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MEGAMOUTH—A NEW SPECIES, GENUS, AND FAMILY OF LAMNOID SHARK (*MEGACHASMA PELAGIOS,* FAMILY MEGACHASMIDAE) FROM THE HAWAIIAN ISLANDS

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Abstract: ***Megachasma pelagios*, a new genus and species of lamnoid shark assigned to the new family Megachasmidae, is described and defined from a single adult male, 4.46 m total length. The holotype and only known specimen was collected approximately 42 km NE of Oahu, Hawaii. Structure and habitus distinctly differ from other lamnoid sharks, particularly in head and tooth morphology and in mesopelagic filter feeding.**

Introduction

On 15 November 1976, the research vessel *AFB-14* of the Naval Undersea Center (now the Naval Ocean Systems Center), Kaneohe, Hawaii, was conducting oceanographic research in waters about 42 km northeast of Kahuku Point, Oahu, at about 21°51′N and 157°46′W. From 1015 to 1415 Hawaiian Standard Time the ship had deployed two large parachutes as sea anchors at a depth of about 165 m in water with a bottom depth of approximately 4600 m. When the parachutes were hauled to the surface, using a small winch with an 180 kg pull shut-off, one of them had entangled in it a large adult male shark 4.46 m (14.6 ft) long and 750 kg (1653 lbs) (Figs. 1–4). Crew members of the *AFB-14* realized that the shark was unusual and brought it aboard with much difficulty. The shark was shipped to the Kaneohe Bay facility of the Naval Undersea Center and tied alongside the dock overnight.

The senior author inspected it the next morning. Preliminary examination indicated that it represented a very distinct, undescribed species, and it was decided that it should be preserved intact. Accordingly, the shark was winched out of the water by the tail using a Navy crane, but the caudal fin broke off and the shark fell into the water and had to be retrieved by divers. The shark was quick-frozen at Hawaiian Tuna Packers, Honolulu, while a large preservation tank

FIGURE 1. Artist's conception of *Megachasma pelagios* in its natural habitat, slowly swimming with open mouth and feeding on planktonic animals. (From a painting by Richard Ellis.)

was constructed. On 29 November 1976, the shark was transported frozen to the Kewalo dock site of the National Marine Fisheries Service for thawing and injection with formalin. Subsequent examination of the shark by the authors and colleagues indicated that it is a lamniform shark (order Lamniformes of Compagno 1973a) that is not assignable to any known genus or family and is herein described as *Megachasma pelagios*, new genus and species, and placed in the new family Megachasmidae.

The discovery of the novel shark was widely reported in newspapers (e.g., Anonymous 1 and 2, 1976, and Dunford 1976). It was dubbed the "Megamouth shark" in reference to its unusually large oral cavity. This common name has since been adopted by several authors (Compagno 1977, 1979, and 1981; Taylor 1977; Tinker 1978; Faughnan 1980; Clark 1981), and we suggest that it be considered as the accepted common name for the species.

This strange shark is extraordinary in its distinctness from other sharks and its great size. Most sharks are small, less than 2 m long at maturity (Compagno 1981). The new shark joins the company of the few giant sharks commonly reaching total lengths over 4 m, including the broadnose sixgill shark (*Hexanchus griseus*), Pacific sleeper shark (*Somniosus pacificus*), Greenland shark (*S. microcephalus*), whale shark (*Rhiniodon typus*), great white shark (*Carcharodon carcharias*), tiger shark (*Galeocerdo cuvier*), and great hammerhead (*Sphyrna mokarran*). The common thresher (*Alopias vulpinus*) and bigeye thresher (*A. superciliosus*) also reach total lengths over 4 m, but these sharks have greatly elongated caudal fins and hence are relatively small-bodied in comparison to the giant species. Although new species of small sharks are discovered fairly frequently, giant sharks are not, and almost all of the great species were described in the 18th and 19th centuries.

Because the only known specimen of *Megachasma pelagios* is an adult male, and because it is very common for female sharks to reach a somewhat larger size than males, it is reasonable to expect larger specimens of this species.

Methods

On 30 November 1976, the thawed shark was placed in a large, above-ground plastic pool filled with seawater. Comprehensive measurements of the shark were recorded, following the procedures of Bigelow and Schroeder (1948). Skin samples were taken from the mouth, tongue, pectoral fin, caudal fin, back below first dorsal fin, and gill-rakers for later examination using a Cambridge S410 Stereoscan electron microscope.

Skin samples from the mouth lining and tongue were sectioned and stained using standard histological techniques. A short incision, approximately 30 cm long, was made on the ventral surface to gain access to the stomach and valvular intestine, and stomach contents were removed. The valvular intestine was removed, slit medially to count the ring valves and to remove intestinal worms for parasitologists (Dailey and Vogelbein 1982), and separately preserved. Samples of muscle tissue and liver were taken for electrophoretic analysis. Extensive sets of still photos were made of the preservation process by the authors and Mr. Paul Meyers of the Naval Undersea Center, who also made 16 mm movies of these techniques.

The body cavity and musculature of the shark were injected with 25 l of 100% formalin (40% aqueous formaldehyde gas solution). The shark was then lifted by crane and cargo sling into a 4 × 3.5 × 1 m fiberglass box and covered with a 40% seawater-formalin solution. After six months in formalin, the specimen was deposited in the fish collection of the Bernice P. Bishop Museum, Honolulu, where it was rinsed for 30 days in water and then placed in 55% isopropyl alcohol. Tooth samples were removed for examination of their morphology, and one tooth was sectioned and stained for tooth histology. A "peel" dissection was made on the right side of the head to examine the neurocranium and jaw structure of the shark, and similar dissections were made on the right pectoral fin and right clasper. Vertebrae were excised from the base of the caudal fin and from beneath the first dorsal fin and sectioned to examine their calcification patterns.

Terminology for descriptive morphology of *Megachasma pelagios* follows Bigelow and Schroeder (1948) and Compagno (1970, 1973a, 1973b, and 1979).

Megachasmidae, new family

Type-genus.—*Megachasma* Taylor, Compagno, and Struhsaker, new genus.

Family Description.—Giant neoselachian sharks of the order Lamniformes (as defined by

FIGURE 2. Holotype of *Megachasma pelagios*, within 12 hours of its capture. Note the extreme protrusibility of the jaws and the gill filaments visible in the first gill opening.

Compagno 1973a) reaching at least 4.46 m length when adult. Trunk cylindrical but not highly fusiform, tapering rearward from the head. Caudal peduncle short, stout, slightly compressed, and without lateral keels or ridges; a shallow, longitudinally oval upper precaudal pit present, but no lower pit. Head broad, very large and long, and not pointed, length greater than abdomen

FIGURE 3. Frontal view. Note Navy research vessel and winch which retrieved shark in background. (Official U.S. Navy photograph.)

between pectoral and pelvic bases. Snout very short, depressed, and broadly rounded, not conical or bladelike. Eyes lateral on head, length less than one-fourth length of longest gill openings. Nostrils small, widths about $\frac{1}{11}$ internarial width, with short, low anterior nasal flaps; nostrils lateral and opposite the first fourth of mouth. Gill openings moderately large, not expanded onto dorsal surface of head; internal gill openings with numerous gill-rakers of a unique type, formed as elongated, slender, cartilage-cored dermal papillae covered by imbricated denticles (Fig. 6). Mouth terminal and very large, broadly arched, extremely long, and extending far behind eyes when jaws are not protruded; jaws strongly protrusible, capable of extension well in front of snout. No true labial furrows or labial cartilages, but with inner labial grooves present along edges of mouth corners.

Teeth similar in upper and lower jaws, weakly differentiated, with moderately long, broad, flattened roots, very short labial root lobes, and very long, broad, expanded lingual protuberance; moderately strong basal ledges and grooves on the labial crown face; a broad, enameloid-free neck on the crown foot; a strong, narrow, lingually hooked cusp with cutting edges confined to its tip, no striations or ridges on the cusp. Teeth not compressed and bladelike, relatively small, and very numerous, over 100 rows in each jaw and in three or four functional series. Toothless spaces on symphyses of jaws extremely broad, especially on upper jaw. Teeth in each jaw half apparently continuously varying and without discrete row groups; no gap or reduced intermediate teeth between teeth in anterior and lateral positions in upper jaw.

Lateral trunk denticles with broad, teardrop, or wedge-shaped, flattened crowns, not erect, hooked, or directed anteriorly or dorsoventrally; pedicels of trunk denticles low and broad (Fig. 11). Wavy grooves of naked skin on the pectoral, pelvic, and caudal fin webs. Pectoral fins relatively narrow, long and blunt-tipped, length from origin to free rear tip about half as long as pectoral anterior margin. Origins of pectoral fins under fourth gill openings. Pectoral fins more than three times area of first dorsal fin, with anterior margins more than three times length of pelvic anterior margins. Pectoral fin skeleton plesodic, with pectoral radials extending into the distal fin web nearly to its edge; ceratotrichia reduced along distal fin margin and not extending proximally to radial musculature of fin. Pectoral fins very small, angular, smaller than first dorsal fin but larger than second dorsal, with an aplesodic fin skeleton. Claspers moderately slender and elongated, with attenuated tips and external spurs (Fig. 11). First dorsal fin moderately large, angular and relatively low, with a narrowly rounded apex and an aplesodic fin skeleton; origin of first dorsal much closer to pectoral fin bases than pelvic bases, and free near tip, well in front of pelvic origins. Second dorsal fin less than one-third area of first dorsal and slightly less than half as high, angular and broad-based, with its origin about over the pelvic fin insertions. Neither second dorsal nor anal bases pivoted. Anal fin about half area of second dorsal, angular and broad-based, with its origin about opposite free rear tip of second dorsal and its free rear tip well in front of ventral caudal origin; insertion of anal separated from ventral caudal origin by space greater than base or anal. Caudal fin with a long dorsal lobe nearly half length of rest of shark, a long ventral lobe about ⅖ as long as dorsal lobe, a deeply notched postventral caudal margin, a weak subterminal notch, and no undulations or ripples on the dorsal or preventral caudal margins; caudal fin not lunate or crescentic, dorsal caudal vertebral axis moderately elevated at an angle to body axis (heterocercal).

