Relationships of the Megamouth Shark, *Megachasma pelagios* (Lamniformes: Megachasmidae), with Comments on Its Feeding Habits

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ABSTRACT

The hypothesis that the megamouth shark (*Megachasma pelagios*, order Lamniformes, family Megachasmidae) is a cetorhinid is rejected by phenetic and cladistic analyses. A phenetic list of characters separating *Megachasma* and *Cetorhinus* is presented. A cladistic analysis of the Lamniformes rejects the hypotheses that *Megachasma* is the sister group of *Cetorhinus* or that *Megachasma* is the primitive sister of all other lamnoids. The Megachasmidae is the primitive sister group to the Alopiidae, Cetorhinidae, and Lamnidae; the Cetorhinidae is sister to the Lamnidae; and the Alopiidae to the Lamnidae and Cetorhinidae. *Mitsukurina* may be the primitive sister group of all other lamnoids, but relationships of other lamnoids with aplesodic pectoral fins is uncertain. The Alopiidae are monophyletic, with *Alopias vulpinus* the primitive sister species of *A. pelagicus* and *A. superciliosus*. The Lamnidae are also monophyletic, but the arrangement of *Lamna* as the sister genus of *Carcharodon* and *Isurus* requires confirmation. Some Cenozoic fossil shark teeth, including *Megascyliorhinus*, may be megachasmids but tentatively fall in their own genus or genera. The Cretaceous *Squalicorax* has some derived cranial features in common with *Megachasma* but otherwise is very different and probably had a macropredatory life-history style. The megamouth shark probably does not passively filter its food while swimming as does the basking shark; it probably expands its buccal cavity and sucks its prey into its mouth. This would be more efficient if the mouth of this shark was luminescent and attracted prey.

Introduction

On 15 November 1976, a U.S. Navy research vessel working off Oahu, Hawaii caught a 750 kg, 446 cm long adult male shark of bizarre and unusual form (Fig. 1A) in a parachute sea anchor and brought it to port despite its flabby bulk. The first "megamouth shark", as it was soon dubbed by the press because of its enormous mouth and jaws, was frozen and preserved intact and is now housed in the Bernice P. Bishop Museum (BPBM), Honolulu, Oahu, Hawaii. On 29 November 1984, a second adult male megamouth shark, 449 cm long and weighing ~705 kg, was captured in a pelagic gill net by a commercial fishing boat off Catalina Island, California and preserved intact in the Natural History Museum of Los Angeles County (LACM) (Lavenberg and Seigel 1985). On 18 August 1988, a third megamouth shark, an adult male 515 cm long and weighing ~690 kg, washed up alive on a beach at Mandurah, near Freemantle, Western Australia and was collected and preserved intact by the Western Australian Museum (G. R. Allen and N. Haigh, Western Australian Museum, Perth, Australia, pers. commun., 1988).

Taylor et al. (1983) described the megamouth shark as *Megachasma pelagios* in the monotypic family Megachasmidae (order Lamniformes, lamnoid sharks). Taylor et al. gave definitions of *Megachasma pelagios* and the Megachasmidae and compared the Megachasmidae with other lamnoid families. Lamnoid derived characters of the Megachasmidae include its elongated ring intestinal valve, reduction of basal ledges and grooves on its teeth, possibly its osteodont tooth histotype (Compagno 1988), absence of subocular ridges, reduced labial cartilages, and vertebral calcification pattern.

Taylor et al. (1983) noted that the megamouth shark shared derived plesodic pectoral fins with the advanced lamnoid families Alopiidae, Cetorhinidae, and Lamnidae and had teeth that are superficially similar to those of the only other lamnoid filter feeder, the basking shark

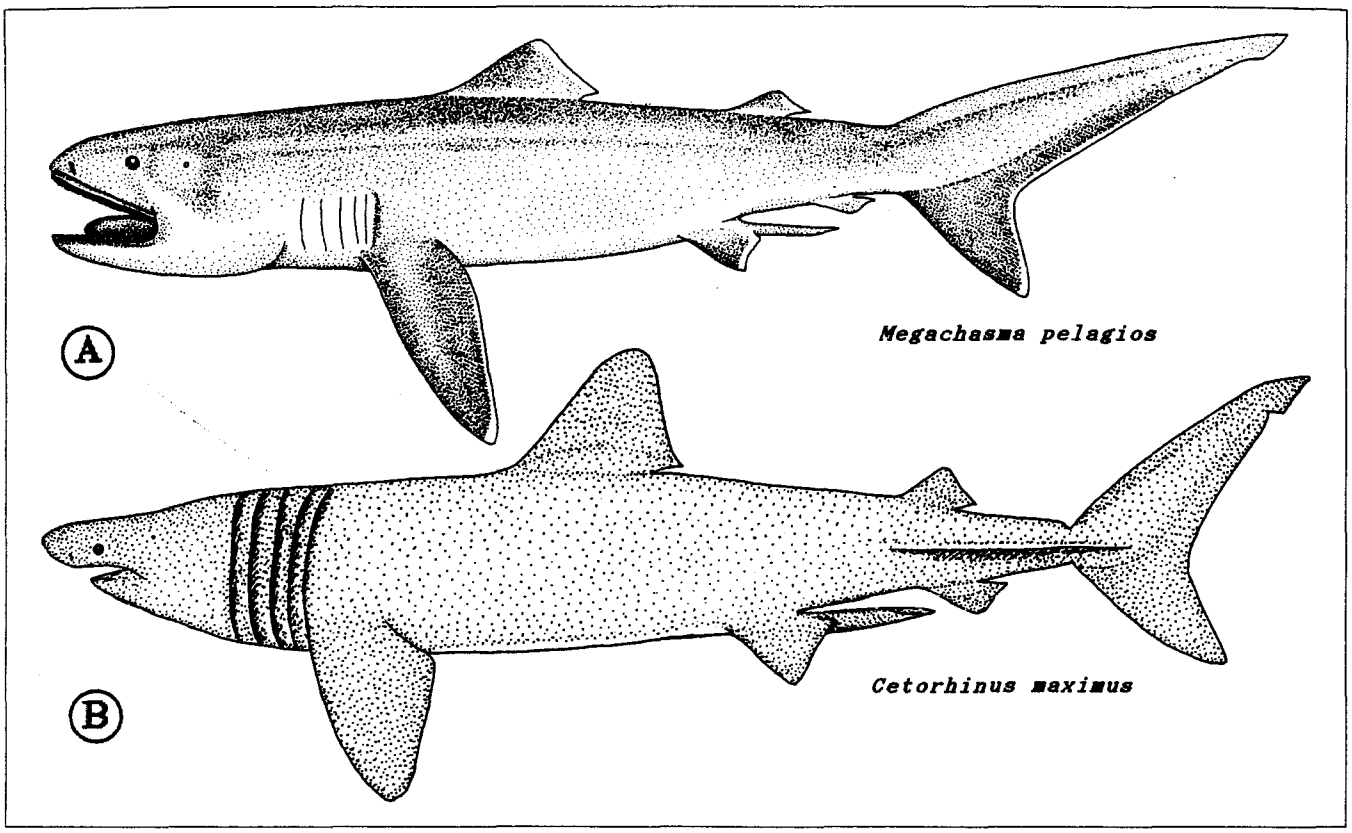


Figure 1.

A, Megamouth shark, *Megachasma pelagios* Taylor, Compagno and Struhsaker, 1983, based on the holotype (BPBM-22730, 4460 mm adult male), from Compagno (1984). B, Basking shark, *Cetorhinus maximus* (Gunnerus, 1765), original drawing based on LACM-35593-1 (7010 mm adult male).

(*Cetorhinus maximus*, family Cetorhinidae). Taylor et al. suggested, as an alternative to placing megachasmids with the advanced lamnoids, that the Megachasmidae might be the primitive sister group of all other living lamnoids. This was based on the presence of strong palatoquadrate orbital processes and the absence of differentiated tooth row groups in *Megachasma pelagios*, which was thought at the time to be primitive relative to other lamnoids. However, Taylor et al. suggested that the simple dentition of the megamouth shark might be secondarily reduced, correlated with its functional replacement by gill rakers.

Maisey (1985) rejected the placement of *Megachasma* as the sister-group of all other lamnoids but was convinced that plesodic pectorals united *Megachasma* with the advanced lamnoid families. He suggested that the megamouth shark was confamilial with the basking shark (Fig. 1B) because of synapomorphies in their jaw suspension, cranial morphology, dentition, and filter-feeding structures. Maisey (1985) stated that *Cetorhinus* and *Megachasma* "seem to form a monophyletic group of specialized filter-feeding lamniforms."

Fossil shark teeth similar to those of the living megamouth shark (Fig. 2J-L) were known from early Miocene deposits of the southern San Joaquin Valley of California since the 1960s (S. P. Applegate, Instituto de Geologia, Universidad Nacional Autonoma de Mexico, Mexico City, Mexico, pers. commun., 1970). These common fossils were difficult to place, and paleontologists and neontologists disagreed as to whether they were primitive carcharhinoid sharks (Scyliorhinidae or Pseudotriakidae) or noncarcharhinoid sharks. Apart from external differences, these teeth have an osteodont histotype unlike the orthodont type of primitive carcharhinoids (see Compagno 1973b, 1988). Similar teeth were subsequently found in the late Oligocene or early Miocene of northern California and central Oregon, Phillips et al. (1976) (B. J. Welton, Chevron Oil Field Research Co., Bakersfield, California, pers. commun., 1983). After the capture of the first megamouth shark and comparison of its teeth with these fossils, it seemed likely that the fossils were megachasmids.

Cappetta and Ward (1977) described *Megascyliorhinus* as a fossil catshark (Carcharhiniformes: Scyliorhinidae), based on *M. cooperi* Cappetta and Ward, 1977 (Fig. 2G-I) from Eocene London Clay. Previously Antunes and Jonet (1970) had described *Rhincodon miocaenicus*, a supposed fossil whale shark (Fig. 2E-F), from the Miocene of Portugal, but

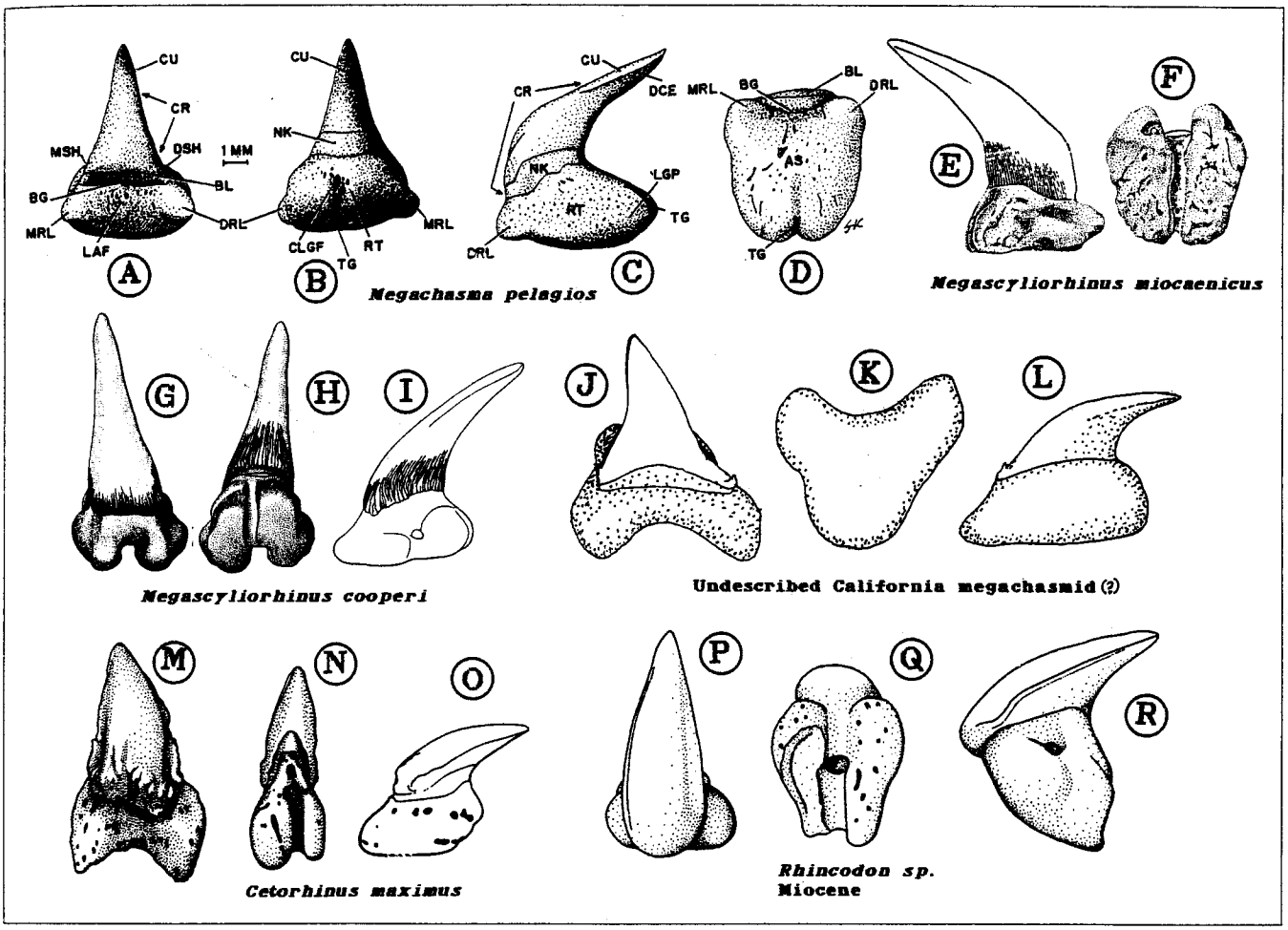


Figure 2.

