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## *ECHINOCHIMAERA MELTONI*, NEW GENUS AND SPECIES (CHIMAERIFORMES), FROM THE MISSISSIPPIAN OF MONTANA

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### ABSTRACT

A new genus and species of chimaeriform, *Echinochimaera meltoni*, is described from the Late Mississippian Bear Gulch limestone of Montana. *E. meltoni* differs from modern chimaeroids in having a complete placoid squamation, an ornamented first dorsal fin spine with simpler synarcuum, a stenobasal second dorsal fin, a subpelvic tenaculum, and prominent dermal cranial armament.

*E. meltoni* and *Marracanthus rectus* are placed in the new suborder Echinochimaeroidei, which is considered a sister group to the Chimaeroidei. The Squalorajoidei and the Myriacanthoidei, Mesozoic Bradyodonti, share few derived characters in common with the Chimaeriformes and are removed from the order. The ptyctodont arthrodires share no phylogenetically significant characters with the Chimaeriformes.

### INTRODUCTION

The chondrichthyan fauna of the Bear Gulch Limestone (Namurian) of Fergus County, Montana, (Lund, 1974; 1977a; 1977b; Lund and Zangerl, 1974) includes several representatives of one species of fish related to the Chimaeroidei, an operculate, holostylic suborder within the order Chimaeriformes. The Chimaeriformes, hitherto known only by Liassic and younger fossils and three families of living fish, have recently been divided into two additional suborders, the Squalorajoidei and Myriacanthoidei, by Patterson (1965). The Chimaeriformes have been grouped with several orders of Paleozoic Chondrichthyes into the

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superorder Holocephali, subclass Bradyodonti (Arambourg and Bertin, 1958; Lund, 1977a).

The members of the Chimaeroidei are united by a number of shared derived characters, among which are the two paired upper and one paired lower cutting and tritoral jaw plates, an elevated and compressed ethmoid region containing an ethmoid canal, extremely expanded orbits lying over the brain, a mobile first dorsal spine and fin pivoted upon a synarcuum composed of fused anterior vertebrae and neural arches and spines, multiple perichordal vertebral rings, tall iliac processes on separate pelvic girdles, and prepelvic tenaculae and a frontal clasper in males (Dean, 1906; Patterson, 1965).

The Jurassic genus *Squaloraja*, the only member of its suborder, differs from the Chimaeroidei in several characters of phyletic importance (see discussion) but most critically in lacking their unique ethmoid specializations. Additionally, independent skeletally supported prepelvic tenaculae seem to be lacking (Patterson, 1965).

The Jurassic Myriacanthoidei resemble chimaeroids in the general configuration of the skull and the presence of a large frontal clasper and synarcuum-based first dorsal fin. The dentition of the myriacanthoids contains three paired upper plates as well as one paired and one median symphyseal lower plate (Patterson, 1965). The myriacanthoid dentition is plesiomorphous in its retention of three paired upper plates in contrast to the chimaeroid condition, probably plesiomorphous, in the retention of a mandibular symphyseal element as well (Dean 1906, Lund, 1977a). An ethmoid canal is apparently absent. The myriacanthoid condition of dermal plates on the neurocranium and mandibular spines, however (Patterson, 1965), is apparently derived relative to the chimaeroid condition.

The Squalorajoidei and Myriacanthoidei contain both plesiomorphous and autapomorphic characters relative to the Chimaeroidei (Lund, 1977a) and have been included within the Chimaeriformes on the assumption (questioned by Dean, 1906) that the Chimaeroidei originated in the early Mesozoic (Patterson, 1965). As it will be demonstrated in this article that the chimaeroids possessed their uniquely derived characters by the Namurian, neither squalorajoids nor myriacanthoids can have more than sister group relationship to them and should not be included within the Chimaeriformes.

Speculations on the relationships of the Chimaeriformes have continued for over a century (see Dean, 1906; Moy-Thomas, 1939; de Beer and Moy-Thomas, 1935; Patterson, 1965; Orvig, 1962). Most interest focuses on the Bradyodonti, poorly known, principally marine, Paleozoic chondrichthyans presumably with holostylic jaw suspensions and few crushing toothplates of tubular dentine (Obruchev, 1967). Very few whole dentitions however, and even fewer holomorphs (Patterson, 1965; Lund, 1977a), are known. Bradyodont dentitions contain small numbers

of plates ranging from those corresponding to the chimaeroid combination through myriacathoid-like combinations to apparently more primitive conditions of three paired upper and three paired lower plates. Further evidence links fused and unfused anterior tooth families of some bradyodonts to tooth families of the "pleuroplax" and "helodus" types, as seen in the freshwater lower Pennsylvanian *Helodus simplex* (Newberry and Worthen, 1866; Patterson, 1968). It is possible to demonstrate a morphologic series of dentitions among *Helodus* and the Bradyodonti by which chimaeroid and myriacanthoid dentitions may be derived on the basis of differential reduction (Lund, 1977a).

Several authors have also suggested the ptyctodont arthrodires as possible relatives of the chimaeroids, initially on the basis of the common possession of tritons of tubular dentine (e.g. Eastman, 1907), and, subsequent to the discovery of well preserved holomorphs of *Ctenurella*, on the basis of similar habitus (Orvig, 1962; Westoll, 1962). Dean (1906) points out, however, that ptyctodonts possess only one upper and one lower pair of jaw plates, too few to be considered ancestral to any holocephalian; Radinsky (1961) illustrates the dangers of using common possession of tubular dentine as a phyletic character, and Patterson (1965) indicates basic histologic differences between ptyctodont tritons on the one hand and the morphologically similar holocephalian and bradyodont plates on the other hand. Other apparent morphologic and histologic dissimilarities between the two groups (discussed below) reinforce the argument that the ptyctodonts are simply a highly specialized group of arthrodires (Denison, 1975), none of which have any synapomorphous relationship to the holocephalians (Zangerl and Case, 1973).

The fish described here is the first known Paleozoic member of the Chimaeriformes. The age of this taxon, Namurian A, and its relationship to younger members of the order, introduces a rich store of new factual information into the debate on chimaeriform relationships.

## SYSTEMATICS

### Order Chimaeriformes

**DIAGNOSIS:** Holostylic chondrichthyans with two pairs of upper dental and one pair of lower dental plates, the ethmoid region high, compressed, and with a median ethmoid canal, orbital region expanded dorsally and posteriorly, a mobile spinous first dorsal fin articulated upon a synarcuum, an aspinous second dorsal fin, diphyccercal caudal fin, and monobasal pectoral fin. The pelvic girdle has a high iliac process and there are well developed pelvic fins in members of both sexes. Males have prepelvic tenaculae articulated with the pelvic girdle as well as pelvic mixopterygia. Squamation may be complete and placoid or limited. Multiple vertebral calcifications per body segment are present.

### Suborder Chimaeroidei

**AMENDED DIAGNOSIS:** Chimaeriformes with an unornamented first dorsal fin spine, a long second dorsal fin supported by separate basidorsals and radials, squamation

reduced to few specialized scales or absent, lateral line canals enclosed by ring scales, prepelvic tenaculae of males articulated with the anterior margin of the pelvic girdle, and a frontal clasper present in males. Dermal cranial armor is absent.

INCLUDED FAMILIES: Chimaeridae, Rhinochimaeridae, Callorhynchidae.

### Suborder **Echinochimaeroidei**, new

DIAGNOSIS: Chimaeriformes with a tuberculated first dorsal fin spine, a stenobasal second dorsal fin supported on a single basal plate, squamation complete and placoid, lateral line canals enclosed by very small denticles, prepelvic tenaculae of males articulated with the posterior margin of the pelvic girdle, a frontal clasper absent in males. Dermal cranial armor of enlarged or fused denticles is present.

INCLUDED FAMILY: Echinochimaeridae, new family.

### Family **Echinochimaeridae**, new

DIAGNOSIS: The family Echinochimaeridae, with the new genus *Echinochimaera* as its type, is distinguished from other chimaeroids in having several paired and a median enlarged compound denticle on the dorsal surface of the head. The first dorsal fin spine bears denticles along its anterior edge, and is laterally tuberculated. Spine and denticles are enlarged distally in males. First and second dorsal fins have small basal plates and long, radiating supporting elements.

### Genus **Echinochimaera**, new

DIAGNOSIS: Echinochimaeroids with four large paired supraorbital denticles in males and one large median postorbital denticle in both sexes. The dorsal fin spine is straight or slightly curved forward distally in mature males, compressed, with a grooved posterior margin for the proximal 2/3 of its length, ornamented laterally by eight to nine small vertically aligned rows of tubercles, and anterodistally by a cluster of denticles that are considerably enlarged in males. Both dorsal fins are short based. A short anal fin is present immediately anterior to the caudal fin.