Neurocranium (Fig. 13) with tripodal rostrum formed of a small, moderately elongated, medial rostral cartilage originating from expanded internasal plate and pair of basally enlarged, triangular lateral rostral cartilages that taper anteromedially to fuse with medial rostral cartilage and form a narrow, flattened, unfenestrated rostral node. Base of medial rostral cartilage elevated by dorsally arched internasal septum above level of bases of lateral rostral cartilages and nasal capsules, so that medial rostral cartilage arches anteroventrally to meet rostral node. Rostrum short, less than half nasobasal length of cranium. Nasal capsules small, greatly compressed, far lateral to each other and separated by flattened internasal septum. Entire anterior surfaces of nasal capsules forming bases of lateral rostral cartilages. Broad subethmoid fossa not extending anterior to nasal capsules. Cranial roof very broad and flat, not arched above the orbits, with a huge transverse anterior fontanelle; basal plate broadly arched. Orbits with low preorbital processes, complete supraorbital crests, and broad, low postorbital processes. A deep pit on each side of ventral surface of cranium between base of suborbital shelf and basal plate in front of stapedial fenestrae, for orbital processes of palatoquadrates. Otic capsules broad and relatively long, without elongated pterotic horns.

Jaws very long and stout, much longer than cranium, extending from the cranial rostral node to well behind the occiput when retracted. Palatoquadrates with long, stout palatine processes lacking dental bullae; strong, low, knoblike, cartilaginous orbital processes, and low, strong quadrate processes. Orbital processes articulating on ventral surfaces of suborbital shelves and basal plate below orbits, quadrate processes far below postorbital processes of cranium and not contacting them. Anterior ends of Meckel's cartilages extending below level of anterior ends of palatoquadrates, no "overbite" of palatoquadrates on Meckel's cartilages. Vertebral column with well-developed cartilaginous centra separated by broad bands of notochordal sheath, but with primary and secondary calcification virtually absent. Intestinal valve with 24 turns.

CLASSIFICATION.—Compagno (1973a, 1977) divided the living elasmobranch fishes, or neoselachians, into four superorders, of which the Galeomorphii or galeomorph sharks clearly includes the new family Megachasmidae and genus *Megachasma*. Megachasmidae has the following galeomorph characters: head and body not greatly depressed and not expanded laterally; spiracles without valves; five pairs of laterally situated gill openings; denticles covering almost entire body, not absent ventrally, nor enlarged on midline of back, and not enlarged on pectoral fins in adult males; pectoral fins without anteriorly expanded triangular lobes covering gills or fused to sides of head above them; propterygium of pectoral fin skeleton not anteriorly expanded; pectoral fins not modified into propulsive organs; pectoral girdle not articulating with vertebral column; vent confluent with pelvic fins; two dorsal fins and an anal fin present; caudal fin heterocercal, with a subterminal notch on the dorsal caudal lobe and with ventral lobe shorter than dorsal lobe; neurocranium with strong suborbital shelves, no antorbital cartilages, ectethmoid processes, or enlarged ectethmoid chambers on the nasal capsules, rostrum not trough-shaped, no basal angle on basal plate, no lateral commissures on otic capsules, and with incomplete postorbital walls; no palatobasal articulation of palatoquadrates with neurocranium; hyoid arch complete, no pseudohyoids; vertebral column without synarcuals, and vertebral centra without concentric calcifications.

The Galeomorphii of Compagno (1973a, 1977) was subdivided into four orders, Heterodontiformes, Orectolobiformes, Carcharhiniformes, and Lamniformes; of these, the family Megachasmidae falls in the order Lamniformes or lamnoid sharks. Lamnoid characters of Megachasmidae include its simple nostrils of the ordinary shark type, entirely separate from the mouth, with small anterior nasal flaps, diagonal incurrent and excurrent apertures, and no perinasal folds and grooves, anterior barbels, or nasoral grooves; a long mouth extending behind the eyes when jaws are retracted; no supraorbital and subocular ridges; eyes circular and laterally without nictitating eyelids, subocular pouches, or postorbital eyelid muscles; osteodont teeth (Fig. 9) with weak basal ledges; posterior teeth not enlarged and formed into molariform crushers; claspers with external spurs on the T-3 cartilage and with elongated, tubular, expanded marginal cartilages; dorsal fins spineless, with segmented basal cartilages; cranium with a tripodal rostrum, nasal capsules not anteroposteriorly elongated and trumpet-shaped; no ethmopalatine grooves for the articulation of the palatoquadrate orbital processes, complete preorbital walls, separate foramina for superficial ophthalmic nerves in orbits and for hyomandibular nerves on otic capsules, and relatively long otic capsules; jaws long, extending posterior to the occiput; mouth gape not restricted anteriorly, labial cartilages, folds and grooves reduced or absent; pectoral fin skeleton with a small propterygium, moderately large mesopterygium, and large metapterygium; mesopterygium and metapterygium not elongated parallel to the axes of their radials, and not proximally shaftlike, distally expanded and without a fenestra between them; preorbitalis or levator labii superioris muscles relatively small and anteroposteriorly positioned on the jaws, with origins on posteroventral surfaces of the nasal capsules, fibers nearly horizontal when jaws are retracted, and insertions far posterior on the adductor mandibulae muscles at the jaw angles; adductor mandibulae muscles anteriorly notched; levator palatoquadrati muscles simple, not subdivided into anterior constrictor and spiracular muscles; no craniomandibular or mandibulocutaneous muscles; and an elongated, ring-valve intestine.

RELATIONSHIPS TO OTHER LAMNOIDS.—Within the Lamniformes, the family Megachasmidae represents a very distinct and singular taxon, well separated from all other families. Other lamnoids of the families Odontaspididae, Mitsukurinidae, Pseudocarchariidae, Alopiidae, Cetorhinidae, and Lamnidae all differ from the Megachasmidae in having a more elongated, more narrowly rounded, conical or bladelike snout; no papillose gill-rakers (denticle gill-rakers present in Cetorhinidae); mouth subterminal on head and less enlarged; tongue smaller; upper anterior and lateral teeth separated by a gap that may or may not have reduced intermediate teeth; tooth rows either less than 60 in each jaw, or more than 200 (Cetorhinidae); toothless space on upper symphysis relatively narrow; no wavy grooves of naked skin on the pectoral, pelvic, and caudal fins; lateral rostral cartilages narrow-based and only covering part of the dorsal surfaces of the nasal capsules or the preorbital processes; base of medial rostral cartilage well below bases of lateral rostral cartilages and with shaft of cartilage below rostral node; nasal capsules nearly spherical, not compressed, and with ventral nasal apertures; cranial roof narrow to only moderately expanded anteriorly, with anterior fontanelle varying from moderate to greatly reduced; orbital processes more or less reduced on palatoquadrates, articulating with the suborbital shelves where present; jaws shorter, beginning well behind the snout tip when retracted; and with primary calcification of the double cones and secondary radii well developed in their vertebral centra.

Members of the family Odontaspididae (including the genera *Eugomphodus* and *Odontaspis*) further differ from *Megachasma* and the Megachasmidae in having prominent, transverse precaudal pits; labial folds, furrows and cartilages present (with the possible exception of *E. tricuspidatus*); nostrils in front of the mouth; teeth with strong labial root lobes, moderate lingual protuberances, narrow necks on the crown, and labiolingually diagonal attachment surfaces; symphyseal, anterior, lateral, intermediate, and posterior tooth-row groups well differentiated along dental bands, with anteriors and laterals enlarged; pectoral fins smaller, shorter, broader, less elongated, and not falcate, and with aplesodic fin skeletons; pectoral fin origins behind fifth gill openings; claspers stouter and blunt-tipped, with blunt clasper spurs; origin of first dorsal fin well posterior to pectoral insertions; second dorsal fin more than half as high as first dorsal; caudal fin shorter, less than half as long as rest of shark; subterminal notch of caudal fin deep; ventral caudal lobe shorter, dorsal caudal margin with rippled edges; rostral node compressed, with vertical fenestra and strut; cranial roof narrow and arched above orbits; and otic capsules with strong pterotic horns.

The family Pseudocarchariidae, which like Megachasmidae has a single, oceanic, highly distinct species (*Pseudocarcharias kamoharai*), differs from *Megachasma* in many characters, including its more slender body and shorter head; slender, cylindrical caudal peduncle with low lateral keels and upper and lower transverse, crescentic precaudal pits; much larger eyes; nostrils anterior to mouth; more elongated gill openings, extending onto dorsal surface of head; teeth with strong labial root lobes, moderate lingual protuberances, a narrow neck on the crown, and labiolingually diagonal attachment surfaces; anteriors, intermediates, and lateroposteriors well differentiated in dental bands; anteriors and anterior-laterals enlarged, pectoral fins smaller, broader, less elongated, and not falcate, with aplesodic fin skeletons; origins of pectoral fins behind fifth gill openings; anal fin with a narrow base and pivotable; caudal fin with a shorter dorsal and ventral caudal lobe; rostrum longer, with appendices, a compressed rostral node, and vertical fenestrae and struts; basal plate and cranial roof extremely narrow, with narrow, slotlike, vertical anterior fontanelle; orbits of cranium very large; pterotic horns present and well developed on otic capsules; palatine processes of palatoquadrates enlarged and forming large dental bullae, articulating with the orbital notches of the cranium; and quadrate processes of palatoquadrates elevated and contacting postorbital processes.