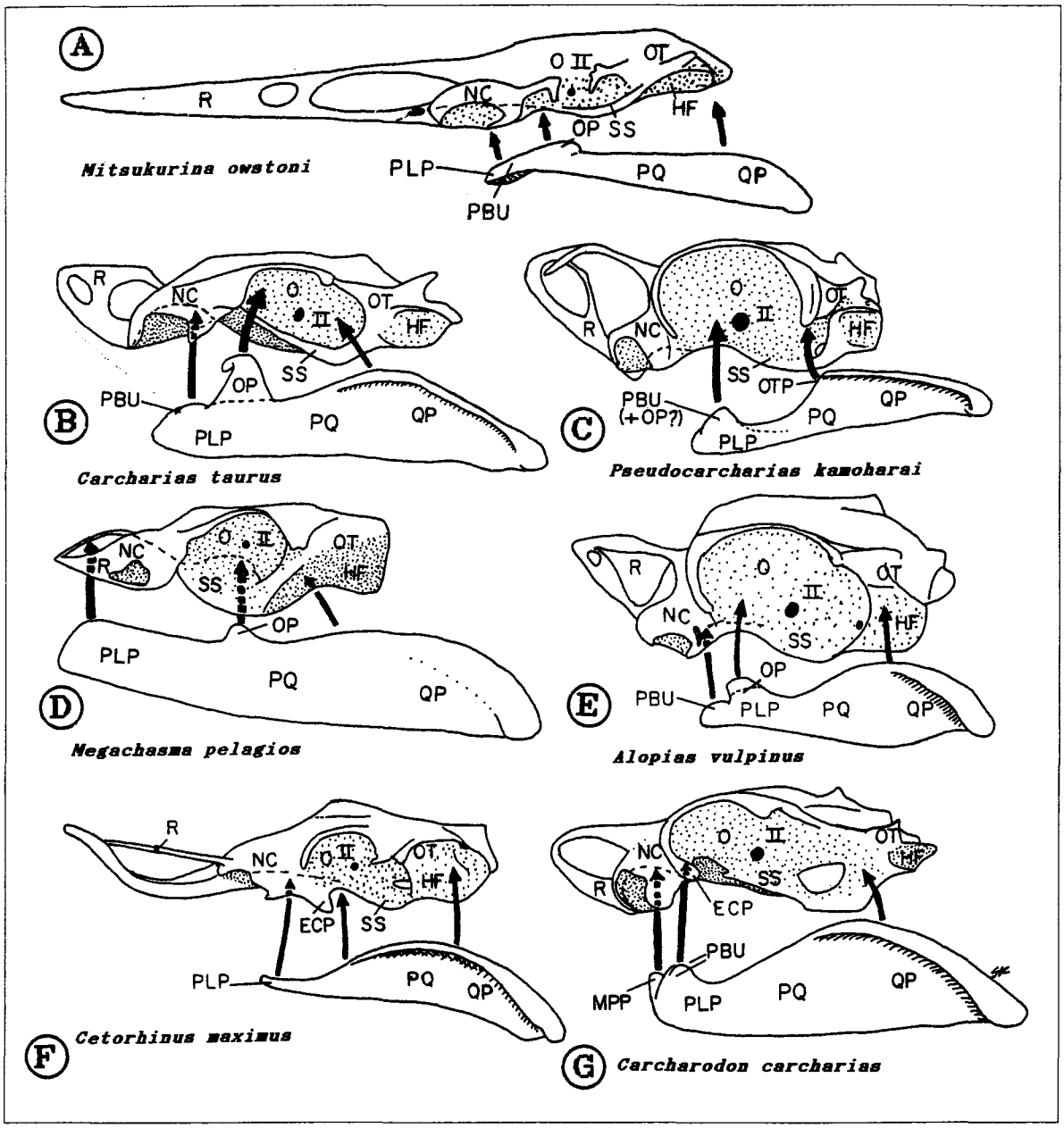
Teeth of megachasmids and other sharks with reduced roots and crowns. A–D, *Megachasma pelagios*, tooth of BPBM-22730 in A, labial; B, lingual; C, lateral; and D, basal views, after Taylor et al. (1983). E–F, *Megascyliorhinus miocaenicus* (Antunes and Jonet, 1970), tooth of the holotype in E, lateral and F, basal view, after Antunes and Jonet (1970). G–I , *Megascyliorhinus cooperi* Cappetta and Ward, 1977, tooth of the holotype in G, labial; H, lingual; and I, lateral views, after Cappetta (1987). J–L, Undescribed megachasmidlike teeth (LACM-VP-10353, Jewett Sand, Pyramid Hill, Kern Co., California, Miocene, Arikareean), original, in J, labial; K, basal; and L, lateral views. M–O, *Cetorhinus maximus*, teech in M, labial; N, basal; and O, lateral views, from Cappetta (1987). P–R, *Rhincodon* sp. from Miocene of France, tooth in P, labial; Q, basal; and R, lateral views, from Cappetta (1987).

Cappetta and Ward transferred it to the Scyliorhinidae and to their genus *Megascyliorhinus*. Cappetta (1987) noted several additional records of *Megascyliorhinus* species from the Lower Eocene to the Pleistocene of Europe, Africa, Australia, New Zealand, South America, and Japan. Cappetta retained *Megascyliorhinus* in the Scyliorhinidae, but noted that this genus has osteodont teeth and may not be a scyliorhinid or a member of the order Carcharhiniformes. Some paleontologists (D. A. Ward, University of London, London, England, pers. commun., 1979; F. J. Pfeil, Pfeil Verlag, Munich, West Germany, pers. commun., 1986) have suggested that *Megascyliorhinus* is a megachasmid and that *Megachasma* may even be a synonym of *Megascyliorhinus*.

This paper reviews the relationships of the megamouth shark to the basking shark and other living lamnoids, and to possible fossil relatives. In addition, the scenario for megamouth feeding presented by Taylor et al. (1983) is reconsidered and modified with further morphological evidence from two of the three specimens of *Megachasma pelagios*.

Taxonomic Characters and Terminology

The taxonomic characters used here are primarily derived from the specimens listed below (see Appendix: Comparative Material of Lamnoid Taxa). The works of Pavesi (1874, 1878), Haswell (1885), Parker (1887), Jordan (1898), Jungersen (1899), Garman (1913), Ridewood (1921), Senna (1925), White (1937), Matthews (1950),



Matthews and Parker (1950), Springer and Garrick (1964), Parker and Stott (1965), and Branstetter and McEachran (1986) were of particular use in supplementing specimens.

Jaw morphology and suspension in lamnoids (Fig. 3) is more variable than in other sharks and shows a number of derived states beyond the primitive type in Alopiidae and Odontaspididae. These have palatoquadrates with large orbital processes (OP) articulating in the orbital notches of the orbit as in carcharhinoids, and large dental bullae that articulate with the subethmoid fossa of the chondrocranium. The derived types are discussed in Compagno (1988) and below. The term "orbital process" is not restricted to dorsomesial articular projections of the palatoquadrate palatine processes in squalomorph and squatinomorph sharks only, as proposed by Maisey (1980, 1985). Orbital processes also include similar processes on the palatoquadrates of some lamnoids and other galeomorph sharks (Compagno 1988).

The chondrocranium of living lamnoids (Figs. 4–7) was especially useful for elucidating the interrelationships of lamnoids. A detailed account of lamnoid cranial morphology is beyond the scope of this account, but will be presented elsewhere.

Lamnoids fall into two groups on the structure of the pectoral fin skeleton. Those genera with aplesodic pectoral fins have the distal radials not extending into the fin web,

Figure 3.

Diagram of jaw suspension types of living lamnoids, and showing cranial-palatoquadrate articulations. A, *Mitsukurina owstoni*, based mostly on RUSI-6206, 1166 mm immature female; derived type in Mitsukurinidae with elongated dental bullae of palatine processes fitting in subethmoid fossa between nasal capsules and slung from orbital notches by loose ethmopalatine ligaments attached to orbital processes. B, *Carcharias taurus*, from CAS 1961-IX:21, 1540 mm immature female; primitive type in Odontaspididae with large dental bullae articulating with subethmoid fossa and with large, semicartilaginous orbital processes articulating with orbital notches. C, *Pseudocarcharias kamoharai*, from LACM-uncat., 1100 mm adult male; derived type in Pseudocarchariidae with dental bullae and orbital processes apparently coalesced, bullae fitting in orbital notches rather than subethmoid fossa, and quadrate processes articulating with postorbital processes. D, *Megachasma pelagios*, from BPBM-22730, 4460 mm adult male; derived type in Megachasmidae with enlarged palatine processes fitting under rostrum, orbital processes fitting in deep, pits in basal plate, and suborbital shelves fitting laterally over palatoquadrates. E, *Alopias vulpinus*, from LJVC-0382, 1605 mm immature female; primitive type in Alopiidae essentially as in Odontaspididae except for reduced jaws. F, *Cetorhinus maximus*, based in part on Maisey (1985), but with cranium modified after LACM-35593-1 and LACM-42649-1; derived type in Cetorhinidae with orbital processes and dental bullae lost and with palatine processes fitting into subethmoid fossa and extending through orbital notches; palatoquadrate movement limited anteriorly by expanded ectethmoid processes, posteriorly by lateral wings of suborbital shelves. G, *Carcharodon carcharias*, from LJVC-0384, 1990 mm immature female; derived type in Lamnidae with no orbital processes, dental bullae and unique mesial processes articulating with subethmoid fossa; ectethmoid processes restrict movement of palatoquadrates anteriorly, lateral wings of suborbital shelves posteriorly.
ABBREVIATIONS: II = foramen for optic nerve; HF = hyomandibular facet; MPP = mesial process at symphysis of palatoquadrates (unique to Lamnidae); NC = nasal capsule; OP = orbital process; OT = otic capsule; PBU = dental bulla of palatine process; PLP = palatine process; PQ = palatoquadrate; QP = quadrate process; R = rostrum; SS = suborbital shelf.

while those with plesodic pectorals have these radials greatly elongated and supporting the fin web. Aplesodic pectoral fins are primitive and plesodic pectorals are derived in living sharks (Compagno 1988).

All living lamnoids have elongated ring intestinal valves (White 1937) with over 15 turns to the valve, which are derived relative to other shark groups. Some lamnoids are further derived in having counts well beyond the 19–30 found in the primitive lamnoids *Mitsukurina* and *Carcharias*. A frequency distribution of valve counts for living lamnoids (Fig. 8) indicates that more derived taxa usually have higher counts.

Several character systems of use in lamnoid systematics, including the hyobranchial skeleton, fin skeletons, clasper morphology, vertebral numbers and ratios, mode of reproduction, and brain morphology are unknown or inadequately known in the megamouth shark and some other lamnoids. These require further investigation and are not included in the analyses here.

Terminology for lamnoid morphology and methodology for its study follows Compagno (1970, 1973a, b, 1979, 1984, 1988) and Taylor et al. (1983). Lamnoid systematics and nomenclature follows Compagno (1984) with one exception. A recent ruling of the International Commission on Zoological Nomenclature (Opinion 1459, 1987) has reinstated the genus *Carcharias* Rafinesque, 1810, which is used here in place of *Eugomphodus* for *C. taurus*.

Phenetic Separation of *Megachasma* and *Cetorhinus*

Maisey's (1985) statement that the megamouth and basking sharks are confamilial is questionable on phenetic arguments. As noted by Taylor et al. (1983), the two genera are vastly divergent in morphology as befits extremely derived specialists with radically different approaches to filter feeding. Even if Maisey (1985) was correct in assuming that *Megachasma* and *Cetorhinus* were sister groups, their morphological distance merits familial separation. Characters separating these genera are summarized as follows.

Characters of *Megachasma*

TRUNK cylindrical but not highly fusiform, tapering rearward from the enormous head (Fig. 1A). Skin soft, muscles very flabby, fins soft and flexible. *Caudal peduncle* slightly compressed and without keels. Upper *precaudal pit* present but lower pit absent, upper shallow and longitudinally oval.

HEAD broad, blunt, very large and long, length greater than abdomen between pectoral and pelvic bases. *Snout* very short, depressed, and broadly rounded. *Nostrils* opposite first fourth of mouth when jaws are retracted. *Mouth* terminal on head and greatly enlarged. Upper jaw and palate iridescent, and lower jaw and tongue covered with black skin that is possibly luminescent. *Jaws* highly protrusible anteroventrally, capable of extending well forward of the snout tip. *Tongue* very large, thick and broad. *Gill openings* moderately large, not extending onto dorsal or ventral surfaces of head. Internal gill openings short, strongly screened by numerous papillose *gill rakers*, which are slender dermal papillae with cartilage cores and covered by normal imbricated denticles. The papillose gill rakers are irregularly situated in tight clusters around the gill openings and are almost certainly not shed.

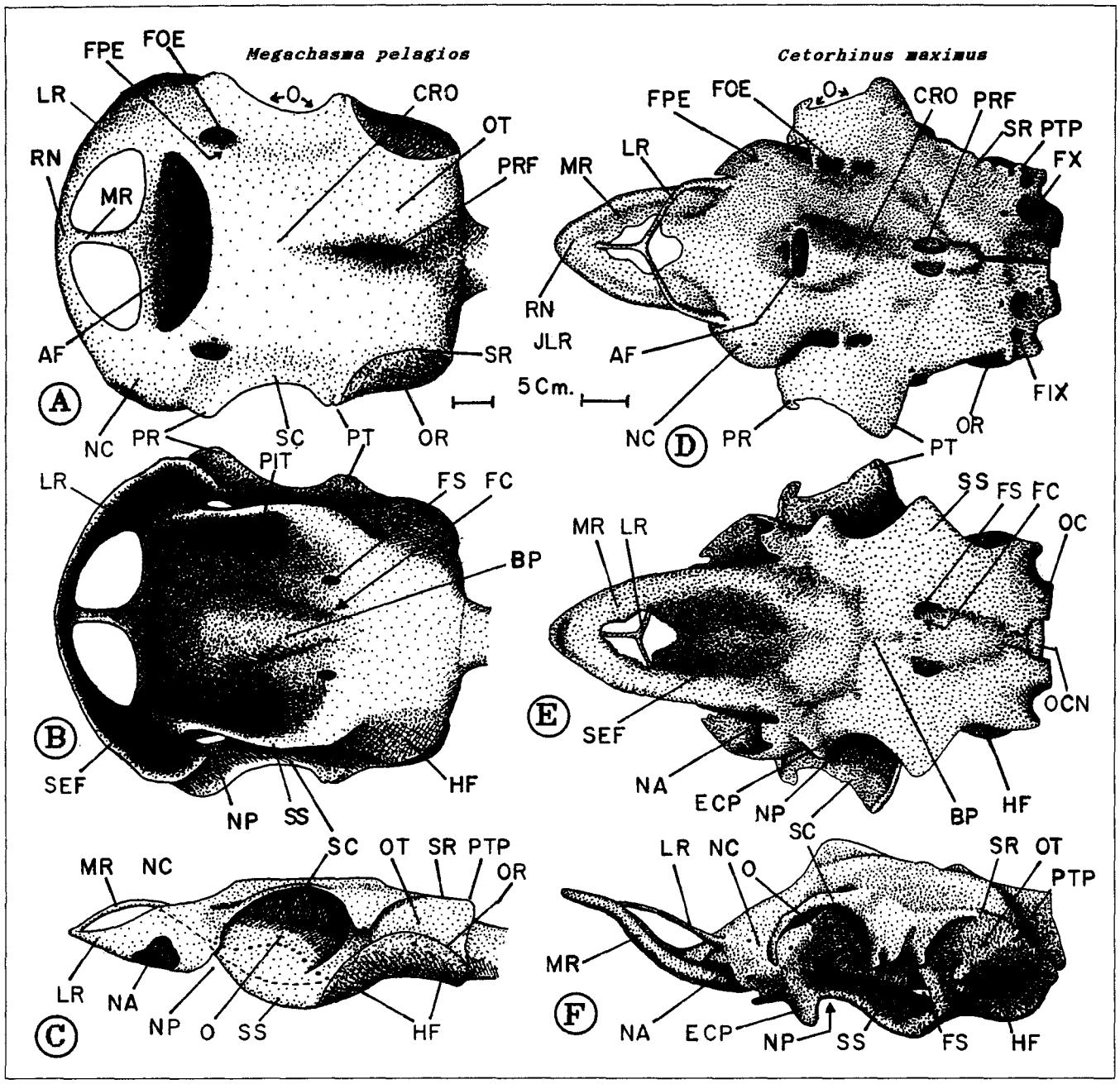


Figure 4.