The rostrum is short and rounded, the orbital region is expanded to almost completely cover the otic region of the braincase. The body is rounded and clearly differentiated from the narrow caudal region. The prepelvic tenaculum is long, thin, well calcified in three segments and capped by a single large hook. The pelvic mixopterygium of each side is long, thin and straight. Squamation of the body and fins is placoid, with each denticle having a stellate base. There is a row of enlarged trifid denticles on each side of the dorsal midline between the second dorsal fin and the origin of the epichordal lobe of the tail.

DERIVATION OF NAME: *Echinochimaera*, a prickly monster.

TYPE SPECIES: *Echinochimaera meltoni*.

### **Echinochimaera meltoni**, new species.

Figures 1-16

TYPE SPECIMEN: MV<sup>1</sup> 5371

REFERRED SPECIMENS: MV 5372, 5374, 5375, 5383, 5384. CM<sup>1</sup> 23656, 25588, 27336, 30626, 30629, 30630, 30631.

HORIZON AND LOCALITY: Mississippian, Namurian A, Bear Gulch Limestone of Fergus County, Montana.

DIAGNOSIS: The only known species of the genus *Echinochimaera meltoni* is a small echinochimaerid, the largest specimen measuring 150 mm, total length. There are nine rays in the first dorsal fin, seven in the second dorsal fin and nine rays in the pelvic fin.

<sup>1</sup>Abbreviations: MV, University of Montana Vertebrate catalog; CM, Carnegie Museum of Natural History.



Fig. 1. *Echinochimaera meltoni*, MV 5371, type specimen, male. Scale is in mm.



Fig. 2. *Echinochimaera meltoni*, CM 25588, female. Scale is in mm.

A maximum of 19 rays can be seen in the epichordal lobe of the caudal fin and 12 in the hypochordal lobe. One to three rays are present in the anal fin.

DERIVATION OF NAME: Named in honor of William G. Melton, Jr., founder and leader of the Bear Gulch project.

#### DESCRIPTION

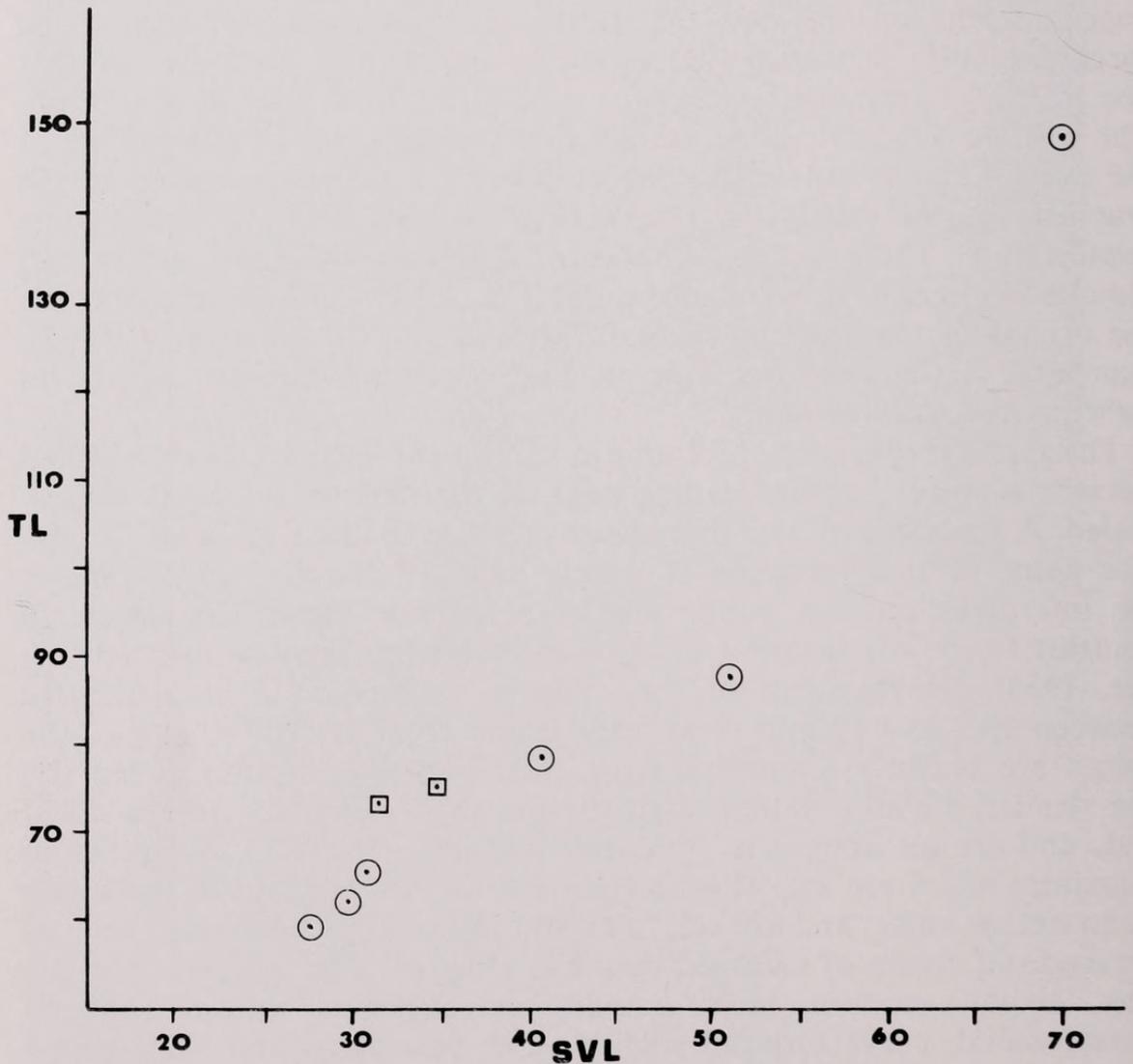
PRESERVATION AND GROWTH: The thirteen presently known specimens have all been flattened during preservation, and show little three dimensionality. Neither neural nor haemal spines are calcified. A complete squamation that covers the body and outlines the fin radials is present in all specimens, (Figs. 1, 2). Dark pigmentation is present only in the orbits, indicating the size and position of the choroid coat of the eye. A ring of denticles in the orbital region indicates the maximum size limit of the cornea.

The relationship between total length and snout-vent length (Fig. 3) appears to be constant over the size range of available and measurable specimens. One specimen that deviates significantly from the straight line in Fig. 3 probably lost several millimeters from the tip of the tail. The relative difficulty of accurately establishing total length has led to the use of snout-vent length for comparative purposes. Spine length graphed against snout-vent length (Fig. 4) also shows a straight-line relationship. There is no significant difference between males and females in either of these relationships. The ratio of the distance between the origins of the first and second dorsal fins to the snout-vent length, expressed as decimal fractions in Fig. 4, shows distinct differences between males and females.

The smallest specimen, 13.2 mm in snout-vent length, lacks a calcified dorsal fin spine, but the leading edge of the first dorsal fin is heavily scaled. A specimen of 19.7 mm snout-vent length has a spine of 7.7 mm. The spine of this specimen is poorly calcified basally, and supports the interpretation that young are born without dorsal fin spines, in contrast to the condition of modern chimaeroids (Bigelow and Schroeder, 1953). Development of the spine is initiated in *Echinochimaera* between 13.2 and 19 mm snout-vent length (Fig. 4). The shapes of the spines are sexually dimorphic from their initiation. Spines of females are slender, slightly shorter than the fin, taper gradually to the distal end, and are set anteriorly with very fine denticles (Fig. 5). Spines of immature males are also shorter than the fin, but taper little, terminate in an obtuse angle, and are set, in all but the smallest specimen, with an anterodistal clump of enlarged denticles (Fig. 6). The spines of the largest, sexually mature, males extend past the distal end of the first dorsal radial, curve forward slightly, and bear large and well spaced denticles distally (Figs. 7, 8).

Changes in spines occur between 30 mm and 40 mm snout-vent length in males. These changes are accompanied by several other mor-

phologic changes, all indicating the onset of sexual maturity. Specimens below 27.5 mm snout-vent length show no calcifications of the fin girdles or axial skeleton. The 27.5 mm specimen and all longer ones show calcification of pectoral and pelvic girdles. Specimens of 32.5 mm and longer show calcified vertebral elements and synarcuums, as does a male of uncertain body length, with a spine length of 15.3 mm (Fig. 7). Males of 40.2 mm snout-vent length and longer are the only specimens that have calcified mixopterygia and prepelvic claspers. Only the two largest males and largest female show advanced calcification of the basal plates and radials of the dorsal fins as well as of the preorbital region of the neurocranium.



