.

Orthodont: An oral tooth with its crown filled with orthodentine, and with a prominent central pulp cavity.

Osteodentine: A primary hard tissue comprising the roots and sometimes the inside of the crown in the oral tooth, with bone-like large reticulating, thick-walled tubules.

Osteodont: An oral tooth with its crown filled with osteodentine, continuous with the root, and without a pulp cavity.

Otic capsules: On the neurocranium, a pair of complex thick-walled capsules containing the inner ears, and located between the orbits and the occiput, and partially separated medially by the cranial cavity.

Overlapping dentition: Teeth along a mesodistal series in which the roots overlap and are not separated by a space. Two types of overlap patterns occur, **alternate overlap**, in which teeth in a series alternate from more labial to more lingual, and **imbricate overlap**, in which the distal end of each tooth lingually or labially overlaps the mesial end of the succeeding tooth, repeating to the distal ends of the dental band. **Alternate-imbricate dentitions** combine both alternate and imbricate overlap. See **independent dentition**.

Oviparity: A mode of reproduction in which female sharks deposit eggs enclosed in oblong or conical egg-cases on the bottom, which hatch in less than a month to more than a year, producing young sharks which are miniatures of the adults.

Ovoviviparity: Generally equivalent to **yolk-sac viviparity**, live-bearing in which the young are nourished primarily by the yolk in the yolk-sac, which is gradually depleted and the yolk-sac reabsorbed until the young are ready to be born. Sometimes used to cover all forms of **aplacental viviparity**, including **cannibal viviparity**.

Paired fins: The pectoral and pelvic fins.

Palatoquadrates: The paired upper jaw cartilages, articulating mesially with each other at the midline or symphysis of the upper jaw, and articulating laterally with the distal ends of the Meckel's cartilages. The palatoquadrates are fused to the neurocranium in all living holocephalans. The palatoquadrates of neoselachians are divided into cylindrical anteromedial sectors or **palatine processes**, which articulate or are otherwise attached to each other at the symphysis; variably modified conical to flattened articular structures or **orbital processes** on the middle of the palatoquadrates for attachment to the neurocranium at the orbital notches; and often elevated posterodistal **quadrate processes** that articulate with the distal ends of the Meckel's cartilages and are loosely or firmly attached to the distal ends of the hyomandibulae. In a few living neoselachians, and many fossil elasmobranchs, the quadrate processes have **postorbital articulations** with the rear surfaces of the postorbital processes of the neurocranium.

Palpebral aperture: The eye opening, defined by the upper and lower eyelids.

Papillae: Elongated finger-like processes of skin, located around the spiracles of torpedo rays, and in the mouths and on the gill arches of other sharks.

Papillose gill rakers: See **gill raker papillae**.

Paralectotype: One of two or more specimens that were syntypes in an original description, but which became a paralectotype or paralectotypes when a subsequent author designated one of the syntypes as a lectotype. Paralectotypes are equivalent to paratypes.

Paratype: Each specimen of a type series other than the holotype. Specimens other than the holotype automatically become paratypes unless the author designates them as referred specimens that are not part of the type series.

Parietal fossa: On the neurocranium, a shallow or deep depression between the otic capsules and at the rear of the

cranial roof, that houses foramina for paired ducts leading to the inner ears and for the spaces around them.

Pectoral fins: A symmetrical pair of fins on each side of the trunk just behind the head and in front of the abdomen. These are present in all cartilaginous fishes and correspond to the forelimbs of a land vertebrate (a tetrapod or four-footed vertebrate).

Pectoral or **shoulder girdle:** See **scapulocoracoid**.

Pedicel: In lateral trunk denticles, a narrow stalk separating the crown from the base.

Pelvic fin: A symmetrical pair of fins on the sides of the body between the abdomen and precaudal tail which correspond to the hindlimbs of land vertebrate (a tetrapod or four-footed vertebrate). Also, **ventral fins**.

Pelvic girdle: See **puboischiadic bar**.

Photophores: Conspicuously pigmented small spots on the bodies of most lantern sharks (family Etmopteridae) and some kitefin sharks (family Dalatiidae). These are tiny round organs that are covered with a conspicuous dark pigment (melanin) and produce light by a low-temperature chemical reaction.

Placenta: See **yolk-sac placenta**.