Chondrocrania of A–C, *Megachasma pelagios*, BPBM-22730, 4460 mm adult male; and D–F, *Cetorhinus maximus*, LACM-35593-1, 7010 mm adult male; in dorsal (A, D), ventral (B, E), and lateral (C, F) views. ABBREVIATIONS: AF = anterior fontanelle; BP = basal plate; CRO = cranial roof; ECP = ectethmoid process; FC = foramen for internal carotid artery; FOE = external fenestra of the preorbital canal; FPE = external profundus foramen; FS = stapedial fenestra; FIX = glossopharyngeal nerve foramen; FX = vagus nerve foramen; HF = hyomandibular facet; LR = lateral rostral cartilage; MR = medial rostral cartilage; NA = nasal aperture; NC = nasal capsule; NP = orbital notch; O = orbit; OC = occipital condyle; OCN = occipital centrum; OR = opisthotic ridge; OT = otic capsule; PR = preorbital process; PRF = parietal fossa; PIT = depression for oribital processes of palatoquadrates; PT = postorbital process; PTP = pterotic process (barely developed in *Megachasma*); RN = rostral node; SC = supraorbital crest; SEF = subethmoid fossa; SR = sphenopterotic ridge; SS = suborbital shelf.

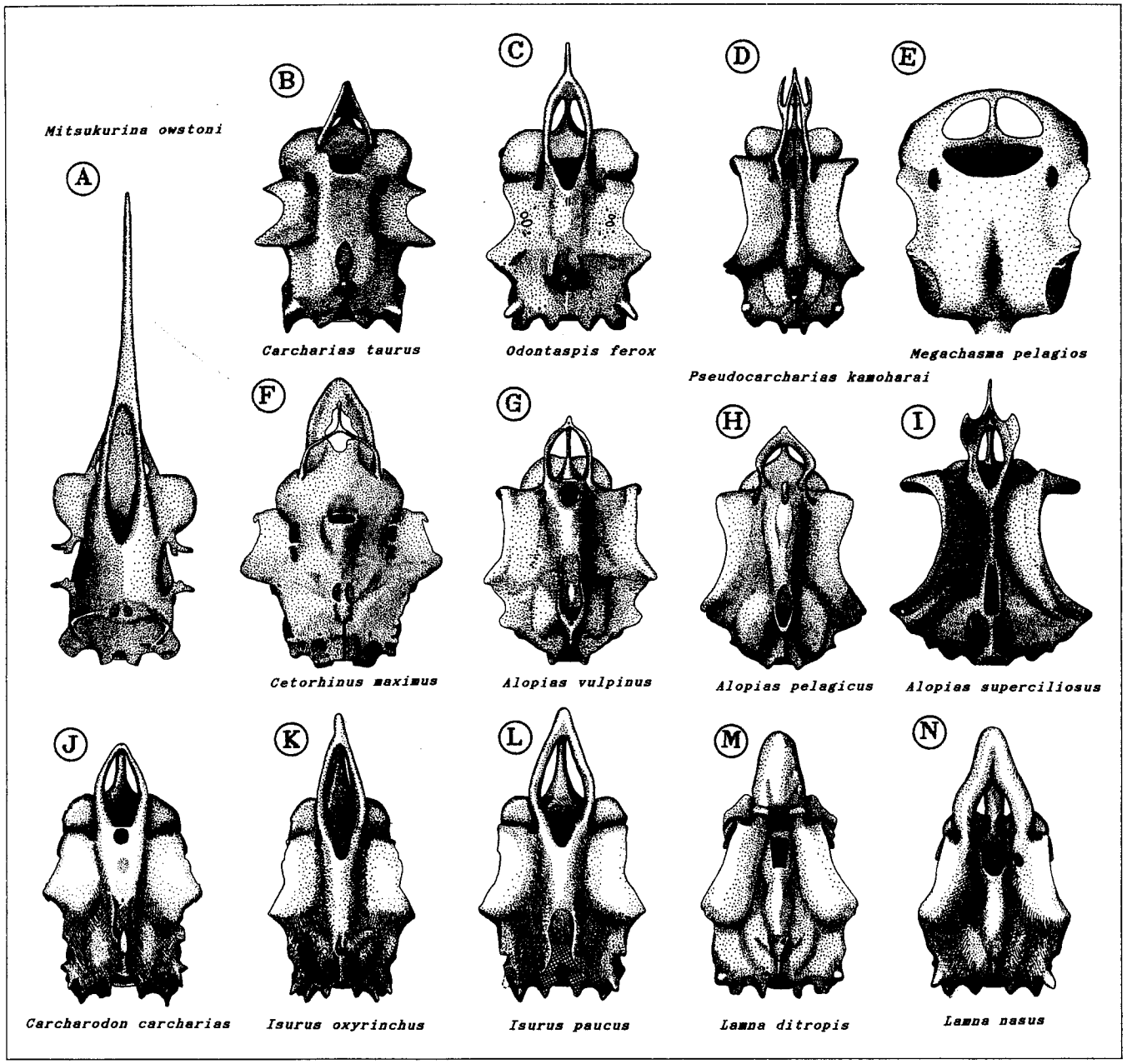


Figure 5.

Chondrocrania of living lamnoids, in dorsal view. A, *Mitsukurina owstoni*, SU-13888, 1130 mm immature female. B, *Carcharias taurus*, CAS 1961-IX:21, 1540 mm immature female. C, *Odontaspis ferox*, LJVC-0272, 2740 mm adult male. D, *Pseudocarcharias kamoharai*, LACM-uncat., 732 mm PCL immature female. E, *Megachasma pelagios*, BPBM-22730, 4460 mm adult male. F, *Cetorhinus maximus*, LACM-35593-1, 7010 mm adult male. G, *Alopias vulpinus*, LJVC-0234, 2057 mm immature female. H, *Alopias pelagicus*, LJVC-0414, 1940 mm immature male. I, *Alopias superciliosus*, LJVC-0355, 2872 mm immature male. J, *Carcharodon carcharias*, LJVC-0187, 2045 mm immature female. K, *Isurus oxyrinchus*, LJVC-0216, 1360 mm immature female. L, *Isurus paucus*, S.P. Applegate uncat., 2175 mm adult male. M, *Lamna ditropis*, LJVC-0112, 2280 mm adult male. N, *Lamna nasus*, LJVC-880127, ~2m.

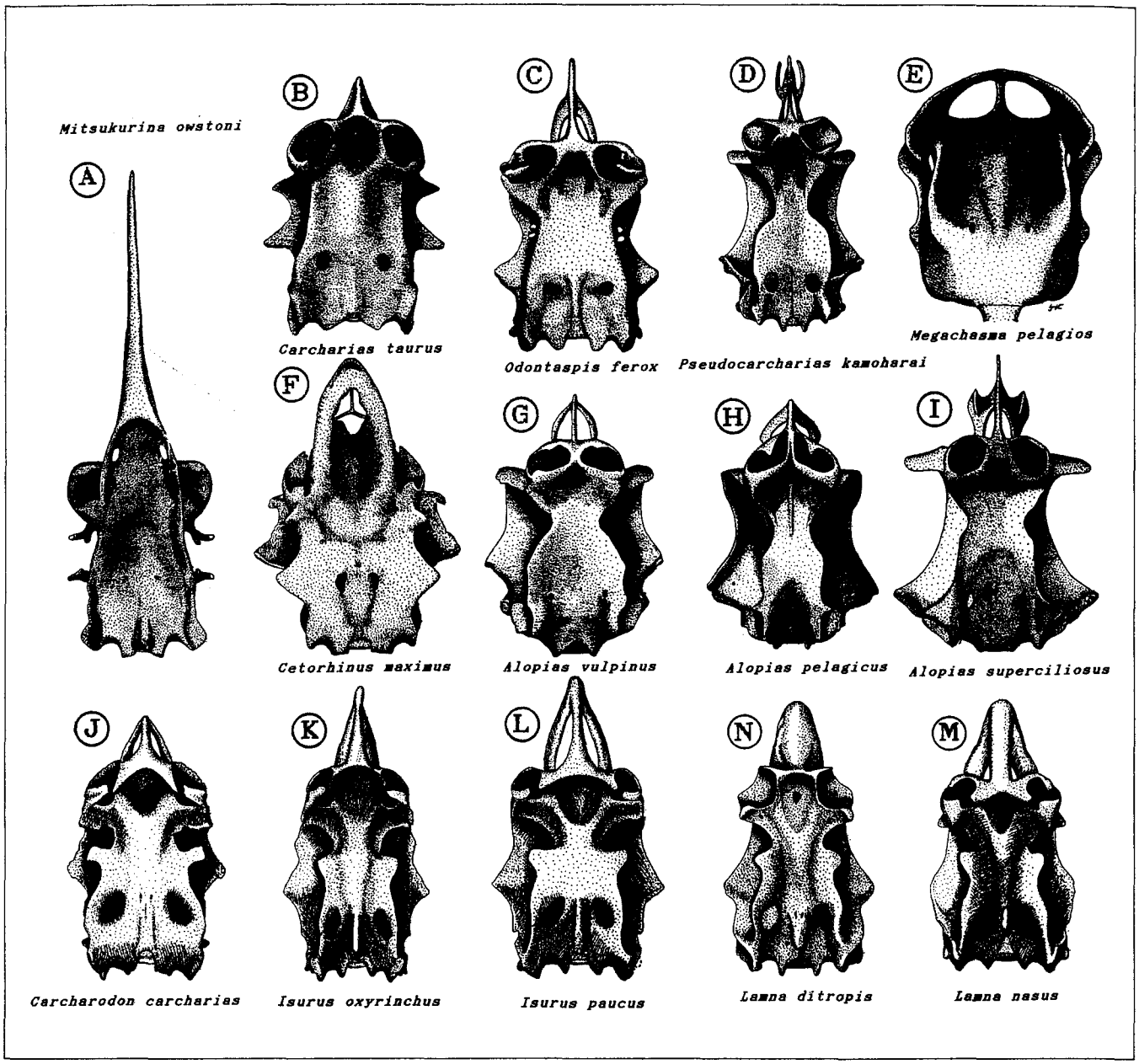


Figure 6.
Chondrocrania of living lamnoids, in ventral view. Same specimens and lettering as Figure 5.

TEETH (Fig. 2A-D) small but about 8 mm. high in adults. Teeth not differentiated into row groups, continually varying, without a gap or small intermediate teeth between anterior and lateral teeth of upper jaw. 108/124 *rows* of teeth present. Very broad medial *toothless spaces* separating dental bands of upper and lower jaws at symphyses, broader on lower jaw than upper. Tooth *roots* moderately long, broad, and flat, with very short labial root lobes, greatly enlarged, expanded lingual protuberances, and obsolete transverse grooves. Tooth *crowns* high, narrow, recurved, flexed, and acutely tipped.

LATERAL TRUNK DENTICLES with broad, teardrop or wedge-shaped, flattened unicuspidate crowns, medial cusps not erect and directed posteriorly. Denticle *pedicles* low and broad. *Denticles* very small and flat, giving skin smooth texture. *Wavy grooves* of naked skin present on the pectoral, pelvic and caudal fin webs.

PECTORAL FINS narrowly leaf-shaped and broad-tipped, length from origin to free rear tip about half anterior margin length. *Pectoral origins* under fourth gill openings. *Pectoral area* about three times first dorsal fin area, anterior margin about 3.2 times pelvic anterior margins.

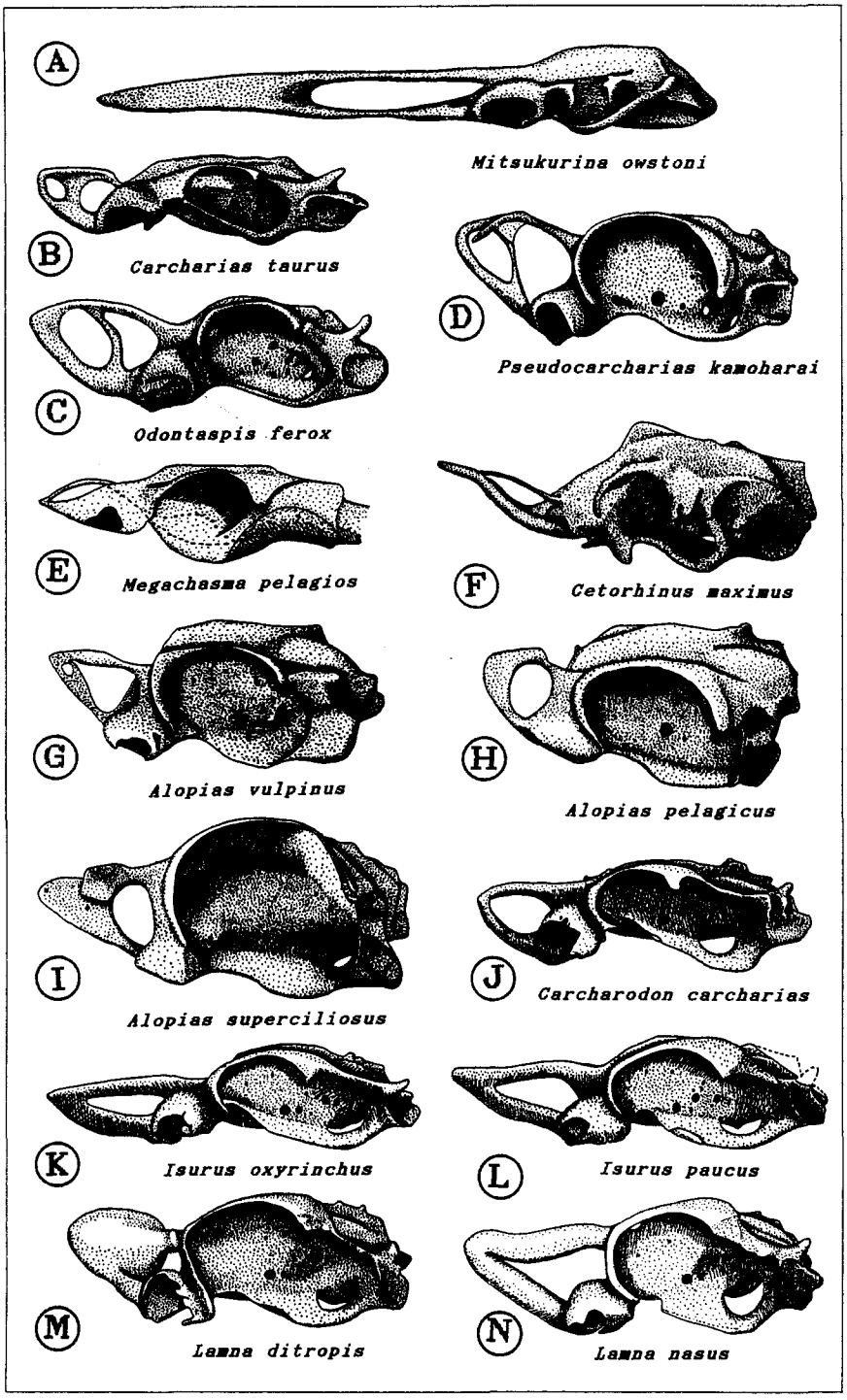


Figure 7.
Chondrocrania of living lamnoids, in lateral view. Same specimens and lettering as Figure 5.