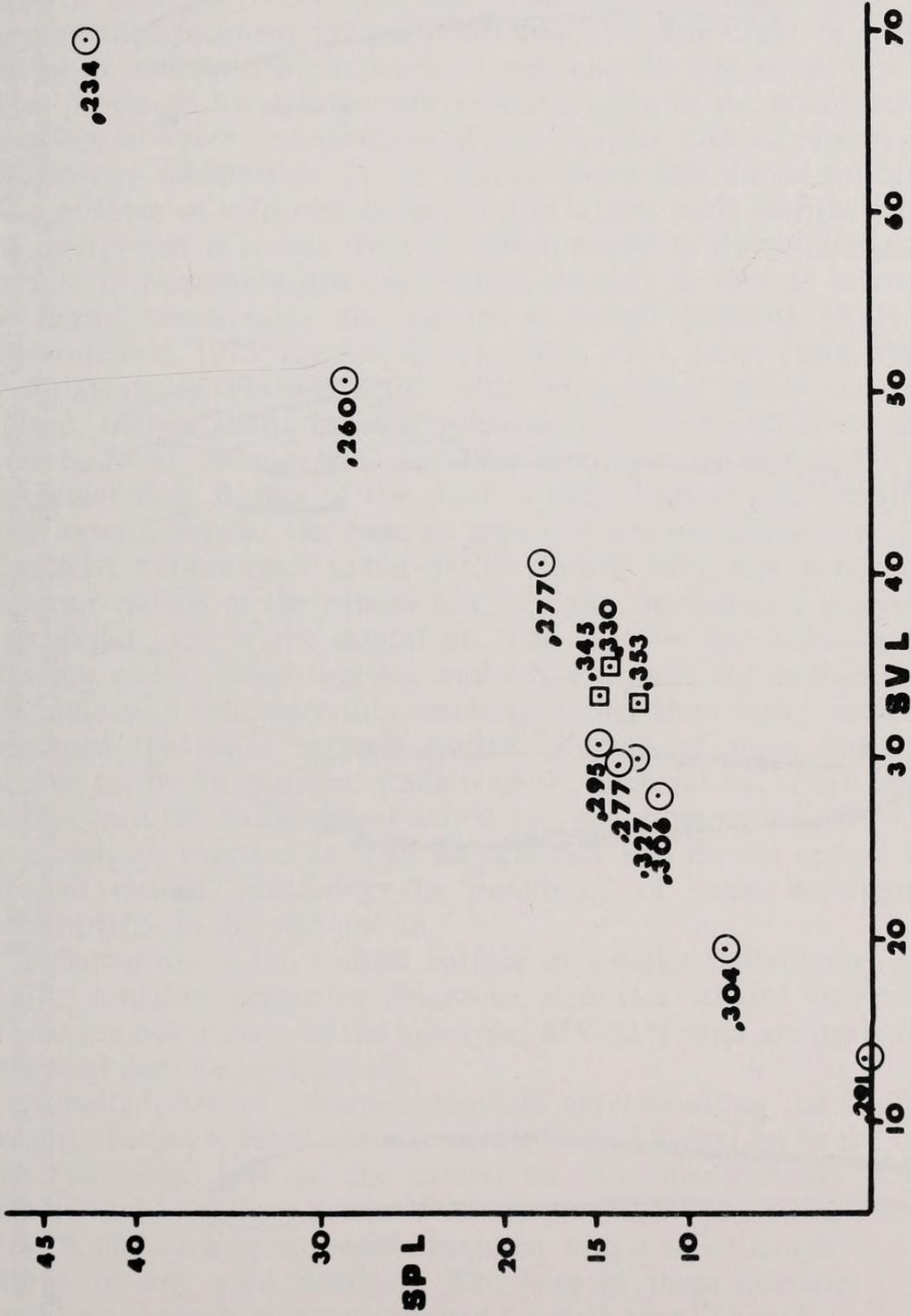
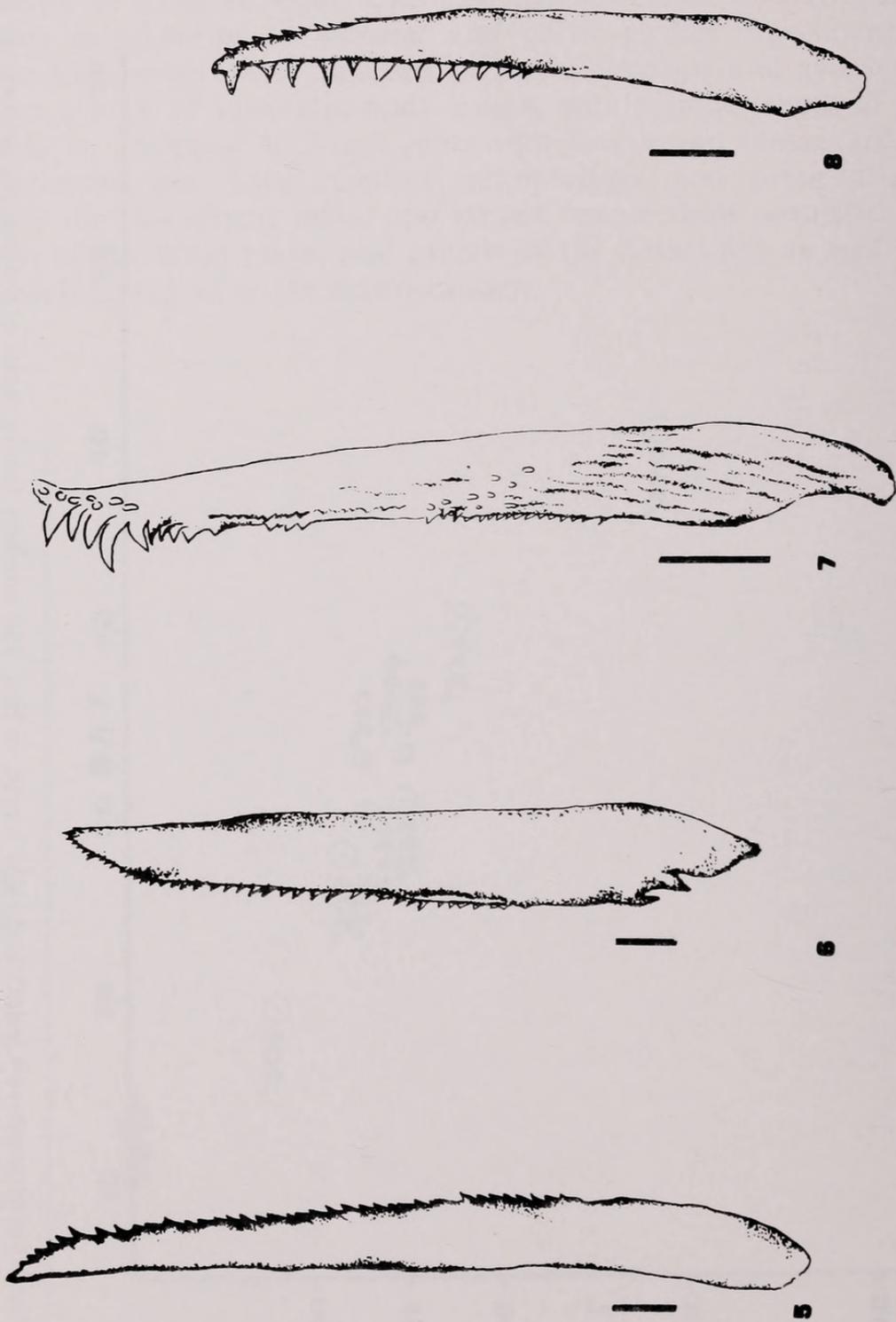


Fig. 4. Relationship between snout-vent length and spine length, in mm. The numbers are the ratios of the distance between the first and second dorsal fins to snout-vent length. Circles are males, squares are females.



Figs. 5-8. *Echinochimaera meltroni*, dorsal fin spines. Fig. 5, CM 25588, female, right side. Fig. 6, CM 23656, immature male, left side. Fig. 7, MV 5372, intermediate male, left side. Fig. 8, MV 5371, type specimen, left side. Scale is 1 mm for Figs. 5 and 6; 2 mm for Fig. 7, 3 mm for Fig. 8.