The benthopelagic family Mitsukurinidae also has a single living, strongly distinct species (*Mitsukurina owstoni*). The Mitsukurinidae differs from the Megachasmidae in lacking precaudal pits; having a greatly elongated, flattened, bladelike snout; smaller eyes; a very narrow, elongated mouth; lower labial furrows; teeth with strong labial root lobes, moderate lingual protuberances, a narrow neck and striations on the crown, and labiolingually diagonal attachment surfaces; symphyseals, anteriors, laterals, and posteriors well differentiated in dental bands, with anteriors and laterals enlarged; lateral trunk denticles with narrow, hooked, semierect crowns; pectoral fins smaller than pelvic fins, shorter, broader, not elongated and falcate, and with aplesodic fin skeletons; pectoral origins behind fifth gill openings; first and second dorsal fins equal-sized, smaller than pelvic and anal fins; anal fin large, broadly rounded, and separated from lower caudal origin by a narrow notch; anal fin origin about opposite or close behind second dorsal origin; no ventral caudal lobe; rostrum of cranium greatly elongated, longer than nasobasal length of cranium, with a compressed, extremely long rostral node; subethmoid fossa extending anterior to the nasal capsules; supraorbital crest reduced to separate preorbital and postorbital processes; and with palatine processes of palatoquadrates deflected ventrally, with prominent bullae.

The three highly specialized lamnoid families Alopiidae, Lamnidae, and Cetorhinidae have numerous additional differences from the Megachasmidae. The Alopiidae further differs from the Megachasmidae in having a shorter head; crescentic upper precaudal pits; larger eyes; nostrils anterior to mouth; shorter gill openings; a much smaller mouth and less highly protrusible jaws; teeth with weaker lingual protuberances, stronger labial root lobes, and differentiated anteriors, lateroposteriors, and (variably) intermediates and symphyseals; claspers very slender, without spurs; pelvic fins plesodic; first dorsal fin higher and plesodic, with its origin well posterior to the pectoral insertions; second dorsal much smaller relative to first dorsal, with a narrow, pivotable base; anal fin smaller, with narrow, pivotable base; caudal fin about as long as rest of shark, with a rippled dorsal margin; rostral node of rostrum compressed, with a vertical fenestra and strut; internasal septum narrow and high; subethmoid fossa very narrow; cranial roof narrow, flat or strongly arched; orbits large to gigantic; and palatine processes of palatoquadrates with small dental bullae.

The Lamnidae differs from the Megachasmidae in the following additional characters: trunk more fusiform; caudal peduncle greatly depressed, with strong lateral keels, and with transverse, crescentic, upper and lower precaudal pits; nostrils anterior to the mouth; gill openings longer, extending partway onto dorsal surface of head; jaws less protrusible; teeth with low lingual protuberances, enlarged anteriors, laterals, and intermediates; pectoral fin origins behind fifth gill openings; second dorsal much smaller relative to first dorsal, with a narrow, pivotable base; anal fin slightly larger than second dorsal, with a narrow, pivotable base; caudal fin shorter, less than half length of rest of shark, nearly symmetrical and lunate in Lamnidae, with a relatively shorter dorsal lobe, ripples in dorsal margin, and a longer ventral lobe; cranial roof narrow and arched; otic capsules with elongated pterotic horns; palatine processes of palatoquadrates with prominent dental bullae articulating with underside of ethmoid region of cranium; and quadrate processes of palatoquadrates very high.

Finally, the family Cetorhinidae with the only other filter-feeding lamnoids of the genus *Cetorhinus,* differs from the family Megachasmidae in the following particulars: trunk more fusiform; caudal peduncle somewhat depressed, with strong lateral keels and transverse, crescentic upper and lower precaudal pits; nostrils anterior to mouth; gill openings much larger, expanded onto dorsal and ventral surfaces of head; jaws little protrusible; pectoral fins with their origins behind fifth gill openings; lateral trunk denticles with erect, hooked, narrow crowns, directed anteriorly and dorsoventrally as well as posteriorly; claspers stout, with broad tips and heavy spurs; first dorsal fin with its origin far posterior to pectoral insertions, and midbase closer to pelvic bases than to pectoral bases; caudal fin shorter, less than half length of rest of shark, nearly symmetrical and lunate, with a shorter dorsal lobe and longer ventral one; medial rostral cartilage very broad, platelike, and ventrally excavated by the broad anterior expansion of the subethmoid fossa; lateral rostral cartilages joining each other posterior to their junction with the rostral node, and extending anterior to that junction as a medial rod; cranial roof moderately broad, highly arched above orbits; supraorbital crests fenestrate basally; and jaws very slender and weak.

The phenetic comparisons between Megachasmidae and other lamnoids presented above are not intended to be exhaustive, but serve to demonstrate the separation of Megachasmidae from related families. They do not broach the question of the relationship of the megamouth shark to other lamnoids. A detailed account of lamnoid interrelationships is beyond the scope of this paper, but suffice it to note here that many of the characters of *Megachasma pelagios,* such as its snout and jaw structure, gill-rakers, dermal grooves on fins, reduced vertebrae, and ethmoid morphology are evidently unique derived characters of this shark that do not offer a clue to its relationships. Its teeth are superficially similar to those of the basking shark (*Cetorhinus maximus*), but this may be parallel evolution of vestigial structures in two very different lamnoid filter-feeders (as suggested by the superficial similarity of the teeth of the orectoloboid whale shark, *Rhiniodon typus*). *Megachasma* most resembles members of the Odontaspididae (especially the genus *Odontaspis*) and Pseudocarchariidae in its body shape, fin shape, relative fin sizes (except for the pectoral fins), fin positions, and relationships of interspaces between fins to fin size. By comparison with the derived families Alopiidae, Cetorhinidae, and Lamnidae, these similarities between Megachasmidae, Odontaspididae, and Pseudocarchariidae may prove to be common primitive characters not of importance in demonstrating phyletic relationships among these families. *Megachasma* shares the derived character state of plesodic pectoral fins with the Alopiidae, Cetorhinidae, and Lamnidae, but presently appears to have little else in common with these derived families.

On the other hand, two characters of *Megachasma*, if correctly interpreted as primitive, suggest that Megachasmidae is the sister-group of all other living lamnoids. The absence of differentiated anteriors, laterals, and intermediates (or a toothless gap between anteriors and laterals) in *Megachasma* may indicate that it is primitive in lacking them, and that all other lamnoids (including *Cetorhinus*) can be united by the presence of these tooth-row groups as a shared derived character. However, the unusually broad, toothless space at the upper symphysis of *Megachasma* suggests another possibility, that it is derived in having lost these row groups, at least in the upper jaw; and that the simple gradient monognathic heterodonty in the dentral bands is secondary and correlated with the evolution of gill-rakers as the primary feeding structures in *Megachasma*.

The second character is the well-developed orbital processes on the palatoquadrates of *Megachasma*, which suggest a primitive condition by comparison with other, non-lamnoid sharks. The reduced (Alopiidae, Odontaspididae, Mitsukurinidae, and Cetorhinidae) or apparently nonexistent (Lamnidae, Pseudocarchariidae) orbital processes of other lamnoids would by this interpretation represent a shared derived character of lamnoids other than *Megachasma*. A detailed assessment of these characters and others, grouping the various lamnoid genera and families will be considered in detail elsewhere (Compagno, in preparation).

A possible fossil relative of *M. pelagios* is represented by isolated small teeth (2–15 mm high) known since the 1960's from early Miocene deposits in the southeastern San Joaquin Valley of California (Shelton P. Applegate, pers. comm.), and subsequently found in other localities in the late Oligocene or early Miocene of northern California (Phillips et al. 1976) and central Oregon (Bruce J. Welton, pers. comm.). The shark represented by these teeth has never been named, but is known from abundant tooth material from southern California. Its affinities have been much debated among palaeoichthyologists, but it appears most likely to be a lamnoid because of its osteodont tooth histology and external tooth morphology. Dr. Bruce J. Welton is preparing a paper describing this shark, and will compare it with *M. pelagios*, of which it is possibly a fossil congener but is distinctly more primitive.

Megachasma, new genus

Type-species.—*Megachasma pelagios* Taylor, Compagno, and Struhsaker, new species.

Derivation of Name.—*mega*, from Greek, large, great; *chasma*, yawning hole, open mouth.

Generic Diagnosis.—Characters of the new genus are those of the new family Megachasmidae (see above).

Megachasma pelagios, sp.nov.

Megamouth Shark

Holotype.—An adult male, 4460 mm total length, Bernice P. Bishop Museum, Honolulu, Oahu, Hawaii, BPBM 22730.

Type-locality.—Hawaiian Islands, about 42 km NE Kahuku Point, Oahu, 21°51′N, 157°46′W, at about 165 m depth in water about 4600 m deep.

Derivation of Species Name.—*pelagios*, from Greek, of the open sea.

Measurements and Proportions.—These are given below as measurements in millimeters, followed by their proportions as percentages of total length and precaudal length, given in that order in parentheses.

Total length: 4460 mm (100% total length, 144.3% precaudal length).

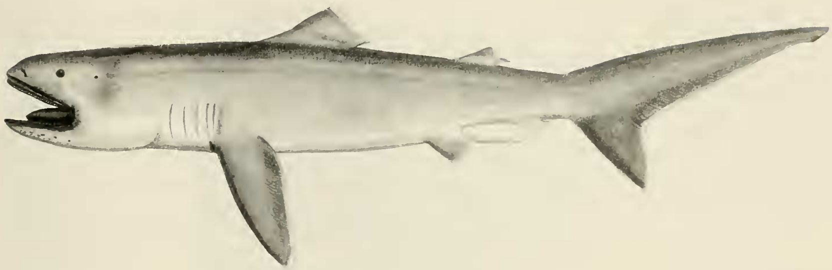

FIGURE 4. Lateral-view drawing of the holotype of *Megachasma pelagios*, with jaws in retracted position. Drawn by L. J. V. Compagno.

Precaudal length (snout to upper caudal origin): 3090 (69.3, 100).