CLASPERS slender and cylindrical, with tapering tips, short glans and small, sharp external spurs.

FIRST DORSAL FIN low, moderately large, with a narrowly rounded apex well in front of fin insertion; first dorsal origin about opposite or slightly behind pectoral insertions, midbase much closer to pectoral fin bases than pelvic bases. First dorsal skeleton low, aplesodic. *Second dorsal fin* low and broad, about twice as large as anal fin. *Anal fin* origin about opposite free rear tip of second dorsal.

CAUDAL FIN not lunate or crescentic, very flexible and elongated, with a long upper lobe about half precaudal length of shark and a third of total length; preventral margin 43% of dorsal margin, subterminal notch weak, and no ripples or undulations present on the caudal margins; caudal vertebral axis at about 20° to body axis.

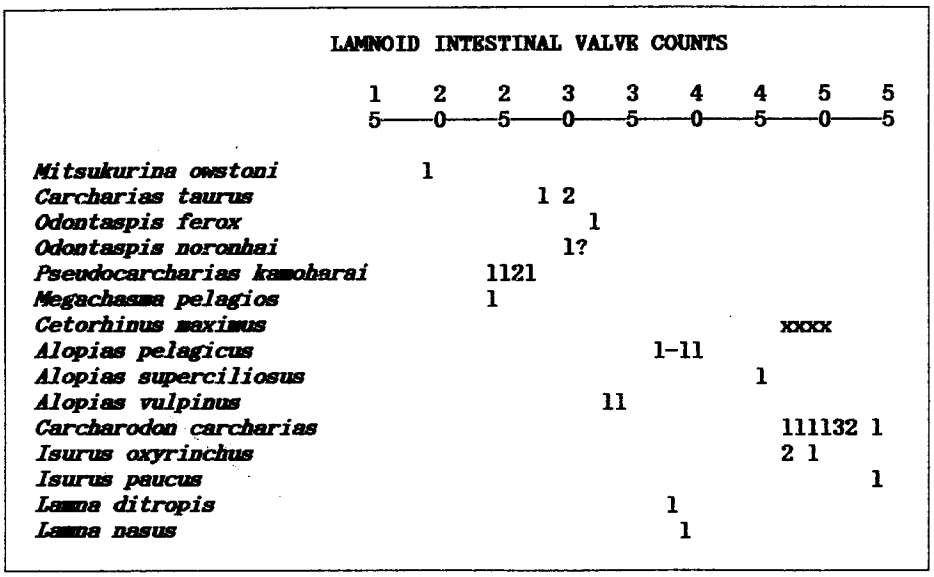


Figure 8.
Intestinal valve counts of living lamnoids. Numbers of specimens counted are indicated, except in *Cetorhinus maximus* for which only a range was available (Matthews and Parker 1950). Count for *Odontaspis noronhai* after Branstetter and McEachran (1986).

CHONDROCRANIUM (Figs. 4A-C, 5E, 6E, 7E) very low and flat, extreme width across preorbital processes about equal to nasobasal length; height of cranium about 40% of nasobasal length. *Rostrum* of simple tripodal form, including a small, moderately elongated, slightly compressed medial rostral cartilage originating from the middle of the internasal plate and a pair of broad-based, triangular lateral rostral cartilages that connect anteriorly in a simple rostral node. *Medial rostral cartilage* a simple rod, without a ventral fossa. Base of medial rostral cartilage elevated by dorsally arched internasal septum above level of bases of lateral rostral cartilages and with shaft of cartilage arching anteroventrally to meet rostral node. Bases of *lateral rostral cartilages* broadly expanded and covering the entire anterior surfaces of the nasal capsules. *Rostral node* of cranium short, narrow, and depressed, without an anteroventral flange. Rostrum short, length from base of medial rostral cartilage to tip of rostral node about 26% nasobasal length, but width across outer bases of lateral rostral cartilages 2.2 times length of rostrum.

NASAL CAPSULES highly compressed, platelike, and wedge- shaped, situated mostly lateral to suborbital shelves; orbitonasal foramina medial to capsules proper. *Nasal apertures* on lateral surfaces of nasal capsules. *Subethmoid fossa* extremely broad and long, expanded anteriorly to below rostral node, between nasal capsules, and posteriorlaterally to merge with orbital pits in basal plate, molded to fit around palatine processes of palatoquadrates when jaws are retracted. External *profundus nerve foramina* well posteriormedial to nasal capsules, opposite midlengths of fenestrae for preorbital canals.

CRANIAL ROOF very broad and flat, not arched above orbits. *Anterior fontanelle* huge, transversely expanded, slightly elevated above level of nasal capsules but with dorsal edge about opposite dorsal edge of orbits. Fontanelle not housed in a separate turret above the cranial roof proper. Width of fontanelle about three times greater than its height and about 53% of nasobasal length. No pit and ridge below lower edge of fontanelle. *Parietal fossa* a single deep elongated slit, with endolymphatic and perilymphatic foramina not immediately visible.

BASAL PLATE very broad, width across orbital notches about 69% of nasobasal length, broadly arched over rear ends of palatine processes of palatoquadrates. Basal plate with a high midventral hump between interorbital septum and internal carotid foramina, but flat between carotid foramina and occiput. A pair of deep, prominent, unique *orbital pits* in the anterior third of basal plate for the orbital processes of palatoquadrates, behind the orbital notches, anterior to the stapedial and carotid openings, and just mesial to the bases of the suborbital shelves. Distance between fenestrae for *stapedial arteries* about 25% of nasobasal length. *Internal carotid foramina* well medial to stapedial fenestrae.

ORBITS nearly circular in lateral view, not expanded behind postorbital processes. *Preorbital processes* low and not much exserted from supraorbital crests. *Supraorbital crests* shallowly concave in lateral and dorsoventral view, tapering posteromesially between preorbital and postorbital processes. *Postorbital processes* short, slightly exserted from supraorbital crests, distance across them much less than distance across preorbital processes. External fenestrae for *preorbital canals* small, behind preorbital processes, and not separating their bases from the nasal capsules. *Suborbital shelves* slightly convex in ventral view, with edges nearly parallel, anterior to stapedial fenestrae, but gently tapering mesially to otic capsules behind them; *orbital notches* extremely shallow, connecting directly to bases of nasal capsules and without ectethmoid processes anterior to them or expanded lateral wings of suborbital shelves behind

them. *Postorbital walls* slanting anteroventrally from below postorbital processes in lateral view.

OTIC CAPSULES with sphenopterotic ridges exserted posterodorsally from the otic capsule, ending in a blunt corner, not expanded as discrete, horn-like pterotic processes. *Opisthotic processes* greatly expanded lateral to sphenopterotic ridges, broadly arched and not undulated. *Hyomandibular facets* broadly crescentic and enormously expanded, covering entire ventrolateral faces of otic capsules and extending in front of postorbital processes onto posterior thirds of suborbital shelves. Hyomandibular facets hardly exserted rearwards from the occiput, rear ends bluntly rounded.

OCCIPUT vertical, vagus and glossopharyngeal foramina small and hardly visible in dorsal view. *Nuchal crest* hardly developed above *foramen magnum*; no medial prominence behind parietal fossa. *Occipital condyles* weak, *Occipital centrum* apparently absent and secondarily lost.

JAWS very long, thick, and stout. *Palatoquadrates* (Fig. 3D) about 1.8 times length of cranium; when retracted palatoquadrates fall with their anterior tips opposite rostral tip and extend from the rostrum to about half their lengths behind the occiput. Palatoquadrates with long, massive, straight *palatine processes* without dental bullae or mesial processes, but with strong, low, and knob-like cartilaginous *orbital processes* that fit in the orbital pits on the underside of the basal plate when the jaws are retracted. Palatoquadrates with low but strong *quadrate processes* which are hardly elevated above palatine processes; quadrate grooves hardly developed on the quadrate processes. Anterior ends of *Meckel's cartilages* ending below anterior ends of palatoquadrates, no "overbite" of latter on Meckel's cartilages. Rear ends of Meckel's cartilages extending well behind joint with palatoquadrates.

VERTEBRAL CENTRA poorly calcified, strong primary calcification of the *double cones* virtually absent and branched secondary *radii* vestigial in the intermedialia, annuli not apparent in vestigial radii; *notochordal sheath* very wide between vertebral centra.

RING INTESTINAL VALVE with 24 turns.

Characters of *Cetorhinus*

TRUNK cylindrical and fusiform, tapering anteriorly from the pectoral fins and posteriorly from the pelvics (Fig. 1B). Skin and muscles firm, fins stiff. *Caudal peduncle* depressed and with strong lateral keels. Both upper and lower *precaudal pits* present, these deep, transverse, and crescentic.

HEAD narrow, conical, pointed, and relatively short, length less than abdomen between pectoral and pelvic bases. *Snout* long, hooked and pointed in young but bluntly conical and bulbous in adults. *Nostrils* well in front of mouth. *Mouth* subterminal on head and moderately enlarged, mouth lining and tongue not iridescent or luminescent. JAWS hardly protrusible anteroventrally, but capable of distending lateroventrally. *Tongue* small and flat. *Gill openings* enormously enlarged, expanded onto dorsal and ventral surfaces of head. Internal gill openings very long, with pretrematic and posttrematic rows of unique *gill raker denticles*. These specialized denticles have compressed bases and hairlike slender crowns that do not greatly impede water flow through the gills but catch small crustaceans on mucous secreted by the pharynx; gill raker denticles are periodically shed.

TEETH (Fig. 2M–O) very small, height less than 6 mm. in adults. Teeth weakly differentiated into row groups, with a gap between anterior and lateral teeth of upper jaw. Over 200 *rows* of teeth present in upper and lower jaws of adults (one counted had 203/229 rows). Narrow *toothless spaces* separating dental bands of upper and lower jaws at symphyses. Tooth *roots* short, narrow, high, and flat, with moderately long labial root lobes, small lingual protuberances, and strong basal grooves. Tooth *crowns* short, thick, not recurved, wedge-shaped, and bluntly pointed.

LATERAL TRUNK DENTICLES with narrow, recurved, unicuspidate, erect crowns with sharp hooked cusps, directed anteriorly and dorsoventrally as well as posteriorly. *Denticles* large, skin with very rough, abrasive texture. No *wavy grooves* of naked skin present on the fin webs, but transverse and longitudinal grooves present on body.

PECTORAL FINS broad, wedge-shaped, and blunt-tipped, length from origin to free rear tip less than half anterior margin length in adults. *Pectoral origins* behind fifth gill openings. *Pectoral area* about equal to first dorsal fin area, anterior margin about twice pelvic anterior margins.

CLASPERS thick and tapering, with a long glans and heavy, blunt external spurs.

FIRST DORSAL FIN high, large, with broadly rounded apex just in front of fin insertion; first dorsal origin behind pectoral free rear tips, midbase about equidistant between pectoral and pelvic bases. First dorsal fin with high semiplesodic fin skeleton. *Second dorsal fin* high and relatively narrow, about as large as anal fin. *Anal fin* origin varying from about opposite second dorsal insertion to opposite second dorsal midbase.

CAUDAL FIN crescentic, stiff and short, with upper lobe about a fourth of precaudal length of shark, preventral margin about 2/3 of dorsal margin in adults, ripples or undulations present on the dorsal caudal margin; caudal vertebral axis at 40 to 45° to body axis in adults.

CHONDROCRANIUM (Figs. 4D–F, 5F, 6F, 7F) very high and arched between orbits but with orbits and otic capsules moderately low, extreme height of cranium about 60% of nasobasal length. *Rostrum* of greatly modified tripodal form: It includes a broad-based, hooked, elongated, greatly depressed medial rostral cartilage originating from the entire width of the internasal plate; and a pair of slender, narrow-based, cylindrical lateral rostral cartilages that connect together in a posterior false rostral node and

extend as a slender medial bar anteriorly to the rear of the true rostral node. *Medial rostral cartilage* complex, formed as a pair of thick lateral bars separated by a thin mesial plate that forms the anterior extension of the subethmoid fossa on the underside of the cartilage, but thickening anteriorly to form the rostral node. Base of medial rostral cartilage not elevated above bases of lateral rostral cartilages and with cartilage arching anterodorsally to meet rostral node. Bases of *lateral rostral cartilages* very narrow, attached to anterodorsomesial edges of nasal capsules and not covering their entire surfaces. *Rostral node* of cranium long, broad, and greatly depressed, with a ventral fossa at its tip. Rostrum long, length from base of medial rostral cartilage to tip of rostral node about 50% of nasobasal length in adult, width across outer bases of lateral rostral cartilages 1.2 in length of rostrum.

NASAL CAPSULES subspherical, situated anterior to suborbital shelves, orbitonasal formaina medial to capsules proper. *Nasal apertures* on ventral surfaces of nasal capsules. *Subethmoid fossa* deep but relatively narrow and long, expanded anteriorly between nasal capsules to below base of medial rostral cartilage but not molded around palatine processes of palatoquadrates. External *produndus nerve foramina* on dorsal midlengths of nasal capsules, well in front of external fenestrae for preorbital canals.

CRANIAL ROOF moderately broad and humped, arched far above orbits. *Anterior fontanelle* small, subcircular, not transversely expanded, far above levels of nasal capsules and orbits; fontanelle housed in a scooplike turret rising above the cranial roof proper. Width of fontanelle about 1.3 times its height and about 14% of nasobasal length. A prominent pit and ridge present below lower edge of fontanelle. *Parietal fossa* formed as a pair of shallow oval depressions separated by a broad ridge, with endolymphatic and perilymphatic formaina visible.