The growth curves and developmental information for *Echinochimaera* lead to some remarkably clear conclusions. These small chimaeroids are born spineless and undergo regular but sexually dimorphic growth patterns. There are no proveable sexually mature females among the specimens presently available, but the onset of sexual maturity in males occurs between 31 mm and 40 mm snout-vent length. This process is heralded by differential growth of the distal part of the first dorsal spine, calcification of the claspers and mixopterygia, and ultimately, calcification of the neurocranium and dorsal fin cartilages. The absence of a frontal clasper in the largest male can therefore only be interpreted as a real absence. Development of differentiated mixopterygia in elasmobranchs and frontal claspers as well as mixopterygia in recent chimaeroids also occurs at sexual maturity (Raikow and Swierczewski, 1975; Bigelow & Schroeder, 1948, 1953; Dean, 1906).

**SQUAMATION:** Placoid scales with thin stellate bases and tapering, ridged, hollow shafts inclined posteriorly at their tips cover the head and body of *Echinochimaera*. They are sparsely distributed on the opercular flap. Ridges of the shaft of each denticle pass onto the base and extend beyond the base to give the stellate appearance (Fig. 9). Denticles outline each radial of the dorsal, anal, and pelvic fins, the anterior radials of the caudal fins, and the anterodorsal margin of the epichordal lobe of the caudal fin. The bases of the denticles of these fins are closely fitted together and curve around the radials (Fig. 10), an indication that only thin webbing, rather than bulky ceratotrichia, occupied the space between radials. Radials of these fins extended almost to the fin margins. Radials of the pectoral fin, which is inserted midway up the flank, are obscured by flank squamation. They are not as closely set together as other fin denticles, and do not appear to curve around radials, indicating the possibility of some development of ceratotrichia in the pectoral fin.

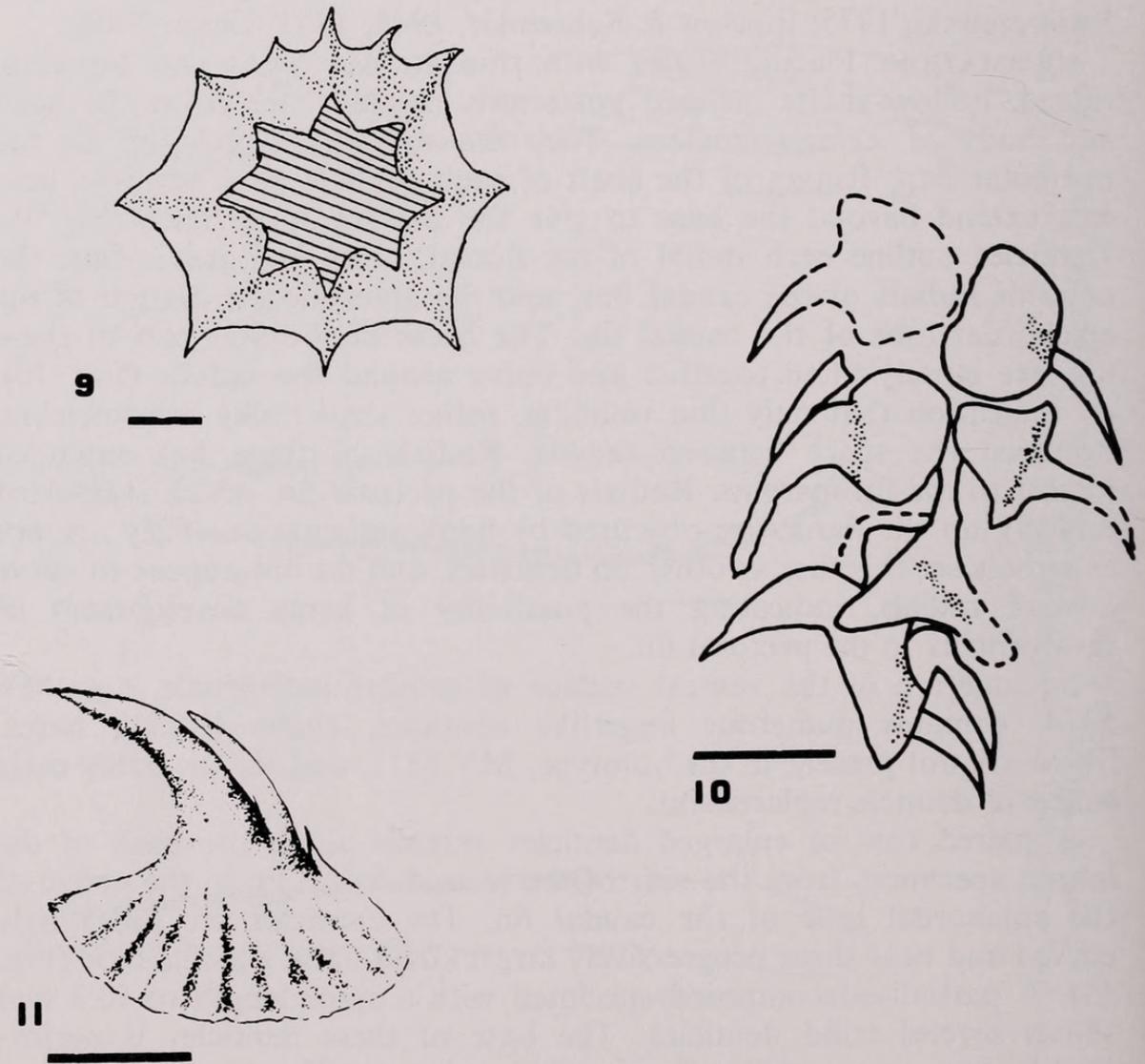
Squamation of the ventral surface of smaller individuals, e.g., MV 5374, contains numerous fingerlike denticles, shafts lacking bases. These are not present in the holotype, MV 5371, and are probably early stages of denticle replacement.

A paired row of enlarged denticles extends along the back of the largest specimen, from the rear of the second dorsal fin to the origin of the epichordal lobe of the caudal fin. The denticles are posteriorly curved and bear three progressively larger cusps upon a single base (Fig. 11). A partially decomposed specimen with a spine length of 15.3 mm shows several trifold denticles. The base of these denticles is perforated by a separate nutrient foramen for each cusp. There is no indication of addition of successive cusps to the denticles. Nine pairs of denticles can be counted in CM 30630.

Very fine, closely set denticles mark the lateral line canals on the

body and tail. The denticles do not form rings enclosing the canals as do those of Mesozoic and Recent chimaeroids.

All specimens except the smallest, CM 30626, bear some indications of a large, complex, strongly curved median postorbital spine. This spine has a broad, thin base, thin walls, a large, open pulp cavity, and many secondary denticles. Prominent thin-walled, narrower spines are found around the base (Fig. 13). The shape and curvature of the spine itself is somewhat variable. The spine projects posteriorly to parallel the long axis. One spine, on CM 23656, apparently arches downward, toward the dorsal midline. Subsidiary basal spines are smooth-surfaced and vary in number and length, but several approach half the length of the major spine in CM 23656 and CM 27336.



Figs. 9-11. *Echinochimaera meltoni*, dermal denticles. Fig. 9, from the posterior flank region. Scale is .1 mm. Fig. 10, CM 23656B, from a lower ray of the first dorsal fin. Scale is .5 mm. Fig. 11, CM 30630, enlarged denticle from the dorsal midline of the caudal region. Scale is 1 mm.