Tip of snout to: upper symphysis, 66 (1.5, 2.1); nostrils, 100 (2.2, 3.2); orbits, 240 (5.4, 7.8); spiracles, 450 (10.1, 14.6); 1st gill openings, 850 (19.1, 27.5); 2nd gill openings, 920 (20.6, 29.8); 3rd gill openings, 1020 (22.0, 33.0); 4th gill openings, 1150 (25.8, 37.2); 5th gill openings (head length), 1180 (26.5, 38.2); pectoral origins, 1110 (24.9, 35.9); pelvic origins, 2270 (50.9, 73.5); 1st dorsal origin, 1540 (34.5, 49.8); 2nd dorsal origin, 2530 (56.7; 81.9); anal origin, 2830 (63.5, 91.6); vent, 2295 (51.5, 74.3).

Distance between: vent and caudal tip, 2165 (48.5, 70.1); 1st and 2nd dorsal origins, 625 (14.0, 20.3); 1st and 2nd dorsal bases, 590 (13.2, 19.1); 2nd dorsal and upper caudal origins, 428 (9.6, 13.9); 2nd dorsal base and upper caudal origin, 395 (8.9, 12.8); pectoral and pelvic origins, 510 (11.4, 16.5); pelvic and anal bases, 330 (7.4, 10.7); anal and lower caudal origins, 315 (7.1, 10.2); anal base and lower caudal origin, 230 (5.2, 7.4).

Eyes (palpebral apertures or fleshy orbits): length, 56 (1.3, 108); height, 54 (1.2, 1.7); width across anterior corners (interorbital), 370 (8.3, 12.0); eyeball diameter, 84 (1.9, 2.7).

Nostrils: width, 30 (.07, 1.0); internarial space, 340 (7.6, 8.8).

Spiracles: diameter, 6 (0.1, 0.2); space between spiracles and eyes, 176 (3.9, 5.7).

Mouth (jaws in retracted position): length, 273 (6.1, 8.8); width, 827 (18.5, 26.8); width across outer edges of jaws, 1025 (23.0, 33.2); length of lower jaw, 820 (18.4, 26.5).

Gill opening widths (heights): 1st, 265 (5.9, 8.6); 2nd, 258 (5.8, 8.4); 3rd, 264 (5.9, 8.5); 4th, 256 (5.7, 8.3); 5th 234 (5.2, 7.6).

Head height: at spiracles, 500 (11.2, 16.2); at 1st gill openings, 625 (14.0, 20.2); at 5th gill openings, 630 (14.1, 20.4).

Trunk height: at 1st dorsal origin, 640 (14.3, 20.7); at pelvic origins, 515 (11.5, 16.7); at pelvic insertions, 440 (9.9, 14.2).

Girth: at 1st dorsal origin, 1800 (40.4, 58.2); at 2nd dorsal origin, 1140 (25.6, 36.9).

Caudal peduncle height: at 2nd dorsal insertion, 341 (7.6, 11.0); at upper caudal origin, 237 (5.3, 7.7).

Caudal peduncle width: at 2nd insertion, 146 (3.3, 4.7); at upper caudal origin, 109 (2.4, 3.5).

Pectoral fins, length of: anterior margin, 837 (18.8, 27.1); posterior margin, 615 (13.8, 19.9); base, 262 (5.9, 8.5); origin to free rear tip, 453 (10.1, 14.7); inner margin, 190 (4.3, 6.1).

Pelvic fins, length of: anterior margin, 264 (5.9, 8.5); posterior margin, 181 (4.1, 5.9); base, 207 (4.6, 6.7); origin to free rear tip, 245 (5.5, 7.9); inner margin, 38 (0.8, 1.2); height, 255 (5.7, 8.3); origin to rear tip of clasper, 575 (12.9, 18.6).

Claspers: inner length from vent to tip, 550 (12.3, 17.8); outer length from clasper base to tip, 355 (8.0, 11.5); width at outer pelvic base, 47 (1.1, 1.5).

1st dorsal fin, length of: anterior margin, 415 (9.3, 13.4); posterior margin, 265 (5.9, 8.6); base, 404 (9.1, 13.1); inner margin, 82 (1.8, 2.7); height, 226 (5.1, 7.3).

2nd dorsal fin, length of: anterior margin, 198 (4.4, 6.4); posterior margin, 158 (3.5, 5.1); base, 191 (4.3, 6.2); inner margin, 80 (1.8, 2.6); height, 104 (2.3, 3.4).

Anal fin, length of: anterior margin, 196 (4.4, 6.3); posterior margin, 80 (1.8, 2.6); base, 159

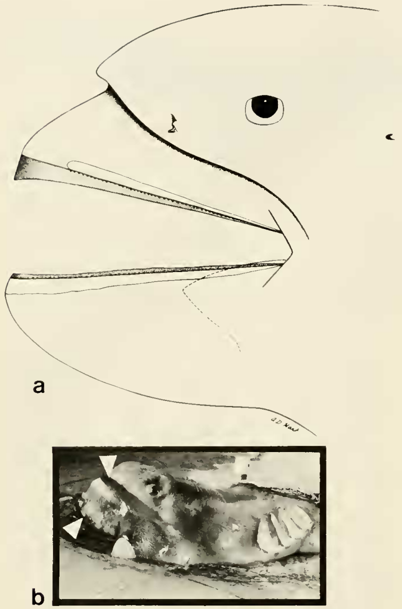

FIGURE 5. (*a*) Schematic head drawing of *Megachasma pelagios* with jaws protruded. (*b*) Photograph of fresh shark with jaws protruded. (Upper arrow points to anteriormost edge of neurocranium; lower arrow to upper jaw and teeth.)

(3.6, 5.1); inner margin, 67 (1.5, 2.2); height, 78 (1.7, 2.5).

Caudal fin, length of: dorsal margin, 1443 (32.3, 46.7); preventral margin, 625 (14.0, 20.2); lower postventral margin, 377 (8.5, 12.2); upper postventral margin, 1220 (27.4, 39.5); subterminal margin, 57 (1.3, 1.8); terminal margin, 96 (2.2, 3.1); terminal lobe or sector, 139 (3.1, 4.5); width of dorsal lobe at postventral notch, 471 (10.6, 15.2); width of ventral lobe at postventral notch, 273 (6.1, 8.8).

Intestinal valve: length, 690 (15.5, 22.3); diameter, 145 (3.3, 4.7); thickness of broadest anterior ring, 25 (0.6, 0.8).

DESCRIPTION (based on the holotype and only known specimen).—Head length from snout tip to 5th gill openings, 26% of total length and 1.6 times distance between pectoral and pelvic fin bases. Head broad, cylindrical, and approximately circular in transverse section at eyes, but somewhat laterally expanded and oval in section over jaws when jaws are retracted; not depressed. Outline of head in lateral view nearly straight dorsally, except for bluntly convex snout, strongly convex ventrally along edges of lower jaws and nearly straight beneath gills; in dorsoventral view, anteriorly rounded and convex and tapering posteriorly to gills. Snout length from tip to edge of mouth about 12.5 times in mouth width. Snout broadly rounded in dorsal view, with lateral margin slightly indented anterior to nostrils; in lateral view, convex dorsally and concave ventrally to fit the front of the retracted upper jaw (Fig. 5). External eye opening (palpebral aperture) or fleshy orbit without anterior or posterior notches, length about 21 times in head length. Irises of eyes black, nearly filling orbits. Eyeballs large, diameter 14 times in head length. Spiracles small, their lengths about $^{1}/_{10}$ orbit length, located about 3 orbit lengths behind eyes and about opposite ventral margins of eyes. Gill openings of nearly equal length, the longest (1st and 3rd) about 4.5 in head length and 4.7 times eye length, the smallest (5th) about $^{9}/_{10}$ length of longest. Edges of gill openings nearly straight, not incised, and with filaments not exposed when jaws are retracted. Gill openings with upper ends falling below level of eyes, and midheight of head at gill openings. Internal gill openings with numerous gill-raker papillae arranged in about 4 rows on their anterior and posterior edges, including both anterior and posterior edges of 1st gill cavity between hyoid and 1st branchial arches and posterior edge of 5th gill cavity on anterior edge of 5th gill arch. Gill-raker papillae small, about 10–15 mm long, densely packed, slender, tapering to blunt point, arranged with tips pointing anteromedially into pharynx, with thick epidermis and dermis covering hyaline cartilage core layered with flattened, imbricated denticles (Fig. 6). Nostrils with large lateral incurrent aperture, anterior nasal flap with an undulated, truncated posterior edge, and low keel on dorsal surface, but no distinct mesonarial flap, small medial excurrent aperture with low posterior nasal flap on its rim. Nostrils lateral to mouth edge and 2.4 times closer to snout tip than to eyes. Nostril width 1.8 in orbit length, 8.8 times in longest gill opening. Inner labial grooves at mouth corners on both upper and lower jaws just lateral to dental bands and medial to vertical fold of skin sheathing adductor mandibulae muscles. Mouth width when jaws are retracted about 1.4 in head length; mouth length

FIGURE 6. Gill-raker papillae of *Megachasma pelagios*. (*a*) Drawing of a group of gill-raker papillae. (*b*) Scanning electron micrograph of the tip of a single papilla, showing the closely imbricated denticles (20× magnification). (*c*) Scanning electron micrograph of denticles from *b*, at higher magnification (51×).

about 3 times in width. A broad fold of skin forming a deep pocket on dorsal surface of upper jaws below snout, and a vertical fold of skin enclosing anterior edges of adductor mandibulae muscles at each mouth corner. Tips of upper jaws can extend at least 6 orbit lengths in front of snout tip, with mouth corners passing anterior to eyes. Tongue extremely large, broadly rounded and thick, enclosing greatly enlarged basihyoid cartilage; tongue almost entirely filling mouth cavity when jaws are closed. Deep pocket under front of tongue, freeing it anteroventrally; pocket about 4 orbit lengths deep from anterior tongue edge to its basal attachment to mouth. Maxillary