BASAL PLATE very broad, width across orbital notches about 57% of nasobasal length, not arched over palatine processes of palatoquadrates. Basal plate virtually flat between interorbital septum and internal carotid foramina, and from carotid foramina and occiput, but with a slight basal angle at carotids. No *orbital pits* in the anterior third of basal plate for the orbital processes of palatoquadrates. Distance between *stapedial fenestrae* about 11% of nasobasal length. Foramina for *internal carotid arteries* on anteromedial edges of stapedial fenestrae.

ORBITS elongated in lateral view, extending about half their lengths behind front edges of preorbital processes and divided into anterior and posterior lobes by them. *Preorbital processes* high, recurved, and exserted from supraorbital crests. *Supraorbital crests* deeply concave in lateral and dorsoventral view, expanding posterolaterally between preorbital and postorbital processes. *Postorbital processes* long, strongly exserted from supraorbital crests, distance across them greater than distance across preorbital processes. External fenestrae for *preorbital canals* enlarged, multiple, expanded anteriorly and posteriorly to perforate bases of preorbital processes and front of supraorbital crests. *Suborbital shelves* undulated in ventral view, with anterior ends exserted as prominent *ectethmoid processes* that extend lateroventrally from nasal capsules and limit travel of palatoquadrates anterior to orbits, deep *orbital notches* extending posteroventrolaterally into acute, broad, triangular *lateral wings*, then abruptly posterodorsomedially to otic capsules. *Postorbital walls* slanting posteroventrally from below postorbital processes in lateral view.

OTIC CAPSULES with sphenopterotic ridges not exserted posterodorsally from the otic capsule, ending in short, blunt hornlike *pterotic processes*. *Opisthotic processes* slightly expanded lateral to sphenopterotic ridges, slightly undulated. *Hyomandibular facets* oval and large, covering ventrolateral faces of otic capsules but not expanded onto suborbital shelves. Hyomandibular facets exserted rearwards from the occiput, rear ends bluntly angular.

OCCIPUT canted diagonally from anterodorsal to posteroventral, vagus and glossopharyngeal foramina huge and prominently visible in dorsal view. *Nuchal crest* strongly developed above *foramen magnum*; a truncated, abruptly elevated medial projection anterior to nuchal crest and just behind parietal fossa. *Occipital condyles* high and stout, *occipital centrum* strongly developed.

JAWS relatively slender and thin. *Palatoquadrates* (Fig. 3F) slightly less than cranial length; when elevated palatoquadrates fall with their anterior tips below the midbases of the nasal capsules and extend about a third of their lengths behind the occiput. Palatoquadrates with slender posteriorly tapering *palatine processes* without dental bullae or mesial processes; *orbital processes* obsolete, reduced to low ridges connecting the ethmopalatine ligaments to the region of the ectethmoid processes and orbital notches. Palatoquadrates with moderately high *quadrate processes* which are prominently elevated above palatine processes; quadrate grooves well developed on the quadrate processes. Anterior ends of *Meckel's cartilages* ending slightly behind anterior ends of palatoquadrates, with an "overbite" of latter on Meckel's cartilages. Rear ends of Meckel's cartilages not expanded behind joints with palatoquadrates.

VERTEBRAL CENTRA strongly calcified, with strong primary calcification of the *double cones* well developed, and prominent branched secondary *radii* and interconnecting *annuli*. *Notochordal sheath* relatively narrow between vertebral centra.

RING INTESTINAL VALVE with 47–50 turns.

Phyletic Relationships of *Megachasma* and Other Lamnoids

Although phenetic distance supports the separation of Megachasmidae and Cetorhinidae, the question remains as to whether these families are sister groups. Maisey (1985, fig. 2) suggested five sets of synapomorphies for *Megachasma*

and *Cetorhinus*: 1) Modified ethmopalatine articulation; 2) Suborbital shelf interposed between palatoquadrate and orbit; 3) Median rostral cartilage partially dorsal to lateral rostral bars; 4) Simplified tooth cusp and root morphology, loss of dental differentiation, increase in numbers of tooth rows; 5) Enlarged gill rakers extending to margins of gill openings, covered by modified oropharyngeal scales.

Maisey's first and second characters refer to supposedly derived similarities in the cranial-palatoquadrate articulation in the megamouth and basking sharks, which he implied were not shared by other lamnoids. In *Megachasma* the orbital processes fit into deep pits in the basal plate (Fig. 3D) and the suborbital shelves wrap dorsolaterally around the palatoquadrates and exclude them from orbital contact. The basking shark has a pair of shallow depressions on the basal plate near the orbitonasal foramina, from which connective tissue arises and extends as the ethmopalatine ligaments to the palatoquadrates (Fig. 3F). Maisey considered these depressions as synapomorphies in the basking and megamouth sharks. However, depressions near the orbitonasal foramina are universal on the basal plates of lamnoid chondrocrania (Fig. 6). In groups with discrete orbital processes (odontaspidids, Fig. 3B; and alopiids, Fig. 3E) or long suspensory ethmopalatine ligaments (mitsukurinids, Fig. 3A), these depressions form part of the orbital suspensory points for the palatoquadrates as in *Cetorhinus*. In *Pseudocarcharias*, with the orbital processes apparently merged with the large dental bullae on the palatoquadrates (Fig. 3C), and in the Lamnidae, with the orbital processes absent (Fig. 3G), the ethmopalatine ligaments have a more diffuse but generally similar arrangement in linking the palatoquadrates with these depressions.

The basking shark also has, as supposed equivalents of the modified suborbital shelves of the megamouth shark, a pair of ventrally expanded ectethmoid processes anterolateral to the palatoquadrates and orbital notches. However, ectethmoid processes, as separate entities from the suborbital shelves, are absent from *Megachasma* and mitsukurinids, pseudocarchariids, odontaspidids, and alopiids. Ectethmoid processes are present in Lamnidae (Fig. 3G) albeit less prominently developed than in *Cetorhinus* (Fig. 3F), and are suggested as synapomorphies of these groups. In cetorhinids and lamnids the ectethmoid processes may serve to restrict anterior travel of the palatoquadrates, and do not exclude the palatoquadrates from the orbits.

No other lamnoids have the unique, highly derived suspensory arrangement of *Megachasma*, which has no synapomorphies with *Cetorhinus* that are absent in other lamnoids. However, *Cetorhinus* can be allied to the Lamnidae by its jaw suspension.

Maisey's third character is absent from *Cetorhinus*, which has a ventrally situated medial rostral cartilage as in lamnoids other than *Megachasma* (Figs. 4F, 7A-N).

Maisey's fourth character set, decreased heterodonty, is probably derived in *Cetorhinus* and *Megachasma*. However, it could be the result of parallel loss or reduction of heterodonty rather than descent from an immediate common ancestor with secondarily homodont teeth. Large teeth with disjunct heterodonty (Compagno 1970) are present in lamnoids that are not filter feeders, but reduced, numerous, weakly heterodont teeth are present in two other nonlamnoid groups of filter feeders, the orectoloboid whale shark (*Rhincodon typus*, family Rhincodontidae) and the devil rays (family Mobulidae). The false catshark (*Pseudotriakis microdon*, family Pseudotriakidae) is a carcharhinoid with gradient heterodonty and numerous small teeth but apparently is not a filter feeder.

Detailed comparison of the tooth morphology of *Megachasma* and *Cetorhinus* reveals important differences. *Megachasma* has teeth with large functional crowns and needle-sharp cusps (Fig. 2A-C) similar to those of more primitive nonfiltering lamnoids (Odontaspididae, Mitsukurina, Pseudocarcharias). In contrast, the crowns of *Cetorhinus* teeth are very reduced, blunt-tipped, and wedge-shaped (Fig. 2M-O), and resemble *Rhincodon* teeth (Fig. 2P,R). The roots of *Megachasma* teeth are derived in their reduced labial lobes, enlarged lingual protuberance, horizontal attachment surface, and possibly in the loss of a transverse groove. *Cetorhinus* teeth retain well-developed labial lobes, transverse grooves, and a small lingual protuberance.

Maisey's fifth character set combines two radically different arrangements for filter feeding. The specialized denticle gill rakers of *Cetorhinus* and supporting filtration structures are unique among Chondrichthyes, and resemble the bony gill rakers and slender gill arches in many filter feeding teleosts. The dense papillose gill rakers of *Megachasma* are like sparser papillose gill rakers in nonfiltering squalomorph sharks and some carcharhinoids (Compagno 1988). The gill rakers of *Megachasma* also resemble the more specialized filter screens of *Rhincodon* and the filter plates of mobulids in being cartilage-cored and covered by skin and normal denticles.

It is unlikely that the divergent filtration setups in *Megachasma* and *Cetorhinus* could be derived from each other or from a common filtering ancestor, but each of the setups could be separately derived from two different types of nonfiltering precursors. That of *Megachasma* is derivable from the more primitive arrangement seen in the Odontaspididae, while that of *Cetorhinus* is derivable from the arrangement found in the Lamnidae. Hence filter feeding cannot be considered a synapomorphic character of *Cetorhinus* and *Megachasma*. The divergent functional implications of the megachasmid and cetorhinid feeding apparatuses are discussed below.

The ranking of the megamouth and basking sharks as immediate sister groups is not supported by the evidence cited above. The following cladistic analysis of the order Lamniformes attempts to relate the megamouth shark to other living lamnoids. The analysis is a first approximation that uses the simple Hennigian noncomputer method

of clustering derived taxa, the schema of cladistic argument, and the rationale for determination of character polarities of Compagno (1988). Questionable polarities are labeled with a query (?). The branches of the lamnoid cladogram (Fig. 9) are numbered according to the text arguments below.

1. Synapomorphies of the order Lamniformes: Lamnoid tooth pattern; reduction of labial cartilages; elongated ring intestinal valve with over 15 turns; uterine cannibalism(?); development of primarily exochordal radii in vertebral centra.

2a. Autapomorphies of *Mitsukurina owstoni* (Mitsukurinidae). Skin thin and soft, fins very flexible, muscles flabby; snout greatly elongated and paddle-shaped; mouth elongated, expanded anteriorly to just behind nostrils; gill region and throat between lower jaws naked, skin there very thin, pliable, and elastic, forming a pelican-like pouch between the Meckel's cartilages and the basihyals and ceratohyals; intermediate teeth lost; anterolateral teeth with extremely slender, needle-like cusps and very thin, flat, expanded labial root lobes; lateral trunk denticles with narrow, conical, hooked, unicuspidate, semi-erect crowns; pectoral fins smaller than pelvic and anal fins; dorsal fins very small and rounded, not angular; anal fin low and elongated, much larger than dorsal fins; insertion of anal fin separated by notch from ventral caudal lobe; caudal fin elongated, dorsal caudal lobe hardly elevated(?), ventral caudal lobe not expanded(?); rostrum greatly elongated, about 1.5 times nasobasal length; tripodal rostrum highly modified, medial rostral cartilage basally expanded to the width of the internasal plate but tapering to a narrow rod distally before joining the rostral node; lateral rostral cartilages connecting anteriorly in a short, common, flattened triangular plate that joins with the rostral node; rostral node a long, greatly compressed, distally angular plate; subethmoid fossa expanded anteriorly into base of medial rostral cartilage but not displacing that cartilage dorsally, fitting anterior ends of palatine processes of palatoquadrates; supraorbital crests absent, preorbital and postorbital processes distally trilobate or bilobate; opisthotic ridges greatly expanded laterally; palatoquadrates with distally bent palatine processes; orbital processes reduced to low ridges on the palatine processes, processes continuous with attenuated, elastic ethmopalatine ligaments that attach to the nasal capsules; mandibular joint of Meckel's cartilages greatly expanded dorsally in a fanlike articular hinge; rear ends of Meckel's cartilages extending well behind joint with palatoquadrates; vertebral calcification reduced, radii simple.

2b. Synapomorphies of all other lamnoids. Transverse ridges lost on tooth cusps in anterolateral teeth, reduced ridges sometimes present on basal ledges; precaudal pits developed; development of enlarged stapedial fenestrae on cranium that house highly convoluted basal arteries. (3).

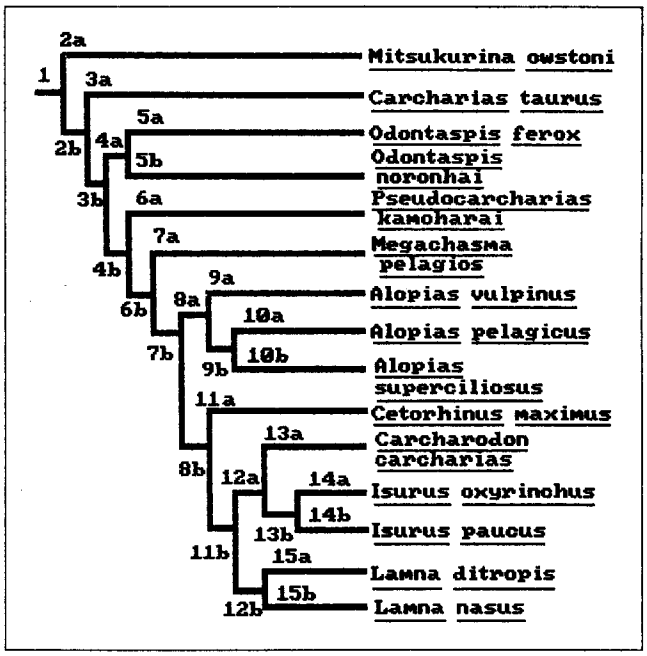


Figure 9.
Cladogram of lamnoid interrelationships. For explanation see text.

3a. Autopomorphies of *Carcharias taurus* (Odontaspididae in part). Posterior shift of first dorsal fin(?); air-gulping buoyancy mechanism; arching of basal plate below anterior part of suborbital shelves(?).

3b. Synapomorphies of all other lamnoids (except taxa above). First dorsal fin much larger than second; no first upper anterior tooth, this replaced by upper symphysical or lost. (4).

4a. Autapomorphies of *Odontaspis* (Odontaspididae in part). Bulbous snout(?); teeth reduced in size; elongated trunk relative to head and precaudal tail; enlarged vertical fenestra in rostrum(?) (5).

4b. Synapomorphy of other lamnoids (*Pseudocarcharias* and "advanced" lamnoids). Reduction of third lower anterior teeth to size and shape of lateral. (6).

5a. Autapomorphies of *Odontaspis ferox*. Intermediate teeth increasing to three to five rows(?); anterolateral teeth usually with two or three pairs of cusplets.

5b. Autapomorphies of *Odontaspis noronhai*. Labial lobes of anterolateral teeth expanded; anal fin reduced; color uniform dark brown.