Placental viviparity: Live-bearing in which the young develop a yolk-sac placenta, which is apparently confined to the carcharhinoid sharks.

Placoid scale: See **dermal denticle**.

Plesodic fin: A pectoral, pelvic, dorsal, or anal fin in which the radial cartilages of the fin skeleton extend far into the distal fin web, often near its edges, and between the supporting ceratotrichia of the fin web. Some fossil sharks also have plesodic caudal fins, in which the expanded haemal arches of the caudal vertebrae extend far into the fin web. In more advanced batoids the radials of the plesodic paired fins become highly branched and segmented, very narrow and slender, and essentially replace the ceratotrichia as supports for the fin webs.

Pores, pigmented: In a few sharks and skates, the pores for the lateral line and ampullae of Lorenzini are conspicuously black-pigmented, and look like little black specks.

Posterior: Rearwards, in the longitudinal direction of the caudal-fin tip or tail filament. Also **caudal**.

Posterior margin: In precaudal fins, the margin from the fin apex to either the free rear tip (in sharks with distinct inner margins) or the fin insertion (for those without inner margins).

Posterior nasal flaps: Low flaps or ridges arising on the posterior edges of the excurrent apertures of the nostrils.

Posterior notch: In the caudal fin, the notch in the postventral margin dividing it into upper and lower parts.

Posterior teeth: Small or sometimes enlarged irregular oral teeth near and at the distal ends of the dental bands, with low crowns and sometimes missing cusps.

Posterior tip: The posteriormost corner or end of the terminal lobe of the caudal fin.

Postocular eyelid muscles: A complex of paired head muscles unique to carcharhinoid sharks that originate around the spiracles and insert on the posterior ends of the upper eyelids and nictitating lower eyelids. Primitively they depress the upper eyelid and elevate the nictitating lower eyelid to close the eye, but in more derived carcharhinoids the eye is closed only by elevation of the nictitating lower eyelid.

Postorbital processes: On the neurocranium, posterolateral projections of the supraorbital crests, below which the postorbital walls originate.

Postorbital walls: On the neurocranium, the posterior boundaries of the orbits, variously reduced vertical plates of cartilage that close the orbits between the postorbital processes and the suborbital shelves, more or less reduced in living neoselachians.

Postventral margin: In the caudal fin, the margin from the ventral tip to the subterminal notch of the caudal fin. See **lower** and **upper** postventral margins.

Preanal ridges: A pair of low, short to long, narrow ridges on the midline of the caudal peduncle extending anteriorly from the anal fin base.

Precaudal fins: All fins in front of the caudal fin.

Precaudal pit: A depression at the upper and sometimes lower origin of the caudal fin where it joins the caudal peduncle.

Precaudal tail: That part of the tail from its base at the vent to the origins of the caudal fin.

Precaudal vertebrae: Vertebrae from the occiput to the dorsal origin of the caudal fin.

Predorsal ridge: A low narrow ridge of skin on the midline of the back anterior to the first dorsal fin base.

Preorbital canals: On the neurocranium, anterior passages for the superficial opthalmic nerves out of the orbits and onto the nasal capsules and rostrum, situated at the anteromesial edges of the supraorbital crests at the rear bases of the preorbital processes; sometimes greatly expanded posteriorly.

Preorbital processes: On the neurocranium, anterolateral projections of the supraorbital crests, below which the preorbital walls originate.

Preorbital walls: On the neurocranium, the anterior boundaries of the orbits, curved vertical plates of cartilage that vary from complete to absent in neoselachians.

Preorbitalis muscles: Paired head muscles that primitively originate on the rear of the nasal capsules or on the preorbital walls, run diagonally rearwards, and insert on the adductor mandibulae at the mouth angles. Orectoloboids and heterodontoids have the preorbitalis vertical, with cross-biased fibres in the latter, and the insertions are along the ventral edge of Meckel's cartilage. In derived orectoloboids the origins of the preorbitalis are expanded onto the cranial roof and the muscles greatly expanded.

Primitively the preorbitalis may primarily serve to protrude the jaws, but they may primarily serve to increase the power of the bite in orectoloboids and heterodontoids. Also termed **levator labii superioris muscles**.

Preventral margin: In the caudal fin, the margin from the lower origin to the ventral tip of the caudal fin.

Pristiophoroid: A saw shark, order Pristiophoriformes, family Pristiophoridae.