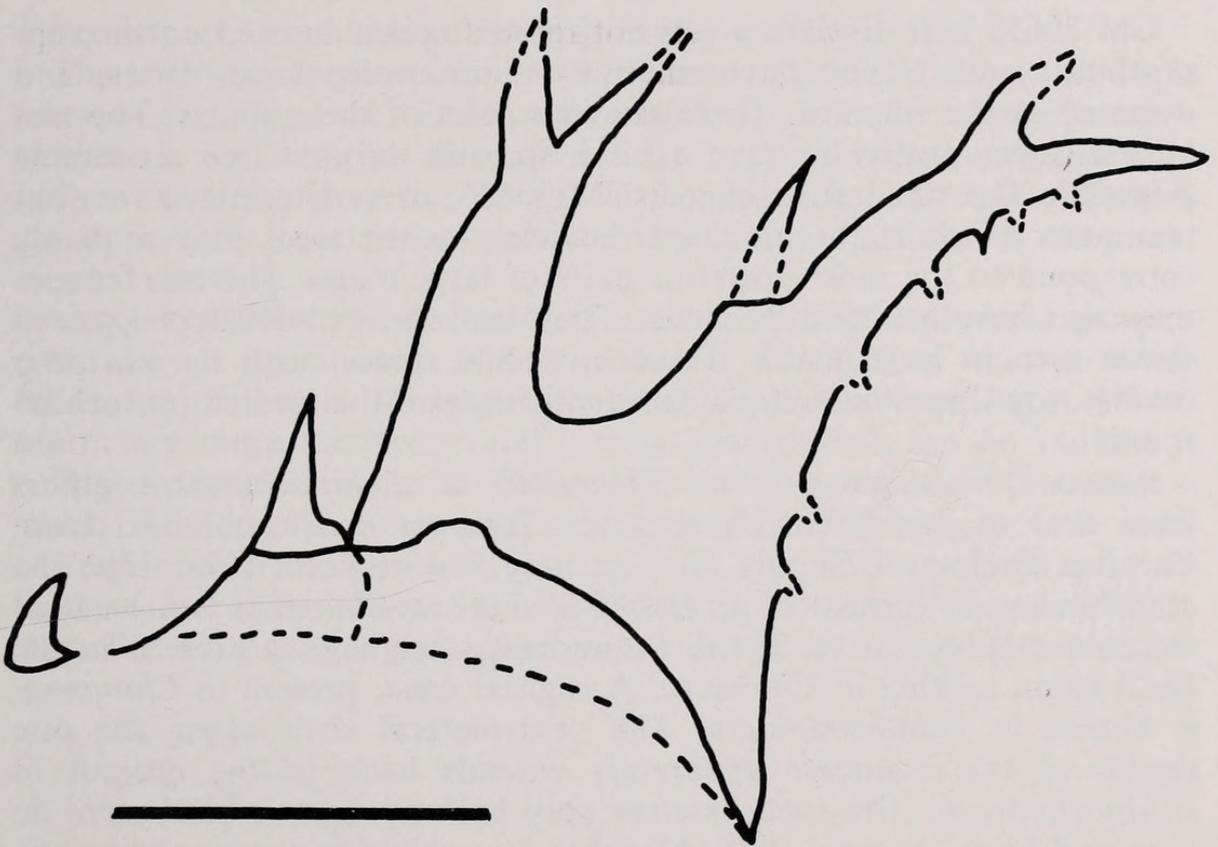


Fig. 12. *Echinochimaera meltoni*, CM 30630A. Supraorbital spines of the right side in mesial view. Scale is 5 mm.

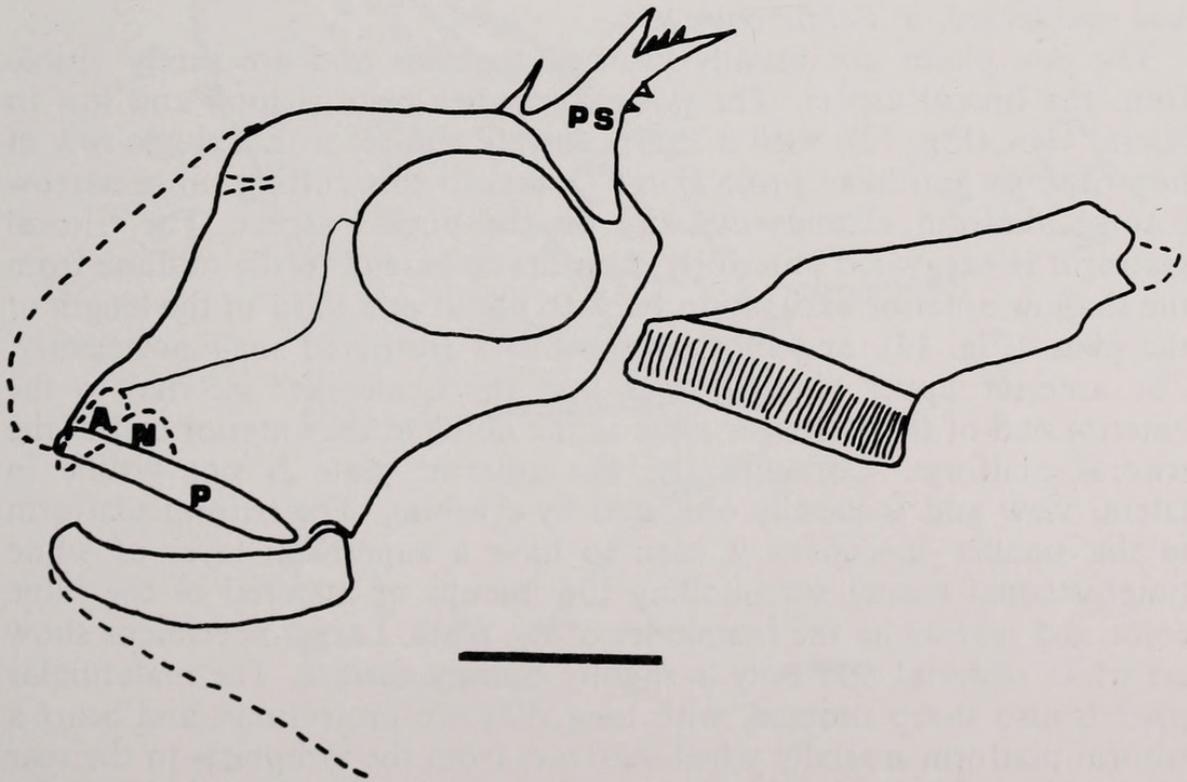


Fig. 13. *Echinochimaera meltoni*, MV 5374, head. A, anterior plate; N, nasal capsule; P, posterior plate; PS, postorbital spine. Scale is 5 mm.

CM 30630 best displays a series of paired spines located on the supraorbital crests. They have relatively thick walls, small bases, and decrease in size forward. There are four pairs of these spines. The two largest (most posterior) have a bifid tip, and the first two are simple (Fig. 12). The smallest specimen, CM 30626, of undetermined sex, has two pairs of short, broad-based denticles on the head that probably correspond to the most posterior pairs of large males. The two females may also have enlarged denticles. They lack the well-developed paired spines seen in large males. These immobile spines, with narrow pulp cavities, are thus modified placoid denticles, as is the median postorbital spine.

NEUROCRANIUM AND JAWS: The skull of *Echinochimaera* differs from that of the recent chimaeroid *Chimaera collei* (obtained from Carolina Biological Supply Co.) in very few respects (Fig. 13). The antorbital wall, formed of a tendinous sheet in *Chimaera* is present as calcified cartilage in the fossil. Supraorbital cartilage is present in the fossil form, lacking in *Chimaera*. A sagittal crest, present in *Chimaera*, is absent in *Echinochimaera*. The ventrolateral shelf along the otic region of the braincase apparently extends back to the occiput in *Echinochimaera*. The shelf extends only halfway back in *Chimaera* de Beer and Moy-Thomas, 1935. All other discernible features and proportions are extraordinarily similar. In view of the morphologic similarity, it is reasonable to propose that rostral and labial cartilages were present, and uncalcified, in *Echinochimaera*.

The jaw plates are usually crushed together and are rarely visible from the buccal aspect. The posterior upper plate is long and low in lateral view (Fig. 13), with a sharp, serrate rim set with a single row of fine villiform toothlike projections. Dorsal to this cutting rim a narrow tritoral platform extends mesially on the buccal aspect. The tritoral platform is excavated anteriorly, appears to extend to the midline from the shallow anterior excavation back to about one third of the length of the plate (Fig. 14), and then narrows to a restricted shelf posteriorly. The anterior upper plate is thick and short, and lies internal to the anterior end of the posterior plate in the notch at the anterior end of the tritoral platform. Consequently, the anterior plate is not visible in lateral view and is usually obscured by crushing. The tritoral platform in the smaller specimens is seen to have a superficial layer of white (interosteonal tissue) surrounding low bumps of material of the same color and texture as the remainder of the plate. Larger specimens show no white material and only a slightly bumpy surface. The mandibular plate is also sharp rimmed, with long villiform projections, and bears a tritoral platform mesially which narrows from the symphysis to the rear of the plate (Figs. 14, 15). The mandibular plates are not fused at the symphysis, but the intermandibular region is very heavily calcified.

The tritoral platform of the anterior end of the upper and lower jaws

is not exposed from a buccal aspect in any specimen.

The rarity of large specimens with intact jaws precludes histologic sectioning at this time. Examination of the jaws under alcohol reveals that there are a series of what appear to be dentinal columns that radiate from the posterior aboral corner of each jaw. These columns are apparently continuous with the villiform projections at the mandibular tips (Fig. 14).

