RELATIONSHIPS OF THE MEGAMOUTH
SHARK, *MEGACHASMA*.—The discovery in
1976 of an unusual species of living shark off
the coast of Oahu, Hawaii, sparked off a number
of popular and semi-technical articles speculat-
ing upon the relationships, mode of life and
feeding habits of the new shark (popularly
dubbed "Megamouth"). A formal description
naming the new genus and species (*Megachasma
pelagios*) has only recently appeared, however
(Taylor et al., 1983). *Megachasma* was included
within the lamniforms sensu Compagno (1973,
1977), in its own family Megachasmidae, on the
basis of an impressive list of phenetic differences
from all other lamniforms (Odontaspidae, Mit-
sukurinidae, Pseudocarchariidae, Alopiidae,
Cetorhinidae, Lamnidae; Taylor et al., 1983).
It was speculated that *Megachasma* is the prim-
itive sister-group of all other living lamniforms,
on the basis of two supposedly primitive char-
acters; the absence of morphologically differ-
entiated anterior, lateral and posterior teeth
characteristic of other lamniforms; and the
presence of a putative "orbital" process on the
palatoquadrate.

The teeth of *Megachasma* are relatively un-
differentiated around the mouth (Taylor et al.,
1983). They are also small and numerous, with
between 50 and 70 tooth rows in each jaw quad-
rant. Taylor et al. (1983) suggested that the
teeth and dental array of *Megachasma* is primi-
tive for lamniforms. Such a hypothesis is refuted
by outgroup comparison with other galeo-
morphs, however, and a comparable pattern oc-
curs in only two other specialized galeomorph
taxa (*Cetorhinus* and the orectoloboid *Rhinio-
don*). Morphologically, *Megachasma* teeth closely
resemble those of some lamnids (e.g., *Lamna,
Isurus*) and odontaspids, pseudocarchariids and
Mitsukurina, apart from an overall reduction in
lateral cusps and the length of the labial root
lobes. *Megachasma* dental morphology (Taylor
et al., 1983:fig. 8) may be characterized as ad-
vanced holaulacorhize (sensu Casier, 1947), in
which the median sulcus ("sillon") of the root
is reduced, conferring upon the tooth a sec-
ondary anaulacorhize condition, as in other
lamniforms. It is possible to interpret *Mega-
chasma* teeth as derived from this lamniform
condition just as readily as to postulate their
primitiveness. In view of this ambiguity, the
dental morphology of *Megachasma* does not pro-
vide satisfactory evidence of relationship be-
yond establishing lamniform affinity.

The dorsal margin of the palatoquadrate in
Megachasma bears a low, rounded articular pro-
cess (the "orbital process" of Taylor et al., 1983:
figs. 13, 14; see Fig. 1 here), resting in a shallow
depression in the floor of the braincase on a
level with the center of the orbit. Taylor et al.
suggest that the presence of an "orbital pro-
cess" in *Megachasma* is primitive. I take issue
both with their identification and their phylo-
genetic assumptions concerning this articula-
tion.