Propterygium: In the pectoral fin skeleton of living neoselachians, the anteriormost basal cartilage, adjacent to the anterior edge of the mesopterygium and with one or more radials attached to its distal end. In batoids with expanded anterior pectoral fin lobes it becomes expanded and segmented into a **propterygial basal** and **propterygial axis**, similar to the metapterygial basal and axis.

Proximal: In any direction, at the near end of a structure.

Pseudopera: On the external clasper glans, a dorsally opening blind pocket along the lateral edge of the clasper, and about opposite the anterior edge of the glans.

Pseudosiphon: On the external clasper glans, a dorsally opening blind pocket along the medial edge of the clasper, and about opposite the cover rhipidion.

Pterotic horn or **process:** On the neurocranium, elongated posterior projections of the sphenopterotic ridges of the otic capsules.

Puboischiadic bar: A transverse flattened or cylindrical plate in the posterior body wall opposite the anterior ends of the pelvic fins, in front of the vent and at the posterior end of the body cavity, that supports a few anterior pelvic radials and a basal cartilage, the basipterygium. The **pelvic girdle.**

Radial cartilages or **radials:** The small, segmented, more distal cartilages of the precaudal fins, attached proximally to the distal edges of the basal cartilages. In the pectoral fin skeleton of living neoselachians, the radials mostly have three segments but range from no segments to 30 or more. The radial segments adjacent to the pectoral basals are the **proximal radials,** the radial segments furthest from the basals are the **distal radials**, and any segments between them are **intermediate radials**.

Radii: In a vertebral centrum in cross-section, branching plates of calcified cartilage in the intermedialia. These have a radial orientation from the centre of the centrum.

Ray: See **batoid**.

Replacement series: A series of oral teeth that are lingual to the functional series, and not in a functional position on the jaw.

Rhipidion: In nonbatoid sharks, a longitudinal, elongated flap attached to the floor of the glans along its base and with its free edge directed laterally. In skates (Rajoidei) rhipidion is used for a soft mass of erectile tissue in the glans, not necessarily homologous to the rhipidion of nonbatoid sharks.

Rhomboidal: In the form of a rhombus or diamond.

Ribs: On the shark vertebral column, short to elongated paired and typically pointed cartilages attached to the basiventral cartilages and extending into the horizontal septum of the segmented trunk musculature or myomeres. Chondrichthyan ribs are therefore dorsal ribs rather than ventral ribs as in bony fishes (which support the body cavity).

Ring valve: A type of spiral intestinal valve in which the valve turns are very numerous and short and resemble a stack of washers.

Root lobe: Sharks often have the roots of their oral teeth divided into separate lobes at their midlengths, which are termed **mesial** and **distal root lobes**.

Root: The proximal part of the oral tooth, made of porous osteodentine and anchoring the tooth in the dental membrane of the jaw.

Rostral keel: In the neurocranium of squaloids, a large vertical plate on the underside of the rostrum and internasal septum, sometimes reduced, and with the cavities of the subnasal fenestrae on either side of the keel.

Rostral node: On the neurocranium, the anterior end of the rostrum of cartilaginous fishes, and the plate formed by the fused anterior ends of the tripodal rostra in many galeomorph sharks.

Rostromandibular muscle: In the orectoloboid family Parascylliidae, paired head muscles that originate on the sides of the adductor mandibulae muscles and insert via long tendons on the medial rostral cartilage. These are possibly for depressing the snout. Not found in any other sharks, though analogous muscles exist in batoids.

Rostronuchal muscles: In the orectoloboid family Parascylliidae, paired head muscles that originate on the dorsal myomeres of the nape, and insert via long tendons on the medial rostral cartilage. These are possibly for elevating the snout. Not found in any other sharks, though analogous muscles exist in batoids.

Rostrum: On the neurocranium, the cartilaginous anteriormost structure which supports the prenasal snout including lateral line canals and masses of ampullae, and is located in front of the nasal capsules and anterior fontanelle. The rostrum is very variable, and in squalomorph sharks is primitively trough or basin-shaped, while it may be primitively rod-shaped or tripodal in galeomorph sharks. It is absent in a few nonbatoid sharks and in many batoids. See **rostrum, tripodal**.