**AXIAL SKELETON:** Neural and haemal arches and spines are uncalcified in all specimens. Stoutly calcified dorsal and ventral hemicentra are present in specimens above 31 mm snout-vent length. Hemicentra are more numerous and closely spaced than are fin radials or enlarged denticles in the caudal region, the only region of the body in which clear segmentation can be estimated. This indicates, as does correspondence of hemicentral proportions with ring centra proportions of *Ishyodus* (Obruchev, 1967) and *Squaloraja* (Patterson, 1965), that the chimaeroid polyspondylous central calcification system is

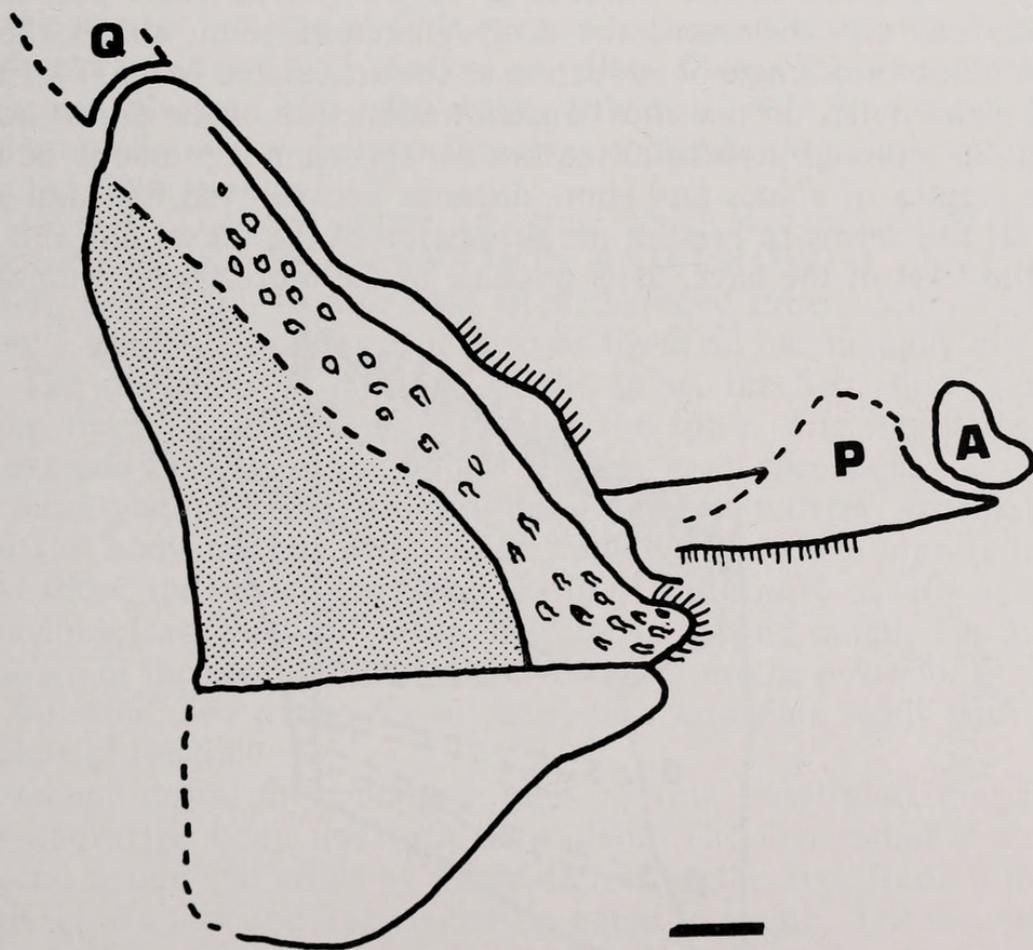


Fig. 14. *Echinochimaera meltoni*, MV 5371, type specimen, left upper and right lower jaws. A, anterior plate; P, posterior plate; Q, quadrate process, presumed calcified cartilage stippled. Scale is 1 mm.

present in these Mississippian fish. Fusion of dorsal and ventral hemicentra, however, is found only in the base of the synarcuum, and is accompanied by fusion of adjacent hemicentra, neural arches, and spines. There is therefore no indication of the number of segments involved in the formation of the synarcuum.

The anterodorsal margin of the synarcuum extends posterodorsally at an angle of about  $30^\circ$  to the vertebral axis. The posterior margin extends vertically around the neural canal, then curves posteriorly, then dorsally, to the posterodorsally concave articular facet. Lateral horns of the synarcuum extend beyond the spine articulation to the level of the rear margin of the spine. The articular facet of the basal plate of the dorsal fin spine is a convex surface that projects anteriorly below the ventral margin of the spine itself.

The arrangement of spine-synarcuum articulation in *Echinochimaera* allows post-mortem adduction of the dorsal fin spine to an angle in excess of  $45^\circ$  anterior to a line perpendicular to the vertebral axis, as seen in the three largest males (Fig. 1). MV 5371, where post-mortem tetany has also dislocated the skull-synarcuum joint, shows the same extreme anterior angle of adduction as the articulated MV 5374. Females and small males do not show anterior adduction of the dorsal fin spine (Fig. 2), although structural reasons for this cannot presently be found. The lengths of spines and short distance between the first and second dorsal fins seems to prevent the depression of the dorsal fins and spines to the level of the back, as is possible in the more recent chimaeroids.

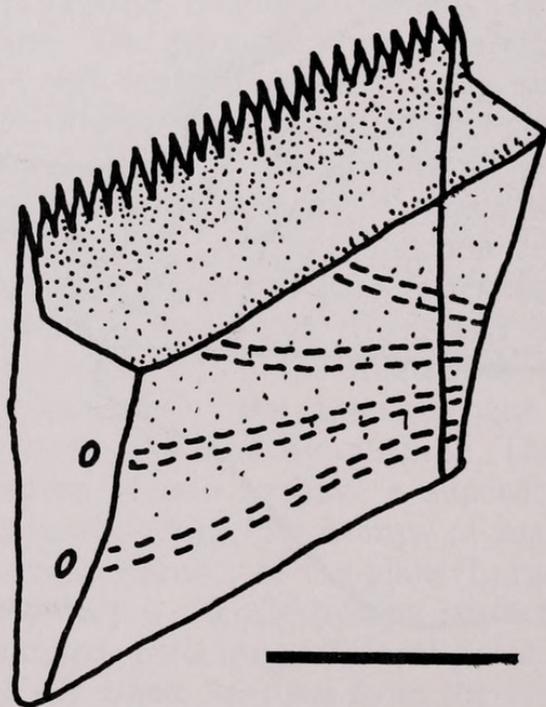


Fig. 15. *Echinochimaera meltoni*, MV 5383, posterior part of the right lower jaw plate in lingual aspect. Scale is 1 mm.

Spines in the more recent forms cannot be adducted forward of a line perpendicular to the vertebral axis.

The synarcuum of *Chimaera* and other Mesozoic and Recent chimaeroids has transversely expanded vertical anterior and posterior margins that are absent in *Echinochimaera*. Dorsal parasagittal musculature originating on the lateral surfaces of the sagittal crest inserts on the anterior margin of the synarcuum of *Chimaera*, some of it extending along the dorsal surface to the crests of the lateral horns posteriorly. Segmental epaxial musculature that inserts lateral to the parasagittal musculature on the neurocranium also attaches firmly to the lateral edges of the posterior margin of the synarcuum. Erector musculature of the spine originates anteroventrally upon the synarcuum of *Chimaera*, posterior and mesial to the anterolateral margin. Depressor musculature originates along the posterior margin, mesial to the epaxial musculature. The relationship between erector musculature, synarcuum and spine of *Chimaera* appears to be essentially the same as that of *Echinochimaera*. Depressor musculature, lacking the broad, vertically oriented posterior laminae of *Chimaera* as an area of origin would have been shorter, thinner, and weaker in effect than the corresponding modern musculature. The relationship between head, synarcuum and epaxial musculature in *Echinochimaera* is significantly less complex than in the Chimaeroidei.

**MEDIAN FINS:** The first dorsal fin spine, which is denticulated along its anterior edge (see **PRESERVATION AND GROWTH**, above, and Figs. 5-8), bears eight to nine rows of well-spaced tuberculations laterally, and a shallow posterior groove to its tip in all but sexually mature males. The dorsal fin is attached to the spine, the first, short radial emerging from the groove at the tip of the spine. The internal pulp cavity extends virtually to the tip of the spine in all specimens.