There is some confusion in the literature as
to what constitutes an orbital process in sharks.
According to Regan (1906), its presence or ab-
sence characterizes the pleurotremates (sharks)
and hypotremates (rays, skates) respectively.
That view is oversimplified, however, and dis-
tinctly different selachian articular patterns may
be recognized in the ethmoidal and orbital re-
gions (Edgeworth, 1935; Holmgren, 1940, 1941;
Maisey, 1980). In galeomorphs and *Heterodontus*
the palatoquadrate may have a ligamentous an-
terior suspension (e.g., carcharinids) or a strong
articulation (e.g., orectoloboids *Heterodontus*),
located in the ethmoid region near the front of
the embryonic trabecular plate. A different ar-
rangement occurs in hexanchoids, *Chlamydose-
lachus*, squaloids, *Squatina* and pristiophoroids.
Here, the palatoquadrate is attached to the in-
terorbital wall, either with or without (*Squatina*)
an articular surface (Edgeworth, 1935). This
articulation is invariably located posterior to the
optic nerve and (if the process is long enough,
as in *Squatina* and *Squalus*) the trochlear nerve,
and is anterior to the efferent pseudobranchial
artery (Maisey, 1980). In squaloids this articu-
lation lies close to the trabecular/polar carti-
lage boundary, but in *Chlamydoselachus* it is much
farther forward, in the anterior part of the orbit
(Allis, 1923:pl. 4, fig. 4). This arrangement is
properly regarded as an orbital articulation, and
the palatoquadrate is said to bear an orbital
process (e.g., Edgeworth, 1935; Maisey, 1980).
Unfortunately this terminology has also been
rather loosely applied to what is really an eth-
moidal articulation. Such an articulation be-
tween the palatoquadrate and internasal sep-
tum of the braincase is apparently primitive,
and occurs in various fossil sharks (Maisey, 1982,
1983; Schaeffer, 1981). Conversely the orbital
articulation has a restricted distribution which,
when taken in conjunction with other anatom-
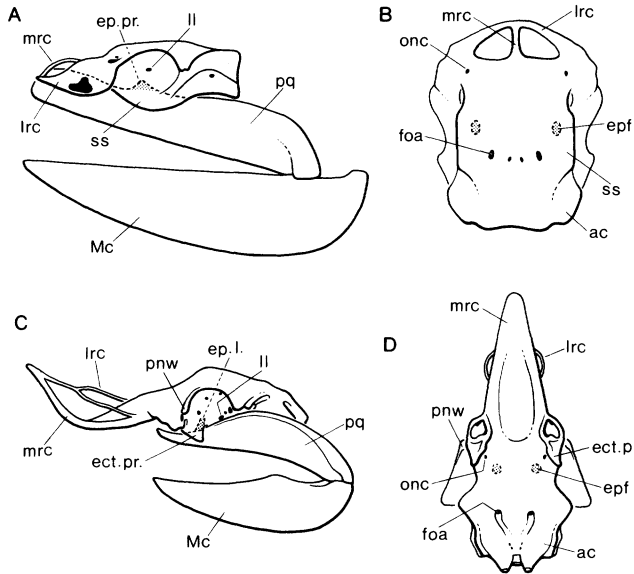ical characters, suggests a derived condition

Fig. 1. Braincase of A) *Megachasma* and B) *Cetorhinus* in ventral view: braincase and jaws of C) *Megachasma* and D) *Cetorhinus* in lateral view. Abbreviations: ac = auditory capsule; ect. pr. = ectethmoid process; epf = ethmopalatine fossa (site of palatoquadrate attachment); epl = ethmopalatine ligament (*Cetorhinus*); eppr = ethmopalatine process (*Megachasma*); foa = fenestra for orbital (external carotid, "stapedial") artery; lrc = lateral rostral cartilage; mc = Meckel's cartilage; mrc = median rostral cartilage; onc = orbitonasal ("preorbital") canal ("ectethmoid foramen"); pq = palatoquadrate; ss = suborbital shelf. *Cetorhinus* after Senna (1925) and AMNH dissection; *Megachasma* after Taylor et al. (1983); not to scale, both much reduced.

uniting these "orbitostylic" sharks (Maisey, 1980).

Perusal of Taylor et al.'s (1983) figs. 13 and 14 reveals an essentially different, basicranial articulation in *Megachasma*. Instead of lying on the interorbital wall of the orbit, the articular process of the palatoquadrate articulates with the basicranium, and is thus far removed from the optic nerve (and presumably from the trochlear nerve and efferent pseudobranchial artery). This articulation of *Megachasma* is therefore extremely unusua. (Fig. 1A). It may conceivably represent a modification of a more anterior generalized ethmoidal articulation, or it may represent a novel, secondarily-acquired articulation. In either case, it cannot be regarded as a primitive arrangement.