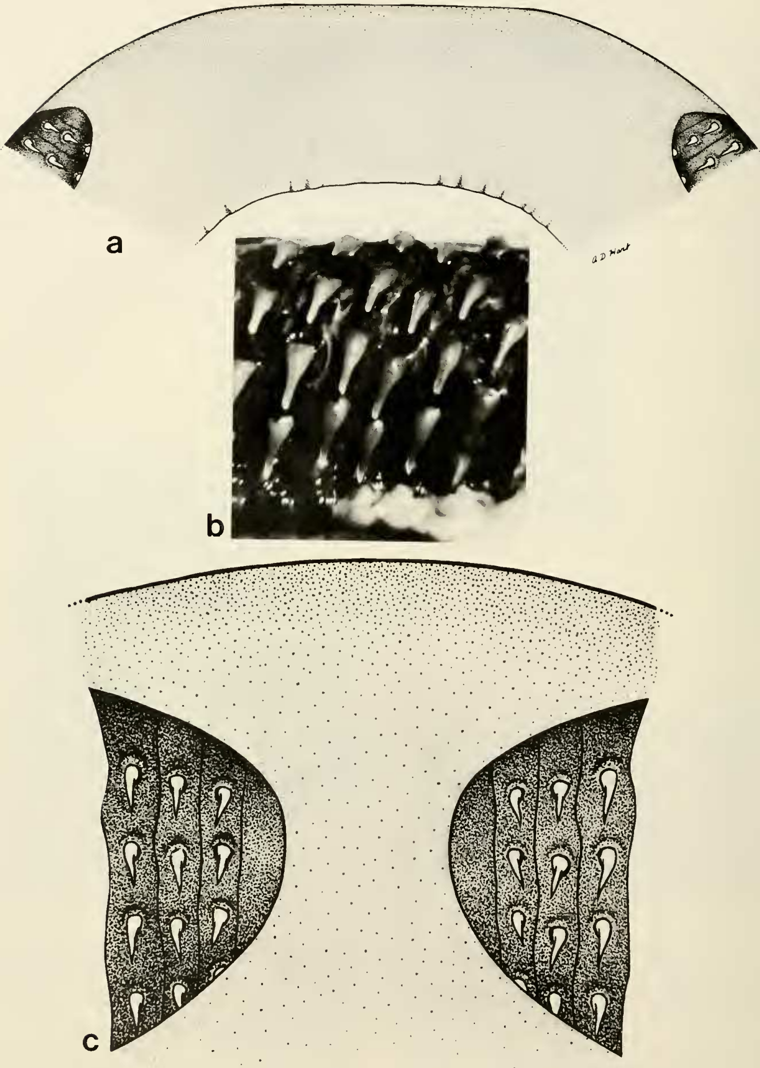

FIGURE 7. Illustrations of (*a*) upper symphysis and (*c*) lower symphysis of *Megachasma pelagios*, showing bare, toothless patches and mesial ends of dental bands. (*b*) Close-up of rows of teeth from upper jaw.

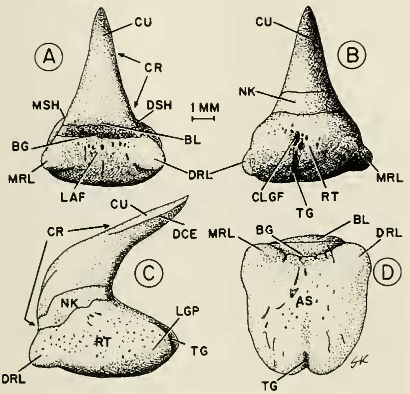

FIGURE 8. Illustration of a lower tooth of *Megachasma pelagios* from about midlength on the lower left dental band in (*A*) labial; (*B*) lingual; (*C*) distal; and (*D*) basal views. Abbreviations: AS, attachment surface of root; BG, basal groove; BL, basal ledge; CLGF, centrolingual foramen; CR, crown; CU, cusp; DCE, distal cutting edge; DRL, distal root lobe; DSH, distal shoulder; LAF, labial foramina; LGP, lingual protuberance; MRL, mesial root lobe; MSH, mesial shoulder; NK, neck; RT, root; TG, transverse groove. Drawn by L. J. V. Compagno.

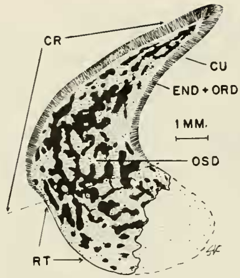

FIGURE 9. Diagrammatic sagittal section of a lower tooth of *Megachasma pelagios* from about midlength on the lower left dental band, lingual protuberance broken off. Abbreviations: CR, crown; CU, cusp; END + ORD, enameloid + orthodentine; OSD, osteodentine; RT, root. The teeth of *M. pelagios* are of the "osteodont" type, with a crown having a core of osteodentine and no pulp cavity or canal. Drawn by L. J. V. Compagno.

valve of upper jaw arcuate and relatively narrow, width less than an eye diameter. No enlarged buccal papillae in mouth cavity, but with scattered circular organs of undetermined function on tongue and mouth.

Teeth very small and relatively numerous, in 56 rows in left upper, 59 rows in left lower, 52 rows in right upper, and 69 rows in right lower jaw halves, or 56–52/59–69; total tooth-row counts 108/128. Teeth not arranged in diagonal files. Symphyseal toothless space about 4 orbit diameters wide in upper jaw and less than one eye-length wide in lower jaw (Fig. 7). Dental bands of upper and lower jaws show strong gradient monognathic heterodonty; starting from small teeth at symphysis, teeth increase in size to about 10 mm high in about 10 tooth rows distal to symphysis, then begin to gradually decrease in size and increase in width relative to height to distal ends of dental bands. Teeth (Fig. 8) have no cusplets, narrow crown shoulders, partial transverse groove on linguobasal attachment surface of root, large centrolingual foramen, and scattered labial foramina below basal ledge. A sectioned tooth (Fig. 9) shows thick osteodentine core in crown, surrounded by relatively thin layers of pallial orthodentine and enameloid, and no pulp canal or cavity; crown osteodentine continuous with that of root, which forms its sole component.

Body stout, trunk circular or vertically oval in section at first dorsal base. Length of head and trunk from snout tip to vent 50% of total length. Trunk relatively short, length from 5th gill opening to vent 1.1 times head length. No predorsal, interdorsal, or postdorsal ridges on midline of back and precaudal lobe; no lateral ridges on body. Precaudal lobe from vent to upper caudal origin short, 19.2% of total length. Height of caudal peduncle at insertion of second dorsal 2.3 times its width there and 1.2 times in distance from insertion of second dorsal to upper caudal origin; height of caudal peduncle at upper caudal origin 2.2 times its width there and 1.7 times in distance from insertion of second dorsal to upper caudal origin. Upper precaudal pit not transverse and crescentic.

Dermal denticles on body very small and flattened, giving skin a smooth texture. Denticles on sides of trunk below first dorsal fin (lateral trunk denticles) loosely spaced, not closely imbricated (Fig. 10), with a strong medial ridge and a pair of strong lateral ridges running entire length of crown, strong medial cusp, but with lateral cusps absent or hardly developed. Denticles on dorsal surfaces of pelvic fins (Fig. 11) similar to lateral

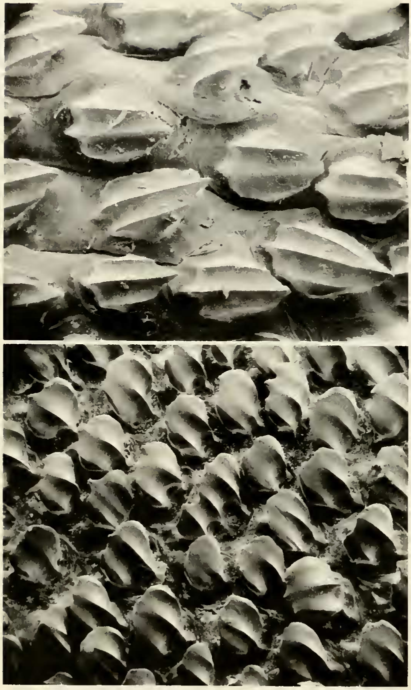

FIGURE 10. Scanning electron micrographs of dermal denticles of *Megachasma pelagios*. (*top*) Lateral trunk denticles from just below the base of the first dorsal fin (60× magnification). (*bottom*) Denticles from the surface of the tongue (67×).

trunk denticles, except for having lower ridges and being closely imbricated. Denticles from tongue are wide-spaced but broader and more transversely oval than lateral trunk denticles. Distal webs of upper surfaces of pectoral and pelvic fins, and dorsal caudal lobe, have conspicuous dark wavy lines, often parallel, which are channels of bare skin between areas of denticulate skin (Fig. 11).

Pectoral fins moderately broad basally but distally elongated, tapering, falcate, and broad-tipped. Anterior margins of pectoral fins moderately convex, apices broadly angular, posterior margins slightly convex, and free rear tips and inner margins smoothly rounded and broadly convex. Length of pectoral fin from origin to free rear tip 1.9 times in its anterior margin length. Apex of pectoral posterior to its free rear tip when fin is appressed to body.

Pectoral fin skeleton with all radials except last 5 on metapterygium greatly elongated, with broad, flattened tips. Radials with numerous segments, the longest with 10; distalmost segments elongated but only about ⅓ length of each radial. Pectoral fin propterygium supporting one radial, mesopterygium with 5 radials, metapterygium with 8 radials on basal segment and 8 on axis. Propterygium small and slightly elongated distally. Mesopterygium moderately elongated distally, fairly broad and wedge-shaped with radials inserted on distal end at an angle to axis of elongation. Metapterygium diagonally elongated across fin base with radials inserted at an angle to long axis. Metapterygial axis of 5 segments, about ⅔ as long as basal metapterygium. Basal and radial cartilages of pectoral fins not highly calcified; fins rather flexible, despite having plesodic skeletons.

Pelvic fins with anterior margin slightly concave anteriorly but convex posteriorly, apex very narrowly rounded, and inner margins slightly concave. Inner margins, posterior margins, and free rear tips of pelvics forming broad triangle.