The basal plate of the first dorsal fin is high and narrow, articulating beyond the body margin with the fin radials. There are nine radials, the first short, the second long, and the third and fourth usually arising by branching from variable positions from the second radial. The anterior margin of the second radial itself emerges from the posterior groove of the fin spine. The remainder of the radials articulate solely with the basal plate of the fin.

The second dorsal fin contains a high, narrow, basal plate that articulates above the body line with the radials. The first radial is stout, the second is thin and arises by bifurcation from the first. Radials three through six are thin and approximately equal in length. The seventh is short and thin, and arises from the sixth radial. The second dorsal fin contrasts strongly with that of chimaeroids, which have a long, low, undulatory dorsal fin of segmental nature.

The low epichordal lobe of the short, small, caudal fin originates above the origin of the hypochordal lobe, with a series of nine or ten

radials of gradually increasing height followed by an approximately equal number of progressively shorter radials. The anterodorsal margin of the epichordal lobe bears a rim of denticles that extends to the high point of the fin. The hypochordal lobe closely follows an anal fin of one long, stout radial and as many as three thinner radials. The first radial of the hypochordal lobe is the longest and stoutest of the fin. The following five radials are successively shorter, and although at least six more can be counted in the holotype, the precise number of these short radials might be somewhat higher than the twelve visible ones.

**PAIRED FINS AND GIRDLES:** The pectoral girdles extend from the dorsal margin of the body, immediately behind the head, to the ventral midline, but are not evidently fused in the ventral midline. The pectoral fins articulate below the middle of the flank. The pectoral girdle is of uniform width throughout. Virtually nothing can be seen of the pectoral fin itself, except that it lay along the midflank, extended about  $3/4$  of the distance from pectoral to pelvic girdle, and had a disposition of covering squamation indicative of an internal structure grossly similar to that of recent chimaeroids.

The pelvic girdle (Fig. 16) has a high iliac process that extends above the level of the vertebral column (Figs. 1, 2). There is an abrupt posterior widening of the girdle below its middle, to the articulation with the apex of the triangular basal plate of the pelvic fin. The posterior margin then curves gently forward toward the slightly anteriorly concave anterior margin (in the female), leaving a thin mesial bar which contacts the contralateral bar in the ventral midline. The basal plate of the fin itself (Fig. 16) has the profile of a low obtuse triangle. The base of the triangle faces mesially, the anterior angle forms the pelvic articulation, and the nine visible fin radials articulate with the apex, posteriorside, and posterior angle. The first ray is stout, the second and third diverge from a single base, and several other bifurcating radials seem to be variably present in different specimens.

The pelvic girdle of sexually mature males bears a posteroventral articular facet immediately above the mesial process and below the articulation for the fin base (Fig. 16). Articulating with this facet is a long axis of two segments, followed distally by a broad based curved spine of uncertain histologic nature but lacking a pulp cavity. This structure evidently corresponds to the prepelvic tenaculum of chimaeroids. Chimaeroid prepelvic tenacula, however, articulate with the anterior margin of the pelvic girdle, and usually bear enlarged denticles (Stahl, 1967, Fig. 10). A single short, curved segment connects the long, simple, gradually tapering distal element of the mixopterygium to a facet near the posterior end of the basal edge of the fin supporting plate. The anterior edge of the pelvic fin of the male bears a short, stout, anteriorly curved first radial which cannot be found in the female.



Fig. 16. *Echinochimaera meltoni*, MV 5371, type specimen, right side stippled. A, axial; BP, basal plate; CL, clasper; PPT, postpelvic tenaculum. Scale is 5 mm.

The prepelvic tenaculum of *Echinochimaera* differs strongly from that of the chimaeroidei. There are no major morphological differences between the girdle-fin-clasper complexes of *Echinochimaera* and the Chimaeroidei.

*Echinochimaeroidei incertae sedis*

*Marracanthus rectus* St. John and Worthen, 1875

*Marracanthus rectus* St. John and Worthen, 1875; p. 466-467, Pl. 22, Figs. 7-9. "Upper Beds of the St. Louis Limestone," Alton, Illinois.

The spines named *Marracanthus* are extremely similar to those of *Echinochimaera* in growth, size, shape, denticulation, and ornamentation. They differ in lacking a distal posterior groove for dorsal fin attachment, in having fewer rows of lateral ornamentation, and fewer anterodistal denticles. Thus, while *Marracanthus* and *Echinochimaera* are demonstrably different spines, they are probably quite closely related and should be included in the same suborder.

DISCUSSION

RELATIONSHIP TO THE CHIMAEROIDEI: *Echinochimaera* shares many uniquely derived structural characters with the Chimaeroidei. The shape and proportions of the skull, jaws, and jaw plates, as well as the position of the branchial basket, differ only in small details from those of the modern Chimaeroidei. The basic structure of the synarcuum, first dorsal fin and spine, the pectoral girdle, pelvic girdle, fin, and clasper are also structures unique to *Echinochimaera* and the chimaeroids. Finally, the nature of the vertebral column, the anal-fin-caudal-fin relationship and diphyccercal tail, and the presence, but not the structure of the prepelvic tenaculum also indicate a very close phyletic relationship between these Mississippian fish and the more recent chimaeroids. *Echinochimaera* clearly has more primitive character states in its complete squamation of placoid denticles, its ornamented dorsal fin spine and in having only small, simple denticles framing the lateral line canals. The lack of a frontal clasper in males is a primitive character that markedly distinguishes these fishes from the chimaeroids. Finally, the postpelvic articulation of the prepelvic clasper is believed to be a primitive character state, under the presently untestable hypothesis that this structure may originally have been derived from anterior pelvic fin radials that articulated with the pelvic girdle. This arrangement of fin radials and girdle may be seen in the petalodont *Heteropetalus elegantulus* (Lund, 1977b).

A complete squamation is unknown among the Chimaeroidei, although *Callorhynchus* does possess some modified denticles (Dean, 1906). Lateral line canals are encased in very fine ring scales in Chimaeroidei from the Mesozoic and later (Patterson, 1965).

The absence of anterior transverse laminae of the synarcuum may be a primitive character state of synarcual evolution. This sustains the view that the synarcuum of chimaeroids originally evolved in connection with strong articulation of a mobile first dorsal spine (Lund, 1977a). The synarcuum of *Arthrodira* was developed in relation to cranial mobility (Stensio, 1945) like the synarcuum of the *Batoidei*, and thus bears only a convergent, coincidental relationship.

*Echinochimaera* has several uniquely derived character states that differentiate it from the *Chimaeroidei*. The second dorsal fin is short based, all radials articulating with a single high basal plate. All *Chimaeroidei* (Obruchev, 1967), *Helodus* (Patterson, 1965), *Chondrenchelys* (Moy-Thomas, 1935), *Heteropetalus* (Lund, 1977), pleuracanthous and anacanthous elasmobranchs (see Lund 1974) bear a serial basidorsal-radial second dorsal fin. This condition is evidently plesiomorphous for the class *Chondrichthyes*.

Sexually dimorphic differentiation of the first dorsal fin spine, as well as lateral supraorbital denticles, is not known in the *Chimaeroidei*. Indeed, the lack of this spine in the youngest specimen also contrasts strongly with the modern chimaeroid condition (Dean, 1906). Further, although adequate information on size dimorphism in the modern forms is lacking, the information available indicates that mature females are usually larger than mature males. (Dean, 1906; Bigelow and Schroeder, 1953). The fin spines of modern *Chimaeroidei* are free from the fin distally, grooved venomous, and thus principally defensive in nature (Evans, 1923). The anteriorly pivoting, anteriorly denticulated and enlarged fin spines of mature male *Echinochimaera*, together with their lateral supraorbital denticles, probably functioned chiefly in intra-specific sexual display and courtship. Ghiselin (1974) (also see Gould, 1974) discusses various strategies involved in sexual selection, one of which seems to explain some features of the occurrence of the Bear Gulch chimaeroids. Elaboration of sexual dimorphism through increased size and ornamentation of males relative to females seems related to gregariousness in some species. It is accompanied in these forms by delayed functional maturity of the males, increased male-male interaction and a high mortality rate of males versus females (Ghiselin, 1974:146-147). It is worthwhile noting that in spite of a precariously small sample size, both the size distribution of specimens and the nature of the sex dimorphism fit convincingly within this model. The more recent chimaeroids have adopted an alternative strategy (Dean, 1906) involving smaller, more mobile males and selection for more effective copulatory devices.