Rostrum, tripodal: The rostrum of the neurocranium in lamnoid and carcharhinoids is primitively tripodal, with a pair of dorsolateral **lateral rostral cartilages** that arise from the posterolaterodorsal surfaces of the nasal capsules or from the preorbital wall, and a **medial rostral cartilage** that arises from the anteromedial surface of the internasal septum. The medial and lateral rostral cartilages extend anteriorly and articulate or fuse at the rostral node. Living orectoloboids have only the medial rostral cartilage although a tripodal rostrum may be present in some fossil orectoloboids, while heterodontoid sharks lack a rostrum as adults but apparently lose it as embryos.

Row: In oral teeth, a single replicating line of teeth, approximately transverse to the longitudinal jaw axis, which includes functional teeth and their replacements, derived from one tooth-producing area on the jaw.

Saw or **saw-snout:** The elongated snout in sawfish and sawsharks, with side and (in sawsharks) ventral teeth formed from enlarged denticles, used to kill, ensnare or dig for prey. Also termed rostral saw.

Scapulocoracoid: The primitively U-shaped cartilage in the body wall just behind the gills and at the anterior end of the pectoral bases, that supports the pectoral fins and articulates with the pectoral basals. The scapulocoracoid consists of a ventral **coracoid bar** connecting its paired **lateral faces** with articular condyles or ridges for the pectoral basals, and a pair of dorsal **scapular processes** dorsal to the lateral faces. The scapular processes sometimes have separate **suprascapulae** above them, but they are sometimes fused with the scapular processes. The coracoid bar has a medial joint or even a separate medial cartilage (sternal cartilage) in a few living sharks, as with many fossil cartilaginous fishes. The **pectoral** or **shoulder girdle**.

Scroll valve: A type of spiral intestinal valve in requiem and hammerhead sharks in which the valve has uncoiled and resembles a rolled-up bib or scroll.

Second dorsal fin: The posteriormost dorsal fin of two in cartilaginous fishes, ranging in position from over the pelvic-fin bases to far posterior on the precaudal tail.

Secondary caudal keels: Low horizontal dermal keels on the ventral base of the caudal fin in mackerel sharks (Lamnidae) and sometimes somniosids.

Secondary lower eyelid: The eyelid below or lateral to the nictitating lower eyelid, separated from it by a subocular groove or pocket, and, in many carcharhinoids with internal nictitating lower eyelids, functionally replacing them as lower eyelids. Some orectoloboids have shallow subocular grooves separating their non-nictitating lower eyelids from weakly developed secondary lower eyelids. They may, however, be able to close their eye openings by retracting the eyeballs.

Semiplesodic fin: In some sharks, a pectoral or dorsal fin with the fin radial cartilages extending partway into the fin web but not to its distal edges, essentially intermediate between plesodic and aplesodic fins.

Series: In oral teeth, a line of teeth along the jaws which is parallel to the jaw axis and includes teeth from all rows present.

Serrations: In oral teeth, minute teeth formed by the cutting edge of the crown that enhance the slicing abilities of the teeth.

Shark: Generally used for cylindrical or flattened cartilaginous fishes with 5 to 7 external gill openings on the sides of their heads, pectoral fins that are not attached to the head above the gill openings, and a large, stout tail with a large caudal fin; that is, all living elasmobranchs except the rays or batoids. Living sharks in this sense are all members of the Neoselachii, the modern sharks and rays. Shark is also used loosely for fossil chondrichthyans that are not neoselachians but have a shark-like form, and even for 'spiny sharks' (acanthodians) and for certain teleosts. Rays are essentially flattened sharks with the pectoral fins attached to their heads and are cladistically nested within the squalomorph sharks, while living chimaeras are the immediate sister group of living neoselachians and are called ghost sharks or silver sharks. Hence shark is used here in an alternate and broader sense to include the rays and chimaeras.

Shoulder: In oral teeth, an arcuate or straight, convex-edged section of the crown foot, without cusplets and similar to a blade but without a cutting edge.

Single oviparity: A mode of egg-laying or oviparity in which female sharks produce encased eggs in pairs, which are not retained in the oviducts and are deposited on the bottom. Embryos in the egg-cases are at an early developmental stage, and take a few months to over a year to hatch. Found in almost all oviparous cartilaginous fishes.

Siphons: A pair of dermal sacs in the ventral abdominal wall of male sharks, connecting posteriorly with the apopyles of the claspers, and extending anteriorly a variable distance from about opposite the pelvic origins to opposite the pectoral bases.