Claspers relatively slender, width at base 7.6 times outer length from pelvic bases to tips, inner length from vent to tip 12.3 percent of total length. Rear tips of claspers reaching almost to midbase of anal fin when claspers are horizontal. Clasper tip elongated, forming a very narrow, slender process (Fig. 11), glans anterior to elongated tip slightly spatulate and flattened, shaft cylindrical. Clasper groove open, with edges not fused dorsally; no pseudopera or lateral clasper groove and fold. Small, sharp-tipped, hardened clasper spur on ventral lobe, lateral to groove. Large, large-mouthed, prominent pseudosiphon on the dorsal clasper lobe.

First dorsal fin with anterior margin slightly concave anteriorly and convex posteriorly, posterior margin nearly straight, free rear tip acute and slightly attenuated, and inner margin slightly concave. Origin about opposite or slightly posterior to pectoral fin insertions, midpoint of dorsal base about 2.6 times closer to pectoral insertions than pelvic origins, dorsal fin insertion anterior to pelvic origins by about 0.8 times first dorsal base, and free rear tip about 2.9 times dorsal inner margin anterior to pelvic origins. Posterior margin slanting posteroventrally from dorsal apex, insertion well posterior to level of

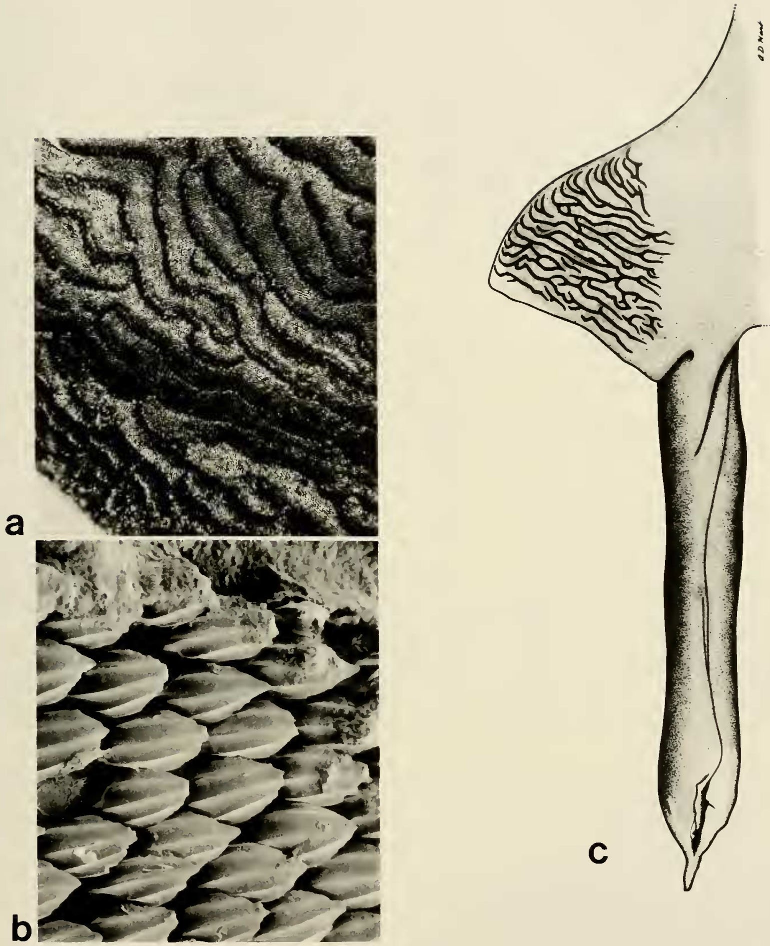

FIGURE 11. Right pelvic fin and clasper of *Megachasma pelagios*, showing channels of naked skin on dorsal surface of pelvic fin. (*a*) Close-up photograph of the channels. (*b*) Scanning electron micrograph of denticles from the anterior edge of the pelvic fin (54× magnification). (*c*) Drawing of the pelvic fin and clasper.

dorsal apex. Base 1.5 times in interdorsal space and 3.6 times in dorsal caudal margin, height 1.8 times in base, and inner margin 2.8 times in height.

Second dorsal fin low, height 0.46 times first dorsal height, base 0.47 times first dorsal base. Anterior margin nearly straight, apex narrowly rounded, posterior margin slightly concave, free rear tip angular and attenuated, and inner margin slightly concave. Free rear tip about over anal fin origin. Posterior margin of second dorsal slanted posteroventrally from apex, insertion

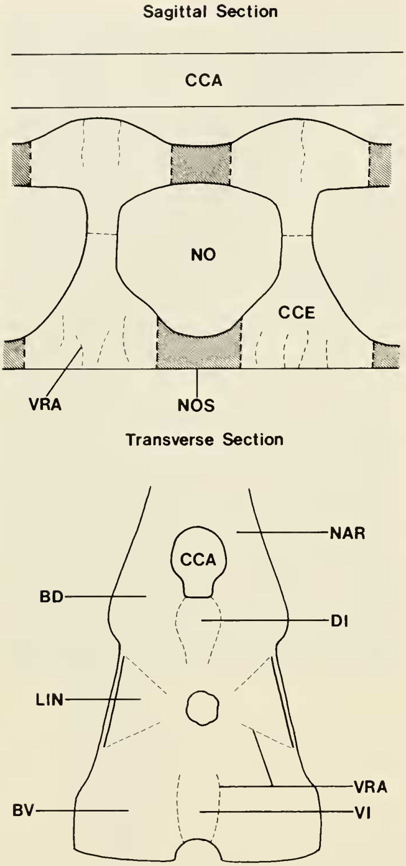

FIGURE 12. Monospondylous precaudal vertebrae of *Megachasma pelagios,* in (*top*) sagittal section, and (*bottom*) transverse section. Abbreviations: *Sagittal section:* CCA, central canal; CCE, cartilaginous centrum; NO, notochord; NOS, notochordal sheaths; VRA, vestigial radii. *Transverse section:* CCA and VRA, as above; BD, basidorsal; BV, basiventral; DI, dorsal intermedial; LIN, lateral intermedial; NAR, neural arch; VI, ventral intermedial. (From drawings by L. J. V. Compagno.)

posterior to apex. Base 2.1 times in distance from insertion to upper caudal origin, height 1.8 times base, and inner margin 1.2 times height.

Anal fin low, height 0.8 times second dorsal height, base length 0.8 second dorsal base. Anterior margin concave anteriorly but convex posteriorly, apex broadly rounded, posterior margin moderately concave or notched, free rear to acute and attentuated, and inner margin slightly concave. Posterior margin of anal fin slanted posterodorsally from apex, with anal apex just below insertion. Base 1.4 times in distance from insertion to lower caudal origin, height 2.0 times in base, and inner margin 1.2 times in fin height.

Caudal fin relatively asymmetrical, with basally broad dorsal lobe, and short terminal lobe. Length of dorsal margin 2.1 times in precaudal length, of preventral caudal margin 2.3 times in dorsal caudal margin, and of terminal lobe from caudal tip to subterminal notch about 10.3 times in dorsal caudal margin. Dorsal caudal margin slightly but continuously convex in lateral view, preventral margin almost straight dorsally but becoming more convex ventrally. Tip of ventral caudal lobe broadly angular, lower and upper postventral margins slightly convex, notch between postventral margins broadly angular, subterminal notch shallowly concave, subterminal margin slightly concave, and terminal margin slightly convex. Subterminal margin length 0.6 times terminal margin length. Ventral lobe of caudal fin aplesodic, not supported by hypural radials but by ceratotrichia and connective tissue only.

Vertebrae (Fig. 12) examined from beneath first dorsal fin (monospondylous precaudal vertebrae) and at base of caudal fin (diplospondylous caudal vertebrae). These found to have extremely reduced calcification, both of the primary double cone of vertebral centra (which is almost entirely formed of uncalcified cartilage and connective tissue in *M. pelagios*), and of intermedial areas between basidorsals and basiventrals. Vertebral centra consist of biconic or bioconcave discs of cartilage, separated by broad bands of unchondrified notochordal sheath and spherical cavities containing notochordal tissue. Calcification in monospondylous precaudal centra restricted to some irregular calcification on lateral centrum body, a layer on ventral part of neural canal, a layer on midventral groove on underside of centrum, and paired thin zones partly bounding intermedial areas between basals, including 2 dorsals, 2 ventrals, and 2 pairs of laterals. These intermedial calcifications resemble radii of other lamnoids, but differ in being only partially developed across intermedial areas and in not forming discrete longitudinal plates. These

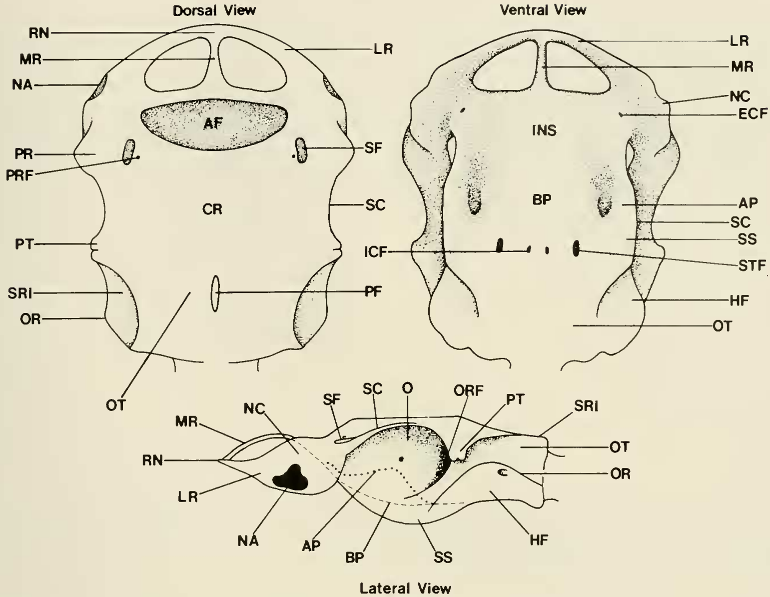

FIGURE 13. Neurocranium of *Megachasma pelagios*, in dorsal, ventral, and lateral views. Abbreviations: *Dorsal view:* AF, anterior fontanelle; CR, cranial roof; LR, lateral rostral cartilage; MR, medial rostral cartilage; NA, nasal aperture; OR, opisthotic ridge; OT, otic capsule; PF, parietal fossa; PR, preorbital process; PRF, profundus foramen; PT, postorbital process; RN, rostral node; SC, supraorbital crest; SF, supraorbital fenestra; SRI, sphenopterotic ridge. *Ventral view:* LR, MR, and OT as above; AP, articular pit; BP, basal plate; ECF, ectethmoid foramen; HF, hyomandibular facet; ICF, internal carotid foramen; INS, internasal septum; NC, nasal capsule; SC, suborbital crest; SS, suborbital shelf; STF, stapedial fenestra. *Lateral view:* O, orbit; ORF, orbital fissure; SC, suborbital crest; SCA, sphenopterotic capsule; all others as above. (From drawings by L. J. V. Compagno.)