The suspensorium of *Cetorhinus*, as described by Senna (1925) and verified by dissection of the head of a young individual in the American Museum collections, resembles that of *Megachasma* in some significant respects. The palatoquadrate of *Cetorhinus* lies in part below the suborbital shelf, so that the dorsal margin of the palatoquadrate fails to occupy the floor of

the orbit (Fig. 1C). The suborbital shelf of *Cetorhinus* is well-developed (Senna, 1925:pl. ix, fig. 2, "p. i."), and is expanded posteriorly to form a broad, triangular platform which merges with the floor of the auditory capsule about halfway along its length. While the suborbital shelf of *Megachasma* is less expanded posteriorly, it extends back as far as in *Cetorhinus* (Taylor et al., 1983:fig. 13; fig. 1 here). Having the suborbital shelf (formed by fusion of the subocular cartilage to the lateral margin of the trabecular plate; de Beer, 1937; Holmgren, 1940) interposed between the palatoquadrate and interorbital wall in *Megachasma* is a remarkable arrangement that is approached (albeit to a much lesser degree) by *Cetorhinus*. More importantly, however, on the ventral surface of the braincase in *Cetorhinus* is a pair of small depressions, located mesial to the ectethmoid process of the postnasal wall, at the junction of the suborbital shelf and interorbital wall as in *Megachasma* (Senna, 1925:pl. ix, fig. 2, "le"). Connective tissue (The "ethmopalatine ligament," according to Senna, 1925:107) arises in this basicranial depression and is attached to the palatine part
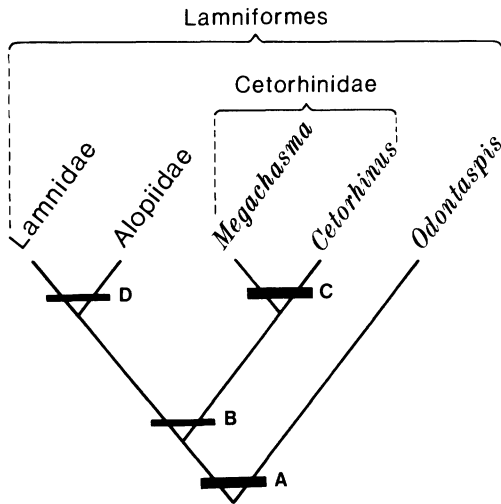
Fig. 2.   Cladogram of phylogenetic hypothesis advanced in the text. *Mitsikurina* and *Pseudocarcharias* omitted for clarity (all are represented here by *Odontaspis*). Characters defending nodes as follows: A, lamniform characters given by Compagno, 1973, 1977; B, plesodic pectoral radials; C, modified ethmopalatine articulation; suborbital shelf interposed between palatoquadrate and orbit; median rostral cartilage in part dorsal to lateral rostral bars; simplified tooth cusp and root morphology, loss of dental differentiation, increase in number of tooth rows; enlarged gill rakers extending to margins of gill openings, covered by modified oropharyngeal scales; D, plesodic dorsal radials.

of the palatoquadrate some distance from the symphysis (Senna, 1925:pl. x, fig. 5, "le"). There is no articular process on the palatoquadrate corresponding to the "orbital process" of *Megachasma*. Nonetheless, the ligamentous "ethmopalatine" attachment in *Cetorhinus* corresponds closely to the basicranial articulation in *Megachasma*, and they are probably homologous. Variation in this basicranial attachment between the two genera may be an expression of somewhat different mandibular kinesis related to their feeding mechanisms (discussed by Taylor et al., 1983:108–110).

From a comparison of their mandibular suspension, *Cetorhinus* and *Megachasma* seem to form a monophyletic group of specialized filter-feeding lamniforms. The erection of a new monotypic family for *Megachasma* may therefore be unnecessary. Notwithstanding the many differences between *Cetorhinus* and *Megachasma*, both genera may be included in the Cetorhinidae on the basis of similarities in their jaw sus-

pension and dental array. The relationships of these genera to other lamniforms remain obscure. The presence of plesodic pectoral radials in *Megachasma* and *Cetorhinus* suggests a closer relationship with mackerel sharks (Lamnidae) and threshers (Alopiidae) than with Odontaspidae, Pseudocarchariidae and Mitsukurinidae. The Cetorhinidae (as defined here) may be the sister-group of Lamnidae plus Alopiidae, which share a plesodic first dorsal fin and some cranial similarities (Fig. 2). In this hypothesis, the characteristic lamniform dental pattern, with modified upper intermediate "eye-teeth" and lobate roots has become secondarily suppressed (Taylor et al., 1983:96), while retaining the secondary anaulacorhize fenestration pattern in the roots.

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