Skull or **cranium:** The skull or head skeleton of sharks includes the **neurocranium** and the **splanchnocranium** or visceral arches. The visceral arches articulate with and are associated with the neurocranium, but, except for the upper jaws of many holocephalans, are not fused to it. Also termed **syncranium**.

Snout: That part of a cartilaginous fish in front of its eyes and mouth, and including the nostrils.

Sphenopterotic ridge: On the neurocranium, a horizontal ridge along the dorsolateral edge of each otic capsule that either ends at the occiput or terminates in an expanded pterotic process.

Spiracle: A small to large opening between the eye and first gill opening of most sharks and rays, representing the modified gill opening between the jaws and hyoid (tongue) arch. This is secondarily lost in chimaeras and some sharks.

Spiral or **conicospiral valve:** An intestinal valve shaped like a corkscrew or augur, with the valve angled anteriorly and medially in the intestine.

Splanchnocranium: That part of the shark skull including the visceral arches. These include the jaws or mandibular arch, the tongue or hyoid arch, and the five to seven gill or branchial arches. Also, **viscerocranium**.

Squalene: A long-chain oily hydrocarbon present in the liver oil of deepwater cartilaginous fishes. It is highly valued for industrial and medicinal use.

Squaloid: A dogfish shark, a member of the order Squaliformes, including bramble sharks, spiny dogfish, gulper sharks, lantern sharks, viper sharks, rough sharks, sleeper sharks, kitefin sharks, and cookiecutter sharks.

Squalomorph: Referring to the Squalomorphii.

Squalomorphii: The neoselachian superorder Squalomorphii, including the hexanchoid, squaloid, squatinoid, pristiophoroid, and batoid sharks.

Squatinoid: An angel shark, order Squatiniformes, family Squatinidae.

Squatinoid caudal fin: Angel sharks (Squatiniformes) are unique among living sharks in having hypocercal caudal fins

that resemble inverted caudal fins of ordinary sharks. The dorsal margin is subdivided into a **predorsal** margin from the upper origin to its **dorsal tip** (analogous to the preventral margin and ventral tips in ordinary sharks), a **postdorsal** margin (like the postventral margin) from the dorsal tip to its supraterminal notch (similar to the subterminal notch), and a short **supraterminal margin** and large **ventral terminal margin** (similar to the subterminal and terminal margins) between the supraterminal notch and the ventral tip of the caudal. The ventral margin has a preventral margin forming a ventral lobe with the ventral tip and the ventral terminal margin.

Stapedial foramen or fenestra: On the neurocranium, a foramen through the posteroventromedial surface of each suborbital shelf into the orbit, for the stapedial or orbital arteries. It may be greatly expanded into a stapedial fenestra in sharks with greatly coiled stapedial arteries or lost in sharks with the suborbital shelves greatly reduced or absent.

Stapediocarotid foramen: On the neurocranium of certain sharks, fusion of the stapedial and carotid foramina on either side produces a single pair of stapediocarotid foramina.

Subcaudal keel: In a few dogfish sharks (family Centrophoridae), a single longitudinal dermal keel on the underside of the caudal peduncle.

Subethmoid fossa: On the neurocranium, a deep cavity on the ventral surfaces of the nasal capsules and the internasal plate, into which fit the palatine processes of the upper jaws.

Subnasal fenestrae: On the neurocranium of squaloids, a pair of apertures in the internasal plate between the nasal capsules that connect the cerebral cavity with two ventral fluid-filled cavities between the nasal capsules and the rostral keel. The fenestrae themselves are covered by tough membranes as with the anterior fontanelle. Subnasal fenestrae are present in most squaloids but reduced in a few derived species, and are not found in other sharks. Their function is obscure but may be sensory. Also termed **basal communicating canals**.

Suborbital shelf: On the neurocranium, a horizontal plate arising on the ventral junction of the orbital wall and basal plate on each side which extends from the nasal capsule to the otic capsule; it forms the floor of the orbit. A well-developed suborbital shelf is apparently primitive for shark-like fishes but is variably telescoped, reduced or lost in many squalomorph sharks and a few galeomorphs.

Subterminal margin: In the caudal fin, the margin from the subterminal notch to the ventral beginning of the terminal margin.