The presence of a complex median postorbital spine in both sexes of *Echinochimaera* is a derived character in relation to the *Chimaeroidei*, all of which tend to elimination of dermal defensive structures other

than the dorsal fin spine. The presence of defensive denticles on the head, and elsewhere, is quite common among Chondrichthyes (Patterson, 1965, 1968; Bendix-Almgreen, 1968).

The jaw plates of *Echinochimaera* agree in number and position with those of the Chimaeroidei. They differ, however, in detail, from the presence of villiform projections to the nature of the tritoral surface.

*Echinochimaera* and the Chimaeroidei share many uniquely derived characters that differentiate them from all other Chondrichthyes. Each group, however, possesses autopomorphous characters that are plesiomorphous in the other. Two conclusions derive from this observation. The first is that the two must share a common ancestor—that is, they are sister groups. The second observation, which follows inevitably from the first, is that therefore the Chimaeroidei did not originate in the Jurassic (Patterson, 1965) but prior to the Namurian A, as suggested by Dean (1906). A brief reevaluation of information on other known Holocephali is necessary at this time.

*Squaloraja* is a depressed holocephalian with a long, thick, flat rostrum and a very long frontal "clasper" (Patterson, 1965). *Squaloraja* shares the number of tooth plates, form of the postrostral braincase, and the structure of the vertebral column and endoskeleton of the pectoral and pelvic fins with the Chimaeroidei. Squamation is placoid and extensive. *Squaloraja* is divergent from the Chimaeroidei in the nature of the rostrum and "clasper," in lacking a first dorsal spine and fin, in having a long, low, batoid-like synarcuum, and in lacking iliac processes or endoskeletally supported prepelvic or subpelvic tenacula. The tooth-plates are not of chimaeroid histology, but are composed of "alternating bands of osteonal and interosteonal tissue" (Patterson, 1965:121). They lack the peculiar localized tritors of tubular dentine and intertritoral cover of outer tissue (Peyer, 1968:79) of chimaeroids, and are not composed of dentinal osteons surrounded by interosteonal tissue, as in typical bradyodont tooth plates (Radinsky, 1961). This condition could conceivably have been derived either from a bradyodont plate, from a chimaeroid condition, or from a condition plesiomorphous to both. It is a totally autopomorphous character state. The lack (loss) of the first dorsal fin and spine, and possibly the absence of iliac processes, might be associated with a flattened body form, as may be the type of synarcuum. The absence of prepelvic claspers is less readily explained in terms of secondary loss. Furthermore, *Helodus*, a distantly derived chondrichthyan, shares most characters of the endoskeleton of the paired fins with *Squaloraja* and the chimaeroids, so that while these characters indicate some affinity, the relationship they indicate might be a distant one indeed.

*Squaloraja* appears to share with the myriacanthoids the elongate rostrum, the absence of an ethmoid canal, and retention of an apparently open precerebral fontanelle (Patterson, 1965:121). The open, if narrow

precerebral fontanelle is a plesiomorphous condition in relation to the highly compressed, elevated chimaeroid ethmoid region and ethmoid canal. The elevation of the ethmoid region is most clearly related to the great anterodorsal expansion of preorbitalis musculature (Raikow and Swierczewski, 1975) and may be relatively independent of expansion of the orbits, as Patterson (1965) indicates. Elongation of the rostrum in *Squaloraja* is thus autapomorphous relative to chimaeroids, but the chimaeroid ethmoid region is apomorphous relative to the squalorajoid condition. Finally the number of tooth plates in *Squaloraja* is the same as that in menaspoids and in some myriacanthoids as well as in chimaeroids (Lund, 1977a).

In summary, *Squaloraja* shares no discernible uniquely derived characters with chimaeroids, except the numerous vertebrae, but does possess many character states in which it is either plesiomorphous or autapomorphous in relation to the chimaeroid condition, and thus is certainly a separately derived group.

The myriacanthoids (Patterson, 1965) are strongly divergent from the chimaeroid condition in having a strong, long, calcified cartilage rostrum of the *Squaloraja* type, in the presence of tuberculated plates on the skull, mandibular spines, and, most strikingly in tooth-plate number and histology. *Myriacanthus* and *Metopacanthus*, the best known members of the group, have three paired upper plates and a symphysial plate, plus a pair of plates in the lower jaw. The two anterior upper pairs of plates have localized tritoral areas, but the pterygoid and all three mandibular plates have an occlusal surface of tubular dentine. A synarcum of chimaeroid type is present, associated with a mobile first dorsal fin and spine. Little else is known about these fish.

The postrostral neurocranium and jaw proportions are quite similar to those of chimaeroids, but as in *Squaloraja*, there is a long, stout rostrum, contrasting strongly with the delicate rostral cartilages of even the longest-snouted chimaeroids (Obruchev, 1967). Tuberculated dermal cranial and mandibular plates are a derived condition in comparison with chimaeroids. Upper tooth plate numbers, however, approximate the highest known cochlodont condition, while lower tooth plate numbers are intermediate between that of "*Platyxystrodus*" and that of menaspoids, *Squaloraja*, and chimaeroids. The disposition of tritoral areas on anterior plates and tubular dentine on the lower and posterior upper plates is again intermediate between the two separately derived conditions.

Thus, while it is not presently possible to determine the evolutionary pathways of tooth morphology between chimaeroid, myriacanthoid, and cochlodontoid, the myriacanthoids provide a clear morphologic link between the two groups. The myriacanthoids cannot consequently be considered close to the chimaeroids phyletically. While the myriacanthoids clearly approach the menaspoid-cochlodont condition, analy-

sis of the cochliodont bradyodonts in addition to what I have done elsewhere (Lund, 1977a) would be futile without additional study material.

*Helodus simplex* (Moy-Thomas, 1936; Patterson, 1965) is a flat headed, many toothed, late Carboniferous fresh-water chondrichthyan which happens to share holostyly and the form of the pectoral and dorsal fins with chimaeroids. Aside from holostyly, the low, wide neurocranium with a broadly open precerebral fontanelle shows none of the modifications necessary to be comparable to the chimaeroid condition. The nature of the skull and dentition reveals a morphotype comparable to what may have been the plesiomorphous condition of the Bradyodonti (Lund, 1977a).

The ptyctodont arthrodires have been frequently suggested as ancestors of the chimaeroids (Orvig, 1962; Westoll, 1962; Stahl, 1967) although the body form seems to be the only character the two groups share. The single paired upper and lower tooth plates of *Ptyctodus*, which lack either a basal layer or the complex relationship of an outer layer to osteodentine and tubular dentine characteristic of chimaeroids are not comparable to those of the latter group (Patterson, 1968; Dean, 1906). The structure of paired and median fins is distinctly divergent, the synarcum is of typical arthrodiran type (Stensio, 1945), and squamation is absent. Finally, while elaborate pelvic fins are present in the form of a funnel, intromittent organs and pelvic fins and girdles, as known in the chondrichthyans, are absent. While there seems little reason to doubt that the pelvic fins of ptyctodonts evolved to facilitate internal fertilization, this feat must have been accomplished by cloacal apposition. The ptyctodont arthrodires represent a highly derived arthrodiran condition, but one far too specialized to be even distantly related to any known holocephalian or bradyodont.

#### CONCLUSIONS

*Echinochimaera meltoni*, the first described Paleozoic chimaeriform, closely resembles the geologically younger members of its order in body form, jaw, and neurocranial structure, in the structure of the pectoral girdle, pelvic girdle, pelvic fin and clasper, and in anal-caudal relationships. While the basic structure of the first dorsal fin-spine-synarcum complex is close to that of the Chimaeroidei, structural differences are evident that strongly suggest a separate adaptive pathway. The steno-basal second dorsal fin and elaboration of armament, the absence of a frontal clasper, and a unique, sub-pelvic, axial, paired tenaculum reinforce the separately derived position of this group in relation to the Chimaeroidei. Large males, with elaborate growth of dermal cranial spines and first dorsal spines, smaller and less common females, and a good morphologic series indicating post-hatching spine formation, all

seem to fit a particular sexual selection pathway which is also divergent from that of the Chimaeroidei. The Chimaeriformes are therefore interpreted as a discrete group that underwent a Paleozoic radiation apart from the Squalorajoidei. The squalorajoids share more derived characters with the Myriacanthiformes than with the Chimaeriformes. The Myriacanthiformes are seen as derived from some holocephalian bradyodont lineage, bearing a sister group relationship to the Chimaeriformes.

Comparison with the ptyctodont arthrodires reveals no phylogenetically significant characters in common.

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