6a. Autapomorphies of *Pseudocarcharias kamoharai* (Pseudocarchariidae). Low keels on sides of caudal peduncle; trunk elongated relative to head and tail; underside of snout between nostrils and mouth with a distinct angular ventral projection, noticeable when jaws are fully retracted; eyes enlarged; labial furrows lost; gill openings moderately enlarged; no symphysial teeth, number of rows of posterior teeth reduced, less than 30 rows of teeth in each jaw; anal fin base narrow, semipivotable; cranium elevated;

rostral node with slender rostral appendices and enlarged vertical fenestra; nasal capsules depressed below level of basal plate, only narrowly separated by internasal septum; internasal septum with a unique wedge-shaped ventral process; subethmoid fossa very narrow; cranial roof very narrow and acutely arched; anterior fontanelle a narrow vertical slot; basal plate and suborbital shelves very narrow; orbits extremely large; postorbital processes extending ventrally to form loose articulations with quadrate processes of palatoquadrates; otic capsule shortened; palatine processes shortened on palatoquadrates; orbital processes merged into high, dorsally expanded dental bullae that articulate with the orbital notches of the cranium rather than the posteroventral surfaces of the nasal capsules; quadrate processes with an angular articular surface that contacts the postorbital processes; vertebral radii slightly reduced; adults to 1.1 m long.

6b. Synapomorphy of "advanced" lamnoids (Megachasmidae, Alopiidae, Cetorhinidae, Lamnidae). Plesodic pectoral fins. (7).

7a. Autapomorphies of *Megachasma pelagios* (Megachasmidae). Skin soft, muscles very flabby, fins soft and flexible (paralleled by *Mitsukurina owstoni*); upper precaudal pit fossate; head enlarged; snout very short, blunt and broadly rounded; nostrils opposite mouth; mouth terminal; mouth with iridescent and possibly luminescent tissue; tongue and pharynx greatly enlarged; numerous cartilage-cored gill raker papillae present; teeth reduced in size but increased in number, over 100 rows in each jaw; medial toothless spaces enlarged; disjunct monognathic heterodonty lost; labial root lobes reduced, lingual protuberances expanded on tooth roots; wavy grooves of skin on fins; pectoral fins of straight, elongated, terminally expanded "oceanic" type; pectoral origins under fourth gill openings; caudal fins elongated, subterminal notch weak, no lateral undulations on dorsal caudal margin; chondrocranium depressed and extremely broad; rostrum extremely short; rostral node simple; medial rostral cartilage elevated above lateral rostrals; bases of lateral rostral cartilages covering nasal capsules; nasal capsules compressed and wedge-shaped, lateral to suborbital shelves; nasal apertures entirely lateral; subethmoid fossa greatly expanded; cranial roof very broad and flat; anterior fontanelle greatly expanded laterally; parietal fossa a single deep slit; basal plate with high midventral hump and deep orbital pits; postorbital walls slanting anteroventrally; opisthotic processes greatly expanded lateral to sphenopterotic ridges; hyomandibular facets expanded onto suborbital shelves; occiput vertical; occipital condyles weak and occipital centrum lost; jaws greatly enlarged, palatoquadrates nearly twice length of cranium and extending to rostral tip when retracted, capable of being protruded far anterior to rostrum; orbital processes articulating with the cranial basal plate and not the orbital notches; palatine processes without dental bullae; palatoquadrates fitting between suborbital shelves, nasal capsules and lateral rostral cartilages when retracted and excluded from orbital contact; quadrate processes low on palatoquadrates, quadrate grooves hardly developed; Meckel's cartilages expanded anteriorly to opposite palatoquadrates, no "overbite"; rear ends of Meckel's cartilages extending well behind joint with palatoquadrates (Taylor et al. 1983, fig. 14); vertebral calcification greatly reduced, radii vestigial, notochordal sheath expanded between vertebral centra.

7b. Synapomorphies of Alopiidae, Cetorhinidae, and Lamnidae. First dorsal fin elevated, fin skeleton partially expanded into fin web (semiplesodic); jaws not strongly protrusible; intestinal valve counts increasing to a range of 33–55. (8).

8a. Synapomorphies of *Alopias* (Alopiidae). Eyes enlarged; pectoral origins under third or fourth gill openings(?); pelvic fins enlarged and plesodic; second dorsal and anal fins greated reduced, with pivoting bases (paralleling the Lamnidae); upper lobe of caudal fin elongated, whiplike and about as long as body; chondrocranium very high between orbits, orbits enlarged; internasal septum high and compressed, with nasal capsules mesially adjacent; otic capsules shortened; mouth, jaws, and teeth reduced in size; vertebral counts increased to over 280 total. (9).

8b. Synapomorphies of Cetorhinidae and Lamnidae. Body spindle-shaped, caudal peduncle depressed and with strong lateral keels; labial furrows absent; gill openings enlarged; caudal fin shortened and lunate; presence of ectethmoid processes on chondrocranium that limit jaw protrusion; suborbital shelves with prominent lateral wings behind orbital notches. (11).

9a. Autapomorphies of *Alopias vulpinus*. Claspers extremely slender, clasper spurs lost(?).

9b. Synapomorphies of *Alopias pelagicus* and *A. superciliosus*. Eyes enlarged relative to *A. vulpinus*; labial furrows reduced or lost; nuchal grooves present above branchial region (inconspicuous in *A. pelagicus*); pectoral fins with broadened tips; ribs of monospondylous vertebrae modified to form an anterior haemal canal protecting the aorta, and extending nearly to cranial occiput; lateral rostral cartilages thickened and laterally expanded; vertical fenestra through rostral node lost; anterior fontanelle blocked and compressed anteriorly by large anterior myodomes for oblique eye muscles in orbits; orbits enlarged posteriorly to opposite stapedial fenestrae; intestinal valve counts increasing to a range of 37–45. (10).

10a. Autapomorphies of *Alopias pelagicus*. Pectoral fins of "oceanic" type, straight and with very broad tips; caudal tip extremely slender; teeth very small; nasal capsules diagonally expanded; basal plate and suborbital shelves very narrow; orbits ventrally depressed on cranium; area on basal plate between hyomandibular facets deeply concave; vertebral radii distally fused in intermedialia; vertebral counts increased to a range of 453–477 total, the highest of any living shark.

10b. Autapomorphies of *Alopias superciliosus*. Nuchal grooves deep, giving head a notched dorsolateral profile; eyes greatly enlarged, orbits modified for a vertical, binocular field of view; intermediates and most posterior teeth lost; first dorsal midbase closer to pelvic bases than pectorals; rostral appendices present on rostral node; rostral node expanded anteriorly as vertical plate; orbits enormously enlarged, with preorbital processes greatly expanded laterally; medial walls of orbit virtually touching each other, with cranial cavity highly compressed between them; optic pedicels reduced to low pads; vertebral calcification simplified, radii reduced in number(?); intestinal valve counts increasing to 45.

11a. Autapomorphies of *Cetorhinus maximus* (Cetorhinidae); Snout hooked in young; jaws hardly protrusible anteroventrally but distensible ventrolaterally; pharynx capable of great distension when feeding; tongue reduced in size; gill openings nearly encircling head; unique denticle gill rakers present; teeth greatly reduced in size and in over 200 rows in adults; no intermediate tooth rows in upper jaw; lateral trunk denticles hooklike and with crowns directed anteroposteriorly as well as ventrally; claspers very large and thick, clasper spurs greatly enlarged; cranium very high between orbits but orbits relatively low; rostrum of unique form, with broad, flat medial rostral cartilage hollowed anteroventrally by the subethmoid fossa, and T-shaped lateral rostral cartilages that fuse in a separate bar before reaching rostral node; bases of lateral rostral cartilages far anterior on nasal capsules; cranial roof arched far above orbits; anterior fontanelle housed in a discrete turret above the cranial roof proper; a pit and ridge below fontanelle; foramina for internal carotid arteries on anteromedial edges of stapedial fenestrae; preorbital processes and supraorbital crests partly separated from cranium by enlarged preorbital canals; postorbital processes enlarged, strongly notched; ectethmoid processes enlarged and ventrally directed; hyomandibular facets enlarged, covering ventrolateral faces of otic capsules; vagus and glossopharyngeal foramina enlarged; palatine processes of palatoquadrates very slender, without dental bullae; vertebral intermedialia with strong annuli; and possibly low vertebral numbers (total count of 110 in two individuals listed by Springer and Garrick 1964); gigantic size, 6–12 + m.

11b. Synapomorphies of Lamnidae. Second dorsal and anal fins greatly reduced in size and attenuated, bases pivoting; claspers with lateral dermal folds; rostral node without a lateral fenestra; nasal capsules depressed below level of basal plate; orbital notches deeply incised; orbits expanded posteriorly to level of pterotic processes; stapedial fenestrae greatly enlarged; mesial processes present at symphysial joints of palatoquadrates. (12).

12a. Synapomorphies of *Carcharodon* and *Isurus*. Jaws and anterior teeth enlarged; lateral cusplets lost on teeth or present only in very young(?); intestinal valves increasing to a range of 47–55; increase in total vertebral counts to a range of 170–197(?); increase in size in adults to at least 4 m maximum. (13).

12b. Synapomorphies of *Lamna*. Secondary caudal keels present; bases of lateral rostral cartilages elevated far above nasal capsules, originating on bases of preorbital processes; orbits elevated above cranial roof; cranial roof narrowed; rostral cartilages swollen and hypercalcified. (15).

13a. Autapomorphies of *Carcharodon carcharias*. Jaws and jaw muscles more enlarged than those in *Isurus*; teeth serrated and compressed, with heterodonty lessened between row groups of upper and lower jaws to produce an integrated slicing dentition; eyes and orbits reduced (?); cranium usually with a discrete epiphysial fenestra, separated from anterior fontanelle by transverse bar; cranium enlarged relative to rest of shark, strengthening jaw support; rostral cartilages reduced, rostral node relatively small; great size, 3.8–6 + m in adults.

13b. Synapomorphy of *Isurus*. Anterior teeth flexed. (14).

14a. Autapomorphies of *Isurus oxyrinchus*. Snout acutely pointed; anterior teeth more highly flexed; cranium elongated; rostrum narrowed; ethmoid region anteriorly expanded.

14b. Autapomorphy of *Isurus paucus*. Enlarged "oceanic" pectoral fins.

15a. Autapomorphies of *Lamna ditropis*. Snout shortened; upper anterior and lateral teeth with oblique cusps; hypercalcified rostral node engulfing rostral cartilages in adults.

15b. Autapomorphy of *Lamna nasus*. Free rear tip of first dorsal fin abruptly white.

The analysis indicates that the lamnoids with plesodic pectoral fins form a derived group, but that *Megachasma* has primitive characters found in aplesodic lamnoids that makes the family Megachasmidae the plesiomorphic sister group of the Alopiidae and Cetorhinidae and Lamnidae. These include its low first dorsal fin with aplesodic skeleton, low intestinal valve counts, highly protrusible jaws, and probably also the odontaspididlike size, shape, and spacing of its dorsal, anal and pelvic fins. This also supports the continued separation of the Megachasmidae and Cetorhinidae. The analysis rejects the hypothesis that the megamouth shark is the primitive sister of all other lamnoids.

The family Cetorhinidae is proposed as the sister group of the Lamnidae, while Cetorhinidae plus Lamnidae is the sister group of Alopiidae. The taxa of living Lamnidae need further study, although the ranking of *Isurus* and *Carcharodon* as sister genera and as the sister of *Lamna* seems reasonably clear. The family Alopiidae shows a very clear arrangement, with the common thresher (*Alopias vulpinus*) being the plesiomorphic sister species of the pelagic thresher (*A. pelagicus*) and bigeye thresher (*A. superciliosus*). Both Lamnidae and Alopiidae show strong evidence of being monophyletic.

There are problems with the cladogram (Fig. 9) and supporting arguments that resemble those found in carcharhinoids (Compagno 1988). As with advanced carcharhinoids the derived lamnoids with plesodic pectoral fins sort out well cladistically, but the more primitive aplesodic taxa presently do not. *Mitsukurina* is plausable as the primitive sister group of all other lamnoids, but also has numerous unique and parallel derived characters that obscure its primitiveness. Alternatively *Carcharias* and *Mitsukurina* might stand as sister groups on dentitional and cranial similarities, and likewise for *Odontaspis* and *Pseudocarcharias*. The present arrangement makes Odontaspididae paraphyletic, but this is on weak evidence and needs further study. The two *Odontaspis* species need detailed anatomical comparison to clarify their relationships to each other and to *Pseudocarcharias*. *Odontaspis noronhai* has a low anal fin and relatively large eyes as does *Pseudocarcharias kamoharai*, and may be related to it. The case for *Pseudocarcharias* as the plesiomorphic sister of the plesodic "advanced" lamnoids is weak, as its lateralized third lower anteriors may have evolved in parallel with those of the higher lamnoids. Some of these problems will be considered elsewhere and may be resolved by additional data on little-known taxa and character systems and by use of computer-aided methods of phylogenic analysis.

A problem with lamnoids that is not apparent with carcharhinoids is that most of the taxa are highly autapomorphic and have relatively few synapomomorphies with one another. Also, most taxa of lamnoids are extinct and are known mostly from fossil teeth; this lack of direct evidence makes comparison difficult and suggests that phylogenetic reconstruction based on living species is only a small fraction of the pattern of lamnoid evolution.

Megachasma and Its Possible Fossil Relatives

A comparison of the teeth of *Megachasma pelagios* as presently known (Fig. 2A–D) with fossil *Megascyliorhinus* teeth and unnamed fossil teeth from California and Oregon suggests that the fossils may be megachasmids but should be retained in separate genera. *Megascyliorhinus* teeth have far smaller, more primitive, more strongly bilobate roots and less recurved cusps (Fig. 2E–I) than those of *Megachasma*. The unnamed fossil teeth (Fig. 2J–L) have lower cusps and stronger labial root lobes than those of *Megachasma* and also have tiny cusplets. A difficulty in comparing teeth of the living *Megachasma pelagios* with megachasmidlike fossils is that the three known megamouth specimens are adult males. It is possible that some of the differences between the teeth of male *Megachasma pelagios* and megachasmidlike fossil teeth are the result of sexual heterodonty. The teeth of adult male *Megachasma* are extremely sharp and might be specially enlarged and modified for use in gripping females during courtship. Adult males of some carcharhinoid sharks have enlarged, modified, hooked cusps and lingually expanded root protuberances (Compagno 1988). However, to my knowledge fossil teeth with *Megachasma*-like elongated cusps, reduced labial root lobes and greatly expanded lingual protuberances have not been found.