intermedial calcified zones interpreted as representing vestigial radii, greatly reduced in *Megachasma* but probably well developed in its precursors. Basal caudal centra similar to monospondylous precaudal centra, except for having intermedial calcifications even more reduced to a set of dorsal and ventral pairs only. The poorly calcified vertebral centra of *Megachasma* recall the septate vertebral columns of large species of *Somniosus* (subgenus *Somniosus*, for *S. pacificus* and *S. microcephalus*) and some other squaloids (see Compagno 1977), with reduction of form and calcification of centra and hypertrophy of notochordal tissue in between centra. The lamnoids *Mitsukurina* and *Pseudocarcharias* have extremely simple centra with double cones and radii reduced to 8 slightly branched plates (2 bounding each intermedial area), but *Megachasma* goes far beyond these genera in reduction of its centra, in calcification, and in intrusion of notochordal tissue. *Mitsukurina* and *Pseudocarcharias* retain normal, close-set double cones, despite their simple radii.

Neurocranium (Fig. 13) dissected on one side only, and reconstructed bilaterally. Cranium relatively large, extremely broad and moderately flat; nasobasal length (from base of medial rostral cartilage to occipital condyles) about 8.9 percent total length and 12.8 percent precaudal length; greatest width of cranium across preorbital processes about equal to nasobasal length, and greatest height from cranial roof to ventral edges of suborbital shelves 0.4 times in nasobasal length and greatest cranial width. Rostrum relatively short but very broad, length of medial rostral cartilage from its base to anterior edge of rostral node about 26 percent nasobasal length; width across outer bases of lateral rostral cartilages 2.2

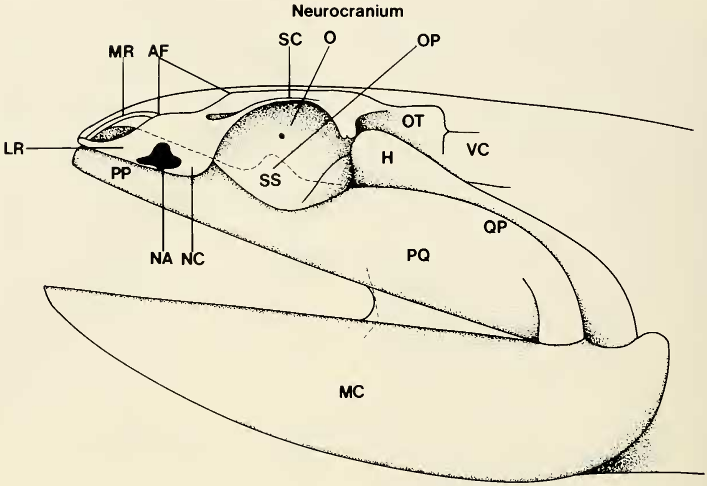

FIGURE 14. Jaw suspension of *Megachasma pelagios*, in lateral view, jaws retracted. Abbreviations: H, hyomandibular; MC, Meckel's cartilage; OP, orbital process; PP, palatine process; PQ, palatoquadrate; QP, quadrate process; VC, vertebral column; all others as in Figure 12. (From drawings by L. J. V. Compagno.)

times length of medial rostral cartilage. Entire ethmoid region of cranium, including rostrum, nasal capsules, and internasal septum, and the anterior basal plate molded dorsally around enlarged palatine processes of palatoquadrates (Fig. 14). Lateral rostral cartilages with broad bases that cover entire anterior surfaces of nasal capsules; diagonally compressed from dorsomedial to ventrolateral, and extending anteromedially as tapering triangular bars to meet rostral node separately on either side. Medial rostral cartilage and its base on internasal septum deflected upward over symphysis of palatoquadrates (jaws in retracted position), so that base originates at a level slightly above lateral rostral cartilages and the moderately depressed, narrow, barlike shaft arches anterodorsally and anteroventrally to rostral node. Rostral node a simple, depressed, narrow plate, not vertically or horizontally fenestrated, anteriorly expanded, vertically compressed, nor with rostral appendices.

Nasal capsules extraordinarily modified, highly compressed, platelike, wedge-shaped structures with nasal fenestra mainly on their lateral faces. Plane of compression of nasal capsules congruent with large-based lateral rostral cartilages, together forming a lateral wall to expansion cavity enclosing palatine processes. Ectethmoid foramen present on dorsomedial surface of each nasal capsule. Large subethmoid fossa on ventral surface of depressed, laterally expanded internasal septum, extending anteriorly beneath rostrum and medially to nasal capsules, and posterolaterally to merge on either side with large orbital process cavity in basal plate. Foramina for nasal canals laterally situated in cranial cavity (not anterolateral), with canals running anterolaterally to nasal capsules.

Basal plate very broad, width across orbital notches about 68 percent nasobasal length, broadly arched over rear ends of palatoquadrate palatine processes (when retracted) but relatively flat posterior to internal carotid foramina. Entire ventral surface of suborbital shelves, basal plate, and internasal septum padded with thick, soft, spongy connective tissue, probably to cushion it from palatoquadrates. Basal plate with pair of internal carotid foramina located about 59 percent nasobasal length behind medial rostral cartilage, separated by a convex space with width 80 percent nasobasal length and 1.1 times in distance between internal carotid foramina and stapedial fenestrae. Stapedial fenestrae small, width about 3 percent nasobasal length, apertures about 1.6 times closer to internal carotid formina than to lateral edges of suborbital shelves. Stapedial fenestrae apparently without greatly convoluted arteries or a rete mirabile elaborated from efferent spiracular arteries. Basal plate nearly horizontal posteriorly, without medial keels.

Orbits nearly circular in lateral view, with large optic nerve foramen slightly dorsal to its center. Orbits moderately large, with horizontal diameters about 43 percent of nasobasal length. Supraorbital crests broad, not fenestrate basally, only moderately concave in dorsal view. Preorbital processes not strongly exserted from supraorbital crests, and extending ventrally to posterior edges of nasal capsules. Small preorbital canal fenestra for superficial ophthalmic nerves present between broad preorbital process and cranial roof on each side; profundus nerve foramen just mesial to fenestra. Postorbital processes ventrally produced almost to level of optic nerve foramen, bifurcate distally. Foramina of orbital wall not examined in detail but including foramina for superficial ophthalmic nerve anterior cerebral veins, optic nerve, and large, deep, trigeminofacialis chamber or orbital fissure. Suborbital shelves nearly vertical, large, thick basally but distally thin, arcuate, and with sides nearly parallel in ventral view.

Otic capsules large and subquadrate, with lengths about 36 percent nasobasal length and width about 82 percent nasobasal length. Hyomandibular facets huge, ventromedially incised, and broadly arcuate, extending along entire length of otic capsules from otic processes anteriorly to partway onto bases of suborbital shelves, but not exserted posteriorly from occiput. Hyomandibular nerve foramina just below opisthotic ridges and about midway along their lengths on otic capsules. Sphenopterotic ridges arching posteromedially in dorsal view, ending posteriorly in a bluntly rounded corner. Opisthotic ridges on dorsal surface of hyomandibular facets low and curved posteroventrally. Occiput flat and not exserted rearwards, with glossopharyngeal and vagus nerve foramina.

Jaws (Figs. 5, 14) poorly calcified; length of palatoquadrates about 16 percent total length, Meckel's cartilages 18.4 percent total length. Palatine processes of palatoquadrates articulating at symphysis and extending for about ⅖ of palatoquadrate length to orbital processes. Meckel's cartilages huge, ventrally arcuate, dorsally nearly straight, thick, and compressed, with long posterior extensions from their mandibular articulations with palatoquadrates. Meckel's cartilages articulating closely at mandibular symphysis.

Manipulation of the jaws of the fresh-caught *Megachasma pelagios* suggested that the jaws are highly protrusible, but not necessarily as a mechanism to quickly eject them outward to capture prey, as in some other lamnoids (most notably *Mitsukurina*), nor to bring the upper teeth to bear on prey items, as in *Carcharodon carcharias*. The jaws may be protruded forward and outward to expand the mouth aperture and form a hoop-net for capturing plankters, though we do not know the exact shape of the jaws deployed in this configuration without photographic documentation of a live *M. pelagios* feeding. The basking shark is able to deploy its much slimmer jaws almost in a circle while feeding and has been photographed many times with jaws expanded (but not protruded); however, the exact shape of the mouth opening in a living, feeding basking shark would be somewhat difficult to work out from a dead, preserved specimen. The jaw structure of *M. pelagios* suggests that the jaws move downward, anteriorly, and outward at the mouth corners, and the distal ends of the hyomandibulae swing anterolateroventrally as protrusion occurs. The mechanism of jaw protrusion is poorly understood with the limited dissection possible during preparation of this description (the desire to limit damage to the specimen prior to making a cast of it prohibited a thorough investigation of the jaw mechanism and the hyobranchial skeleton and musculature), but the large, straplike, diagonal preorbitalis muscles may help to pull the jaws forward.