Subterminal mouth or **ventral mouth:** Mouth located on the underside of the head, behind the snout. Also termed an **inferior mouth**, in reference to its ventral position but not its function. A **superior mouth** (not found in living cartilaginous fishes) is on the dorsal surface of the head.

Subterminal notch: On the caudal fin of most nonbatoid sharks and at least one batoid, the notch in the lower distal end of the caudal fin, between the postventral and subterminal margins, and defining the anterior end of the terminal lobe.

Superficial ophthalmic nerve foramina: Foramina for the roots of the superficial ophthalmic nerves in the medial wall of the orbits, separate from the orbital fissure. These foramina are confluent with the orbital fissure in many sharks.

Supraorbital crest: On the neurocranium, an arched horizontal plate of cartilage forming the dorsal edge of the orbit on each side; it arises from the medial orbital wall and the cranial roof and extends horizontally from the preorbital process to the postorbital process. It is apparently primitive for shark-like fishes but is variably reduced or absent in some living elasmobranchs.

Supraorbital or **brow ridge:** A dermal ridge above each eye, particularly well-developed in heterodontoids and some orectoloboids.

Symphyseal or **symphysial groove:** A longitudinal groove on the ventral surface of the lower jaw of some orectoloboid sharks, extending posteriorly from the lower symphysis.

Symphysial teeth: Larger oral teeth in one row on either side of the symphysis, distal to medials or alternates where present. Symphysials are broader than medials and usually have asymmetrical roots.

Symphysis: The midline of the upper and lower jaws, where the paired jaw cartilages articulate with each other.

Syntype: Two or more specimens used and mentioned in an original description of a species, where there was no designation of a holotype or a holotype and paratype(s) by the describer of the species.

Systematics: Scientific study of the kinds and diversity of organisms, including relationships between them.

Tail: That part of a cartilaginous fish from the cloacal opening or vent (anus in chimaeroids, which lack a cloaca) to the tip of the caudal fin or caudal filament, and including the anal fin, usually the second dorsal fin when present, and caudal fin.

Taxon, plural **taxa:** A taxonomic group at any level in a classification. Thus the taxon Chondrichthyes is a class with two taxa as subclasses, Elasmobranchii and Holocephali, and the taxon ***Galeorhinus***, a genus, has one taxon as a species, ***G. galeus***.

Taxonomy: Often used as a synonym of systematics or classification, but narrowed by some researchers to the theoretical study of the principles of classification.

Term foetus: See **foetus**.

Terminal 3 cartilage: A wedge-shaped or elongated cartilage articulating with the posterior edge of the ventral marginal cartilage and over the ventral terminal cartilages. It supports a variety of structures, including clasper spines and spurs, the shields of many skates (Rajoidei), and the mesorhipidion of some carcharhinoid sharks.

Terminal lobe: In the caudal fin of most nonbatoid sharks and at least one batoid, the free rear wedge-shaped lobe at the tip of the caudal fin, extending from the subterminal notch to the posterior tip.

Terminal margin: In the caudal fin, the margin from the ventral end of the subterminal margin to the posterior tip.

Terminal mouth: Mouth located at the very front of the animal. Most cartilaginous fishes have subterminal mouths, but some species (viper sharks, wobbegongs, angel sharks, frilled sharks, whale sharks, megamouth sharks, and ***Manta***) have it terminal or nearly so.

Thorn: In many batoids, most angel sharks and the bramble shark (***Echinorhinus brucus)***, enlarged, flat conical denticles with a sharp, erect crown and a flattened base (which may grow as the shark grows).

Tongue arch: See **hyoid arch**.

Transverse groove: In oral teeth, a deep groove transverse on the lingual root surface, transecting it into mesial and distal root lobes.

Transverse notch: In oral teeth, a distinct notch in the proximal labial edge of the root at about its midlength.

Transverse ridges: Small narrow ridges on the labial and lingual surfaces of the crown, apicobasally oriented and sometimes extending to the cusp edges.

Tribasal pectoral fin: A pectoral fin skeleton with three basal cartilages, the propterygium, mesopterygium, and metapterygium, primitively found in most euselachians including living neoselachians.

Trilobate lower lip: In advanced orectoloboids, shallow orolabial grooves divide the lower lips into a medial section and a pair of lateral sections.

Tropeic folds: Longitudinal paired ridges on the ventral midline of the abdomen in frilled sharks (Chlamydoselachidae).