Compagno (1988) mentioned material of a Cretaceous anacoracid shark, *Squalicorax "falcatus"* (possibly = *S. pristodontus*) in the LACM paleontological collections, including a largely intact chondrocranium with associated teeth and jaw fragments (LACM-VP-16056), and material of the vertebrae, teeth, and even a whole-bodied specimen which shows a high precaudal vertebral count and plesodic pectoral fins. G. Hubbell (JAWS International, Miami, Florida, pers. commun., 1988) kindly provided photographs of two other *Squalicorax* specimens in private collections for comparison with the LACM material, including an intact head and a nearly complete skeleton missing gill arches and some fin elements.

The *Squalicorax* chondrocranium (reconstruction, Fig. 10) is suggestively like that of *Megachasma* in its extreme width and general shape, except for the ethmoid region, which is highly truncated in the *Squalicorax* cranium examined and may be missing most of the rostrum (as suggested by other *Squalicorax* specimens). The characteristic modifications of the ethmoid region and basal plate of *Megachasma*, which allow the cranium to sit atop the palatine processes of the palatoquadrates, are absent in *Squalicorax*. The palatoquadrated are too fragmentary in the material examined to determine the exact nature of the orbital articulations of the palatoquadrate in *Squalicorax*, but there is no indication of a specialized megachasmid arrangement. The cranium of LACM-VP-16056 is highly calcified but crushed flat, and peripherally damaged so that details of the nasal capsules, rostrum, and orbits are uncertain. The strongly calcified jaws and vertebrae, stiff plesodic pectoral fins, caudal fin with strong ventral lobe, and large, serrated cutting teeth of *Squalicorax* suggest that it was an active, formidable macropredator rather than a sluggish filter feeder. The cranial similarities of *Megachasma* and *Squalicorax* may be superficial only, and may not be indicative of relationship, but this is uncertain with the present material.

A Revised Scenario for Megamouth Feeding

Taylor et al. (1983) compared the filter feeding apparatuses of the megamouth, basking, and whale sharks and noted important differences between them. They suggested that "*Megachasma* can be imagined as slowly swimming through schools of euphausiid shrimp and possibly other prey with jaws widely opened, occasionally closing its mouth and contracting its pharynx to expel water and

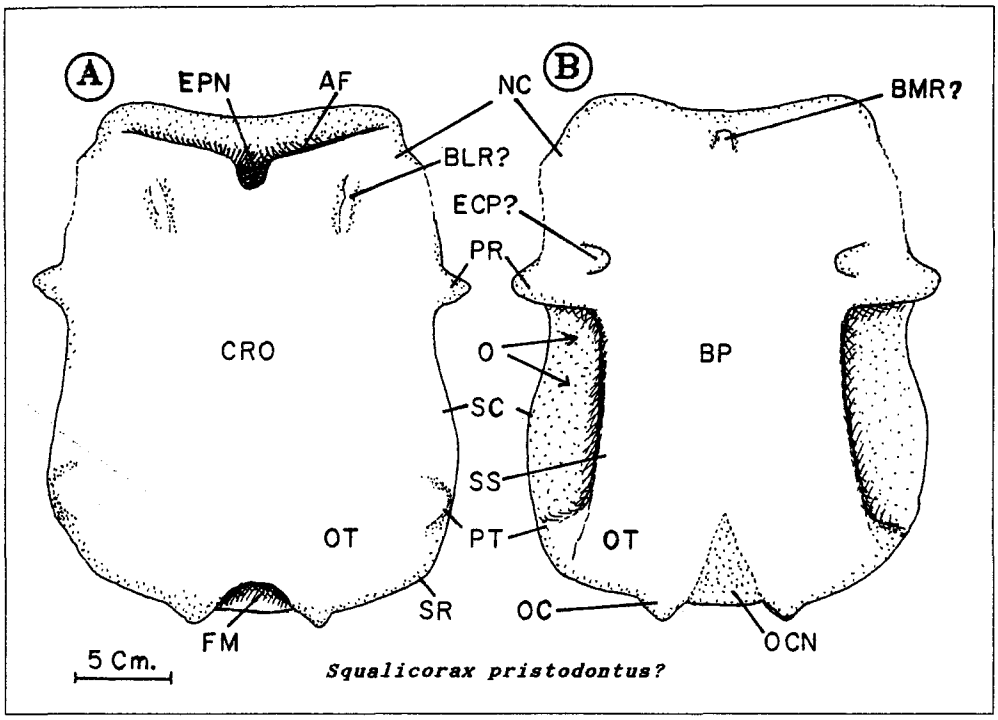


Figure 10.

Reconstruction of partial chondrocranium of *Squalicorax "falcatus"* (? = *S. pristodontus* [Agassiz, 1843]) in A, dorsal; and B, ventral views, based on LACM-VP-16056 (Upper Cretacous, Logan Co., Kansas). ABBREVIATIONS: AF = anterior fontanelle; BLR? = possible base of lateral rostral cartilage; BMR = possible base of medial rostral cartilage; BP = basal plate; CRO = cranial roof; ECP? = possible ectethmoid process; EPN = epiphysial notch for pineal organ; FM = foramen magnum; NC = nasal capsule; O = orbit; OC = occipital condyle; OCN = occipital centrum; OT = otic capsule; PR = preorbital process; PT = postorbital process; SC = supraorbital crest; SR = sphenopterotic ridge; SS = suborbital shelf.

concentrate its prey before swallowing it" (Taylor et al. 1983, p. 109).

Although the exact details of feeding behavior in the megamouth shark await observations on a live, feeding specimen, additional inferences can be made from morphological observations on the first two specimens. It is apparent that our earlier scenario (Taylor et al. 1983) was unduly influenced by the known feeding habits of the basking shark, which has often been seen and photographed swimming with mouth agape at the surface (Davis 1983; Stevens 1987). The strong swimming basking shark can efficiently pass a large volume of water through its pharynx and swallow part of its own bow wave along with the copepods and other invertebrate prey scattered in it. However, the weak body musculature, soft fins, restricted internal gill openings, and jaw morphology of the megamouth shark do not facilitate efficient feeding by this method. The megamouth shark might tend to shove water and prey ahead of it because water could not pass at any great rate between the densely packed papillose gill rakers and through the relatively small internal gill openings.

The slender jaws of the basking shark are hardly protrusible but swing ventrally on the cranium and spread laterally like a hoop, stiffening the almost circular mouth like the frame of a butterfly net (Fig. 11B), while the pharynx, hyobranchial arches and gill raker denticles are depressed and distended ventrolaterally. The heavy, long jaws of *Megachasma pelagios* are probably not widely distensible laterally, but, as shown by the Oahu and Catalina specimens, are highly protrusible anteriorly (Fig. 11A). The Catalina specimen, preserved with jaws maximally protruded, has its hyoid arch reversed in direction, with the hyomandibulae and ceratohyals anteroventral to their normal positions. This depresses the tongue, basihyobranchial skeleton and pharynx ventrally. The goblin shark, *Mitsukurina owstoni*, shows a similar hyoid reversal and pharyngeal depression when its jaws are protruded far forward (Fig. 11C).

Taylor et al. (1983) suggested that the megamouth shark had a bioluminescent mouth but could not prove it because of the poor preservation of the Oahu specimen. Sections of the black skin from the lower lip and tongue of the

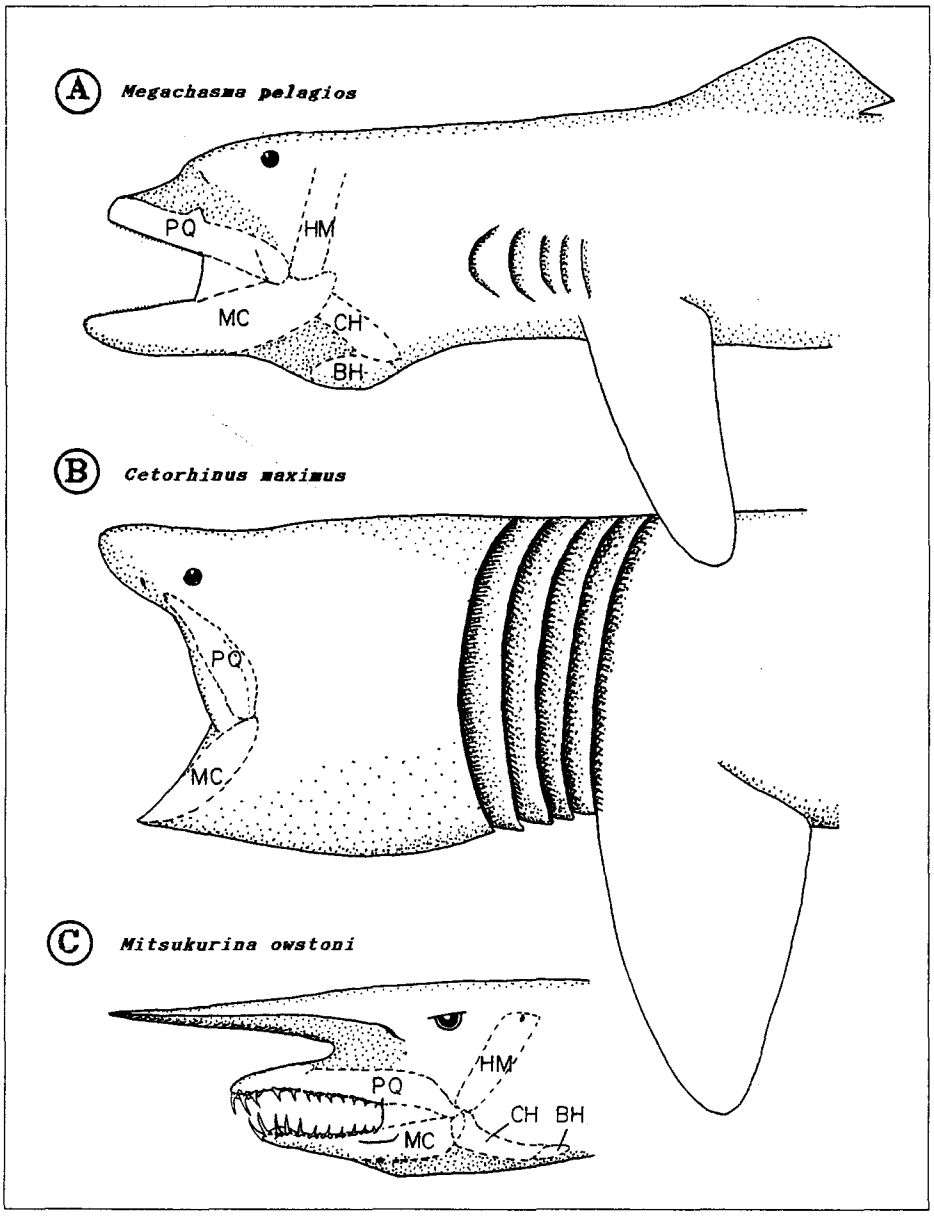


Figure 11.
Jaw mobility in the megamouth, basking, and goblin sharks. A, *Megachasma pelagios* (top) head with jaws protruded anteroventrally and hyoid arch reversed, composite of LACM-43745-1 and BPBM-22730. B, *Cetorhinus maximus* (center) head with jaws and hyobranchial arches distended lateroventrally in feeding posture but with jaws not protruded, composite of LACM-35593-1 and photos of feeding basking sharks in Davis (1983) and Stevens (1987). *C, Mitsukurina owstoni*, prebranchial head with jaws protruded and hyoid arch reversed as in the megamouth shark, composite of SU-13888 and RUSI-6206. ABBREVIATIONS: BH = basihyal; CH = ceratohyal; HM = hyomandibula; MC = Meckel's cartilage; PQ = palatoquadrte.

better preserved Catalina specimen revealed possible luminescent tissue (J. A. Seigel, Natural History Museum of Los Angeles County, Los Angeles, CA, pers. commun., 1985), along with iridescent, reflective upper jaw tissue (Taylor et al. 1983; Lavenberg and Seigel 1985). The nature of the lower jaw tissue may be resolved by investigations on the recently caught Australian specimen. Diamond (1985) discussed the use of a reflective, luminescent mouth to the megamouth shark as a "light trap" to attract its prey.

The above observations suggest a revised scenario for the feeding of the megamouth shark that is consistent with its feeding apparatus and its probable sluggishness. The megamouth shark can be imagined as slowly swimming through aggregations of euphausiid shrimp and other prey or floating in such aggregations with its jaws retracted and mouth open (Fig. 12A). If luminescent tissue is present on the upper jaw, the luminous, reflective tissue may be attractive to potential prey when producing light, and may serve to concentrate its near the mouth and jaws of the shark. Suddenly the megamouth shark protrudes its jaws, which reverses and depresses its hyoid arch, drops its tongue and pharynx, greatly increases the volume of its pharynx, and, like a gigantic bellows or underwater slurp gun, sucks the prey inside (Fig. 12B). The megamouth shark then closes its mouth and retracts its jaws; this action raises the pharynx and huge tongue, decreases the pharyngeal volume, and expels the water out through its closely screened internal gill openings (Fig. 12C). The shark swallows its food, opens its mouth again, and waits

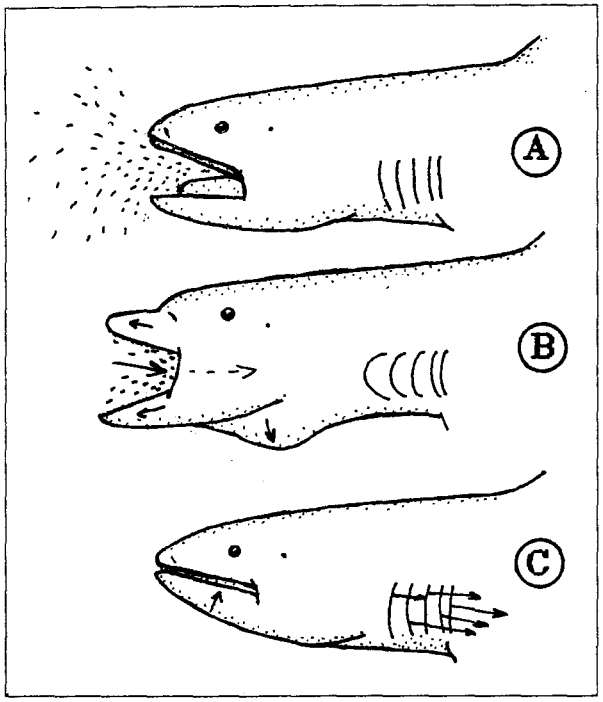


Figure 12.
Sequence of feeding action in *Megachasma pelagios*, based on the first two specimens. A, Mouth open with jaw retracted (top), luminescent organs would attract prey if present. B, Jaws protruded, hyoid arch reversed, and pharynx depressed, sucking prey into mouth. C, Mouth closed, hyoid arch and pharynx lifted, expelling water from gills. For further explanation see text.

for more victims to concentrate around its mouth, or slowly swims elsewhere to locate undisturbed patches of prey.