The jaw musculature was not investigated in detail, but sufficient information was collected to determine that the jaw muscles are similar to those in other lamnoids. Levator palatoquadrati muscle simple, originating on sphenopterotic ridges of otic capsules and running posteroventrally to insert on quadrate processes of palatoquadrates. Adductor mandibulae muscles moderately large but small and weak compared to the huge jaws, and limited anteriorly by mouth corners. Levator hyomandibuli muscles broad and relatively large.

The viscera were not examined in detail, ex-

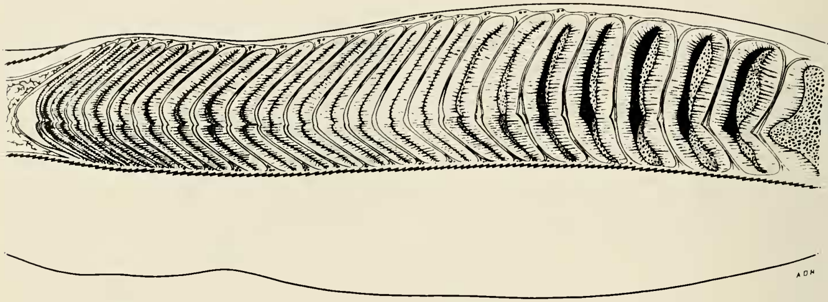

FIGURE 15. Drawing of the valvular intestine of *Megachasma pelagios* with the dorsolateral quadrant removed to show the ring valves with highly fimbricated edges (anterior to the right).

cept to note that the liver is relatively small (though very oily) and that the valvular intestine is an elongated ring-valve type rather similar to that of other lamnoids (Fig. 15). Each ring has a densely fimbriated surface, apparently to increase the absorptive surface, with a maximum thickness of 23–25 mm at the pyloric end of the intestine but becoming increasingly thin towards the rectum.

Color. When preserved, dorsal surface of head, trunk and tail, dorsal surfaces of pectoral and pelvic fins, dorsal fins, center of anal fin, and caudal fin dark gray to blue-black; sides of body lighter, underside of body and fins light gray, except for underside of head and lower jaw which are dark gray and mottled with black, undersurface of pectoral fins which have an abruptly black anterior margin about an eye diameter wide, and underside of pelvic fins with a dusky anterior margin. Tips and posterior margins of dorsal surfaces of pectoral and pelvic fins abruptly white, as are posterior margins of dorsal and anal fins and postventral caudal margins. Tissue of oral cavity and tongue blackish in preservative, but with oral lining silvery when fresh.

FEEDING HABITS AND BIOLOGY

The stomach contents were a thick reddish soup abundantly stocked with the euphausiid shrimp *Thysanopoda pectinata,* a species attaining a median length of 31 mm (Hu 1978). According to Hu (1978), *T. pectinata* off the west coast of Oahu (21°15′–20′N, 158°15′–30′W) shows a moderate day and night migration pattern. During the day most are caught between 350 and 750 m depth, with some ranging up to 300 m and down to 1100 m, but at night the bulk are between 150 and 500 m depth, with some up to 75 m and down to 525 m. Apparently, when captured, *Megachasma pelagios* would have been in the upper depths (165 m) where these euphausiids are commonest at night, and quite possibly might have been feeding on them when it became entangled in the parachute.

The megamouth shark unites an eclectic combination of habitus characters that (along with its apparent epipelagic habitat and filter-feeding habits) suggests an unusual mode of life. Deepwater epibenthic and epipelagic sharks often show a decrease in specific gravity and increase in hydrostatic support by the enlargement of their abdominal cavity and liver volume to produce a large, oily, hepatic "float." *M. pelagios,* in contrast, has reduced specific gravity in the form of extremely poor calcification; a soft, almost entirely hyaline cartilage skeleton; very soft, loose skin; and flabby, loose connective tissue and muscles. These features, and its soft, rubbery precaudal fins; lack of a keel on the caudal peduncle, weak precaudal pit; lack of dorsal caudal ripples; and highly flexible, asymmetric caudal fin suggest that *M. pelagios* is a slow, weak swimmer.

It is interesting to compare *M. pelagios* with the other two species of large, filter-feeding sharks: the basking shark and the whale shark. The basking shark is the only lamnoid filter-feeder besides megamouth, but in contrast has many adaptations for a higher activity level and sustained powerful swimming, including a strongly calcified skeleton, firm muscles, stiff fins, dense skin, and tough connective tissue; a huge, oily liver and elongated body cavity; a more fusiform body, lunate caudal fin, strong caudal keels and precaudal pits, and huge gill openings. The filter apparatus of *Cetorhinus*, with its vast gill cavities and slender, smooth, streamlined gill-raker denticles, is clearly adapted for a higher rate of water flow than is possible with the smaller gill cavities, more restricted internal gill apertures, and less streamlined gill-raker papillae of *Megachasma*. The basking shark is a slow but strong swimmer, which has often been observed and photographed while feeding at or near the surface with its mouth distended to form a circular scoop. Although its mouth is relatively smaller than that of megamouth, the basking shark is probably a much more efficient dynamic filterer because of its stronger swimming abilities and high-flow filter apparatus. The prey of the basking shark is far smaller than what is known for megamouth, consisting entirely of microscopic crustaceans (especially copepods). The basking shark prefers cool to cold coastal waters rich in nutrients and plankton.

The whale shark resembles the basking shark in its strong swimming adaptations, except that it has a less fusiform body, flattened anteriorly; a shorter body cavity and much smaller liver; and much smaller external gill openings (but larger than those of megamouth). The filter apparatus of *Rhiniodon* differs from that of *Megachasma* and *Cetorhinus* in not being confined to the margins of the internal gill openings; instead, the gill filter elements of *Rhiniodon* cross and bar these openings. They are compressed, triangular, cartilage-cored, connective-tissue-covered, parallel plates that transversely bridge the internal gill openings and connect adjacent holobranchs. The plates have highly lobulated pharyngeal margins that form an interconnected network, or dense filter grid, and are divided into paired dorsal and ventral groups of plates or screens over each internal gill opening. The dense screens of *Rhiniodon* are obviously efficient filters, but are incapable of sustaining a high flow of water through them. However, this filter apparatus, combined with a broad but very short, transverse mouth; very long, broad, low pharynx, and relatively small gill openings apparently adapts the whale shark to a combination of suction feeding (as in *Ginglymostoma* and other orectoloboids) and filter-feeding not found in *Megachasma* and *Cetorhinus*. The bellowslike pharynx and filter screens of the whale shark may provide it with a more versatile feeding apparatus than in *Cetorhinus* (and presumably *Megachasma*) by allowing it to suck in and filter out a wide variety of prey animals, independent of the shark's forward movement. Although the whale shark can ingest small crustaceans, it also eats squid and commonly takes small schooling fishes such as anchovies and sardines, and even small albacore and tuna (Bigelow and Schroeder 1948). It is not known whether *Rhiniodon* can filter out crustacean prey as small as the copepods favored by *Cetorhinus*, but almost certainly the euphausiids eaten by *Megachasma* are in the prey-size range of the whale shark, which is a warm-temperature to tropical, coastal to oceanic, slow but strong-swimming shark, often seen basking or cruising at the surface and feeding on schools of fishes. It often positions itself vertically beneath a school of prey, unlike the horizontal attitude *Cetorhinus* maintains while feeding at the surface.

The soft, flabby body and fins, low-flow branchial filter apparatus, and small gill openings suggest that *Megachasma* is less active and possibly a less efficient filter-feeder than *Cetorhinus* or *Rhiniodon*. Nevertheless, this species has a specialized, presumably efficient mechanism for capturing small oceanic animals in its oversized jaws which are enlarged to increase the diameter of its "net" and thickened to provide adequate support from its rubbery hyaline cartilage. The greatly distensible mouth and pharynx, closely packed gill-raker papillae, and large tongue probably help to expel water from the pharynx when it closes its mouth. *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 concentrate its prey before swallowing it.

Inspection of the mouth of megamouth 24 hr after capture revealed a bright silvery lining punctuated by small circular porelike structures. At the time it was speculated that these might be bioluminescent organs, but we have no evidence of this. Histological sections of mouthlining were made but were problematical because of the deteriorated state of the tissue.

That *Megachasma* may not be a more active filter-feeder such as *Cetorhinus* or *Rhiniodon* may be related to its tropical deepwater oceanic habitat, which has a relative paucity of nutrients and prey in comparison to the cool coastal surface waters favored by *Cetorhinus* and the tropical coastal waters preferred by *Rhiniodon*. Various mesopelagic teleosts have reduced skeletal and other tissues as adaptations to a nutrient-poor environment, and *Megachasma* may be similarly limited to a reduced level of tissue development and hence a low activity level for a filter-feeding shark, far less than is possible in the habitats frequented by *Cetorhinus* and *Rhiniodon.*

Two distinctive scars, one on the throat, another behind the right pectoral fin, suggest that megamouth may be the only known selachian victim of *Isistius brasiliensis,* the "cookie-cutter" shark, that is believed responsible for similar marks found on tuna, porpoise, and billfish caught in Hawaiian waters (Jones 1971). The soft skin and midwater habitat of megamouth may make it vulnerable to *Isistius* attacks.

Megachasma pelagios, itself the representative of a new family of sharks, is the host of a new family of tapeworms Mixodigmatidae (order Trypanorhynchida), described by Dailey and Vogelbein (1982) for the new genus and species *Mixodigma leptaleum.* These parasitic tapeworms from the valvular intestine presented taxonomic problems over placement in existing trypanorhynch families comparable to the difficulties encountered in attempting to place *Megachasma pelagios* in an existing lamnoid shark family.

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