Truncate: Blunt, abbreviated.

Trunk: That part of a cartilaginous fish between its head and tail, from the last gill openings to the vent, including the abdomen, back, pectoral and pelvic fins, and often the first dorsal fin.

Umbilical cord: A modified yolk stalk in placental viviparous sharks, carrying nutrients from the placenta to the foetus.

Unpaired fins: The dorsal, anal, and caudal fins.

Upper eyelid: The dorsal half of the eyelid, separated by a deep pocket (conjunctival fornix) from the eyeball. The upper eyelid fuses with the eyeball and the pocket is lost in all batoids.

Upper origin: In the caudal fin, the anterodorsal beginning of the epaxial or upper web of the caudal fin, at the posterior end of the dorso-caudal space (see measurement illustrations).

Upper postventral margin: In the caudal fin, the upper part of the postventral margin of the hypaxial web, from the posterior notch to the subterminal notch.

Uterine cannibalism or **cannibal viviparity:** A mode of reproduction in which foetuses deplete their yolk-sacks early and subsist by eating nutritive eggs produced by the mother (see **oophagy**) or first eat smaller siblings and then nutritive eggs (see **adelphophagy**).

Vent: The opening of the cloaca on the ventral surface of the body between the inner margins and at the level of the pelvic fin insertions.

Ventral: Downward, in the vertical direction of the abdomen. See **dorsal**.

Ventral fin: See **pelvic fin**.

Ventral lobe: In the caudal fin, the expanded distal end of the preventral and lower postventral margins, defined by the posterior notch of the caudal fin.

Ventral margin: In the caudal fin, the entire ventral margin from lower origin to posterior tip, either a continuous margin or variably subdivided into preventral, postventral, subterminal and terminal margins.

Ventral marginal: In the clasper skeleton, a flat semicylindrical cartilage that is partially fused to the lateral edge of the axial cartilage, and forms the lateral wall of the clasper groove.

Ventral terminal: On the skeleton of the clasper glans, an often triangular, elongated, curved, plate-like cartilage that articulates or is attached to the lateral or ventrolateral edge of the end-style and to the posterior end of the ventral marginal cartilage.

Ventral tip: In the caudal fin, the ventral apex of the caudal fin where the preventral and postventral margins merge.

Vertebra, plural **vertebrae:** A single unit of the vertebral column, including a vertebral centrum and associated cartilages that form neural arches and ribs or haemal arches.

Vertebral axis: That part of the vertebral column inside the base of the caudal fin.

Vertebral column: The entire set or string of vertebrae or 'backbone' of a shark, from the rear of the chondrocranium to the end of the caudal base. Living elasmobranchs range from having as few as 60 vertebrae (some squaloids of the family Dalatiidae) to as many as 477 vertebrae (thresher sharks).

Visceral arches: See **splanchnocranium**.

Viviparity: Used in two ways in recent literature, as being equivalent to **placental viviparity** only, that is for carcharhinoid sharks with a yolk-sac placenta; or for all forms of live-bearing or **aplacental viviparity**.

Web, fin: See **fin web**.

Yolk sac or **yolk sack:** Almost all sharks start embryonic development somewhat like a chicken, as a large spherical yolky egg inside an elongated shell, the egg case. A small disk of dividing cells represents the pre-embryo or blastula atop the huge yolk mass. The blastula expands around the sides and ventral surface of the yolk mass, and differentiates into an increasingly shark-like embryo, the yolk sac or bag-like structure containing the yolk, and a narrow tubular yolk stalk, between the abdomen of the embryo and the yolk sac.

Yolk stalk: The connecting passage between embryo or foetus and yolk sac, which allows yolk to pass from the sac into the embryonic gut.

Yolk-sac placenta: An organ in the uterus of some ground sharks (order Carcharhiniformes), formed from the embryonic yolk-sac of the embryo and maternal uterine lining, through which maternal nutriment is passed to the embryo. It is analogous to the placenta of live-bearing mammals. There are several forms of yolk-sac placentas in carcharhinoid sharks, including entire, discoidal, globular, and columnar placentas (see Compagno, 1988).

Yolk-sac viviparity: Live-bearing in which the young are nourished primarily by the yolk in the yolk sacs, which is gradually depleted and the yolk sacs reabsorbed until the young are ready to be born.

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