This scenario is not dependent on luminescent organs being present in *Megachasma*, because it may be able to feed on prey concentrations without their possible attractive effect. However the megachasmid feeding mechanism would be enhanced by a luminous oral lure. The extreme size of the jaws, the long pharynx, the *Mitsukurina*-like hyoid reversal, and the unusual cranial morphology of *Megachasma*, which permits the upper jaws to tuck in under the cranium, are apparent adaptations to producing a relatively large increase of pharyngeal volume and sudden inward flow of water when the shark protrudes its jaws.

Megachasma may have evolved its distinctive feeding apparatus from an odontaspidlike primitive jaw mechanism by exaggerating its jaw size and acquiring papillose gill rakers while harnessing and modifying the primitive lamnoid mode of jaw protrusion for suction-feeding. The basking shark, in contrast, could have evolved its feeding apparatus from a lamnidlike antecedent with restricted protrusion, but virtually eliminated protrusion in favor of jaw distension and a teleostlike method of filter feeding that is unparalleled amongst chondrichthyans.

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Appendix: Comparative Material of Lamnoid Taxa

Abbreviations for catalog or other numbers of lamnoid specimens examined in this study follow Leviton et al. (1985) and Compagno (1988):

BPBM—Bernice P. Bishop Museum, Honolulu, Hawaii
CAS—California Academy of Sciences, San Francisco
ISH—Institut für Seefischerei, Hamburg
LACM—Natural History Museum of Los Angeles County
LJVC-nnnn (e.g., LJVC-0251)— L.J.V. Compagno cataloged collection
LJVC-nnnnnn (LJVC-year/month/day, e.g., LJVC-840208)—L.J.V. Compagno field number;
MCZ—Museum of Comparative Zoology—Harvard

ORI—Oceanographic Research Institute, Durban
PEM—Field number of Port Elizabeth Museum, South Africa
RUSI—J.L.B. Smith Institute of Ichthyology
SOSC—Smithsonian Oceanographic Sorting Center
SU—Stanford University fish collection, now housed at CAS
USNM—United States National Museum of Natural History, Washington, D.C.

Mitsukurinidae: *Mitsukurina owstoni*

South Africa—RUSI-6206, 1166 mm immature female, Western Cape, west of Cape Town.
Japan—SU-13888, 1130 mm immature female (cranium dissected), Sagami Sea; USNM-50972, 335 cm adult female, skeleton, near Kosu, Sagami Bay.

Odontaspididae: *Carcharias taurus*

Western Atlantic—CAS 1961-IX:21, 1200 mm immature male and 1540 mm immature female (cranium and jaws removed from latter), no data.
South Africa—LJVC-831113, 1265 mm immature female, skeleton, Eastern Cape, Sardinia Bay; LJVC-840108, 2215 mm adolescent male, cranium, Eastern Cape; LJVC-840108, 2455 mm adolescent male, cranium, Eastern Cape; LJVC-840123, ~2.5 m adult male, cranium, Eastern Cape; LJVC-851228, 2250 mm adolescent female, Eastern Cape; LJVC-870103, 2200 mm adolescent female, jaws, Eastern Cape; LJVC-870805, 995 mm term fetus, skeleton, Natal; RUSI-27025, 1236 mm immature male, Algoa Bay.
Japan—MCZ-1278, 920 mm term fetus, Sagami Sea, HOLOTYPE of *Carcharias owstoni* Garman, 1913.

Odontaspis ferox

California—CAS-27022, ~3.2 m adult, cranium; CAS-27023, 1600 mm immature male, San Onofre; LJVC-0272, 2740 mm adult male, skeleton, San Clemente Island.
Hawaiian Islands—BPBM-9334 and BPBM-9335, 297 cm, heads only, both from Oahu, off Barber's Point.
South Africa—RUSI-6234, 1114 mm immature female, Natal.

Odontaspis noronhai

Dried jaw, possibly from Seychelles Islands, from D. J. Ward.

Pseudocarchariidae: *Pseudocarcharias kamoharai*

Central Atlantic—ISH-587, one female fetus, 415 mm, and 3 males, 397, 390, and 407 mm, from 1.1 m female, lat 12°07′N, long. 23°08′W.
South Africa—RUSI-6205 (ORI-1745), 930 mm adolescent female, lat. 33°29′S, long. 16°43′E, northwest of Cape Town; LJVC-880921, 972 mm adult male, Western Cape, washed up on beach, Blouberry Strand.
East Africa—RUSI-6181, 871 mm adult male, RUSI-6210, 970 mm adult male, longlined near Zanzibar(?).
Central Pacific—BPBM-18043, 823 mm adult male, lat. 20°02′N, long. 154°39′W, off Hawaii, Hawaiian Islands; CAS-32482, 933 mm adult male, lat 20°10′N, long 154°39′W, off Hawaii, Hawaiian Islands; RV *Charles H. Gilbert* 101-37, 955 mm female, lat. 21°20′N, long. 158°26′W, west of Oahu, Hawaiian Islands; RV *Townsend Cromwell* Cruise 44, Stn. 18, lat. 11°53′N, long. 144°49′W; LACM-uncat., 732 mm PCL immature female and 1100 mm adult male, both from lat. 7°33′S, long. 129°45′W, near Marquesas Islands.

Megachasmidae: *Megachasma pelagios*

BPBM-22730, 4460 mm adult male (dissected), off Oahu, Hawaiian Islands, HOLOTYPE of *Megachasma pelagios* Taylor, Compagno, and Struhsaker, 1983; LACM-43745-1, 4488 mm adult male, off Catalina Island, California. Possible megachasmid teeth, undescribed taxon: LACM-VP-10353, two teeth from Jewett Sand, Pyramid Hill, Kern Co., California, Miocene (Arikareean).

Cetorhinidae: *Cetorhinus maximus*

CAS-1953-IX: 23, dried jaws and gill rakers; LACM-35593-1, 7010 mm adult male, cranium, claspers, and other skeletal parts, off Avila Beach; LACM-42649-1, 5640 mm female, cranium and other parts, off San Pedro.

Alopiidae: *Alopias pelagicus*

Eastern Pacific—LJVC-0171, 1913 mm immature spec., cranium, Mazatlan, Mexico; LJVC-0414, 1970 mm immature male, cranium and other parts, lat. 11°53′N, long. 103°21′W; SIO-H52-19-5A, 560 male fetus and 585 female fetus, Galapagos Islands, off Fernandina.
South Africa—LJVC-870806, 3180 mm adolescent male, skeleton, Natal; LJVC-871125, 3330 mm adolescent female, cranium, jaws, vertebrae, Natal; RUSI-6247, 277 cm immature female, Natal, Durban.
Northern Indian Ocean—SOSC 79, RV *Anton Bruun* Cruise 5, near Stn. 282, 1372 mm immature female, lat. 16°14.5′N, long. 63°27′E, north Indian Ocean; SOSC 79, RV *Anton Bruun* Cruise 5, Stn. 288, 475 mm male fetus and 515 mm female fetus, lat. 9°36′N, long. 55°00′E, north Indian Ocean; SOSC 79, RV *Anton Bruun* Cruise 5, near Stn. 289, 727 mm female fetus, 3 male fetuses 660, 670, and 705 mm, lat. 7°17′N, long. 55°00′E, north Indian Ocean.
Taiwan—SU-21252, 614 mm male fetus, Takao.
Japan—SU-23415, 385 mm male fetus, Misaki.

Alopias superciliosus

Eastern Pacific—CAS-27072, 3715 mm adult male, off San Clemente Island; LJVC-0355, 2872 mm immature male, cranium and other skeletal parts, east-central Pacific, lat. 03°16′S, long 128°18′W; S.P. Applegate uncat., cranium, no data.
Florida—S. Gruber uncat., 2 male fetuses, one cleared and stained, 207 and 213 mm, from adult taken off Miami, Florida.
South Africa—RUSI-6248, 363 cm adult male, parts, Natal, Durban; PEM-790603, 4285 mm adult female, Eastern Cape, off Cape Recife.

Alopias vulpinus

California—S.P. Applegate uncat., 1308 mm immature male, cranium, S. California, Manhattan Beach Pier; S.P. Applegate uncat., cranium, (?)locality; CAS-30830, 1445 mm immature female, skeleton, San Francisco Bay; LACM-35592-1, 3099 mm female, head only, Los Angeles, Santa Monica Bay; LJVC-0234, 2057 mm immature female, cranium, Muir Beach; LJVC-0382, 1605 mm immature female, skeleton, Moss Landing; LJVC-0387, 1555 mm immature male, skeleton, Morton's Beach near Half Moon Bay; LJVC-0388, 1472 mm immature female, skeleton, Monterey Bay, Manressa State Beach near Rio Delmar; LJVC-0404, 1500 mm immature male, jaws, vertebrae, Moss Landing; LJVC-0473, 4200 mm

adult male, cranium and claspers; LJVC-0474, 3700 mm immature female, cranium; SU-40908, 1752 mm immature female, no data.

South Africa—RUSI-8654, 3480 mm female, Eastern Cape, off Port Alfred; RUSI-26219 (LJVC-870130), 2022 mm immature male, Eastern Cape, off Port Alfred; LJVC-880229, 2882 mm adolescent male, Mossel Bay; RUSI-27024 (LJVC-870228), 2236 mm immature female, head and vertebrae, Langebaan, Saldanha Bay.

Lamnidae: *Carcharodon carcharias*

California—CAS-uncat., from J. D. McCosker, 1670 mm immature male, skeleton, Bodega Bay; CAS-53045, 1460 mm immature male, Ventura, off Ventura Marina; LJVC-0187, 2045 mm immature female, cranium, jaws, Tomales Bay near Inverness; LJVC-0261, 2340 immature male, cranium, Half Moon Bay; LJVC-0384, 1990 mm immature female, cranium, gill arches, jaws, fins, Half Moon Bay; LJVC-0475, 1290 mm immature male, cranium, jaws, gill arches, claspers, Baja California; LJVC-0478, 393 cm adult male, claspers, Año Nuevo; LJVC-0481, 4597 mm adult male, claspers, southeast of Anacapa Island; LJVC-0483, 5334 mm, cranium, Santa Cruz Island.

South Africa—LJVC-841026, 3058 mm immature female, cranium, Eastern Cape, Algoa Bay, Bird Island; LJVC-840126, 2000 mm immature male, Eastern Cape, Algoa Bay; LJVC-850226, 1585 mm immature male, Eastern Cape, Algoa Bay, Bird Island; PEM-801005, 2150 mm, New Brighton Beach, jaws only; LJVC-860502, 1510 mm immature male, Ciskei, Mgwalama; LJVC-860618, 2375 mm immature female, cranium, Eastern Cape, Algoa Bay; Gans Bay Fisheries Cooperative (LJVC-870303), 6000 mm female, jaws, fins, vertebrae, W. Cape, Gans Bay; LJVC-870805, 3027 mm immature female, cranium, vertebrae, Natal, Brighton Beach; LJVC-870830, 3826 mm adult male, cranium, vertebrae, teeth, fins, W. Cape, Koeberg; LJVC-871126, 2 adolescent males, 2830 and 2935 mm, crania and vertebrae, Natal; RUSI-12998, 1400 mm immature male, Algoa Bay; RUSI-6253, 1788 mm immature female, Natal, Umhlanga Rocks.

Isurus oxyrinchus

California—S.P. Applegate uncat., cranium, no data, S. California; LJVC-0216, 1360 mm immature female, cranium, jaws, vertebrae, off San Diego.

South Africa—LJVC-820816, 2330 mm adolescent female, cranium, jaws, vertebrae, Eastern Cape; LJVC-840122, 1982 mm immature female, cranium, jaws, vertebrae, Eastern Cape; LJVC-840726, 1773 mm immature female, cranium and LJVC-850405, 1400 mm immature female, skeleton, Eastern Cape, off Cape Recife; LJVC-870211, 1600 mm immature male, cranium, vertebrae, Eastern Cape, off Cape Recife; LJVC-870416, 1650 mm immature male, cranium, vertebrae, Eastern Cape, off Cape Recife; LJVC-880221, 1060 mm immature female, Eastern Cape, off Cape Recife; LJVC-870805, 2750 mm adult male, cranium, claspers, Natal; LJVC-uncat., dried jaw from huge individual, est. 396 cm, Western Cape, off Cape Town; RUSI-6916, 101 cm male, RUSI-6917, 284 cm male, RUSI-6918, 130 cm male, RUSI-6919, 120 cm female, RUSI-6920, 123 cm male, RUSI-6921, 82 cm male, RUSI-6922, 102 cm male, and RUSI-6923, 78 cm male, all dried jaws from Natal.

Isurus paucus

Western North Atlantic—LJVC-880125/LFM-8, 1096 mm full-term fetal female, from J. G. Casey.

Japan—S.P. Applegate uncat., 2175 mm adult male, cranium, claspers, teeth, Tokyo Fish Market.

Central Pacific—USNM-197429, 1380 mm immature female, PARATYPE of *Isurus alatus* Garrick, 1967.

Lamna ditropis

California—LJVC-0112, 2280 mm adult male, cranium, jaws, vertebrae, claspers, Monterey Bay, off Monterey; LJVC-0113, 2200 mm female, cranium, jaws, vertebrae, Monterey Bay; LJVC-0385, 1829 mm immature male, cranium, gill arches, vertebrae, fins, off Pescadero; LJVC-0476, 2200 mm adult male, cranium, claspers, Monterey Bay, Monterey Canyon; LJVC-0477, adult male, head only, Monterey Bay, Monterey Canyon; LJVC-0494, ~1 m, jaws, vertebrae, Monterey area; LJVC-uncat., 983 mm immature male, Northern California.

Lamna nasus

Western North Atlantic—LJVC-880127, head of ~2m individual, from J. G. Casey.

Italy—B. Welton uncat., 2476 mm, tooth set, caught off Sicily.

Southern Indian Ocean—SOSC, RV *Anton Bruun* Cruise 5, Stn. 309, 960 mm immature female, lat. 42°23′S, long. 74°56′E.

Anacoracidae:

Squalicorax "falcatus" (? = *S. pristodontus*)

LACM-VP-16056, chondrocranium, jaw fragments, and teeth, Upper Cretaceous, Logan Co., Kansas.

Note: While this paper was in press, Nakaya (pers. commun., 1988; Nakaya 1989) reported a fourth magamouth shark (also an adult male over 4 m long) that was stranded on the beach at Hamamatsu City, Shizuoka Prefecture, south-central coast of Honshu, Japan (34°42′N, 137°42′E). This was photographed by beachgoers but was washed out to sea and lost before scientists were notified of its presence and could collect it.