FRESHWATER STINGRAYS OF THE GREEN RIVER FORMATION OF WYOMING (EARLY EOCENE), WITH THE DESCRIPTION OF A NEW GENUS AND SPECIES AND AN ANALYSIS OF ITS PHYLOGENETIC RELATIONSHIPS (CHONDRICHTHYES: MYLIOBATIFORMES)

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Source: Bulletin of the American Museum of Natural History, 2004(284) : 1-136

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/0003-0090(2004)284<0001:FSOTGR>2.0.CO;2

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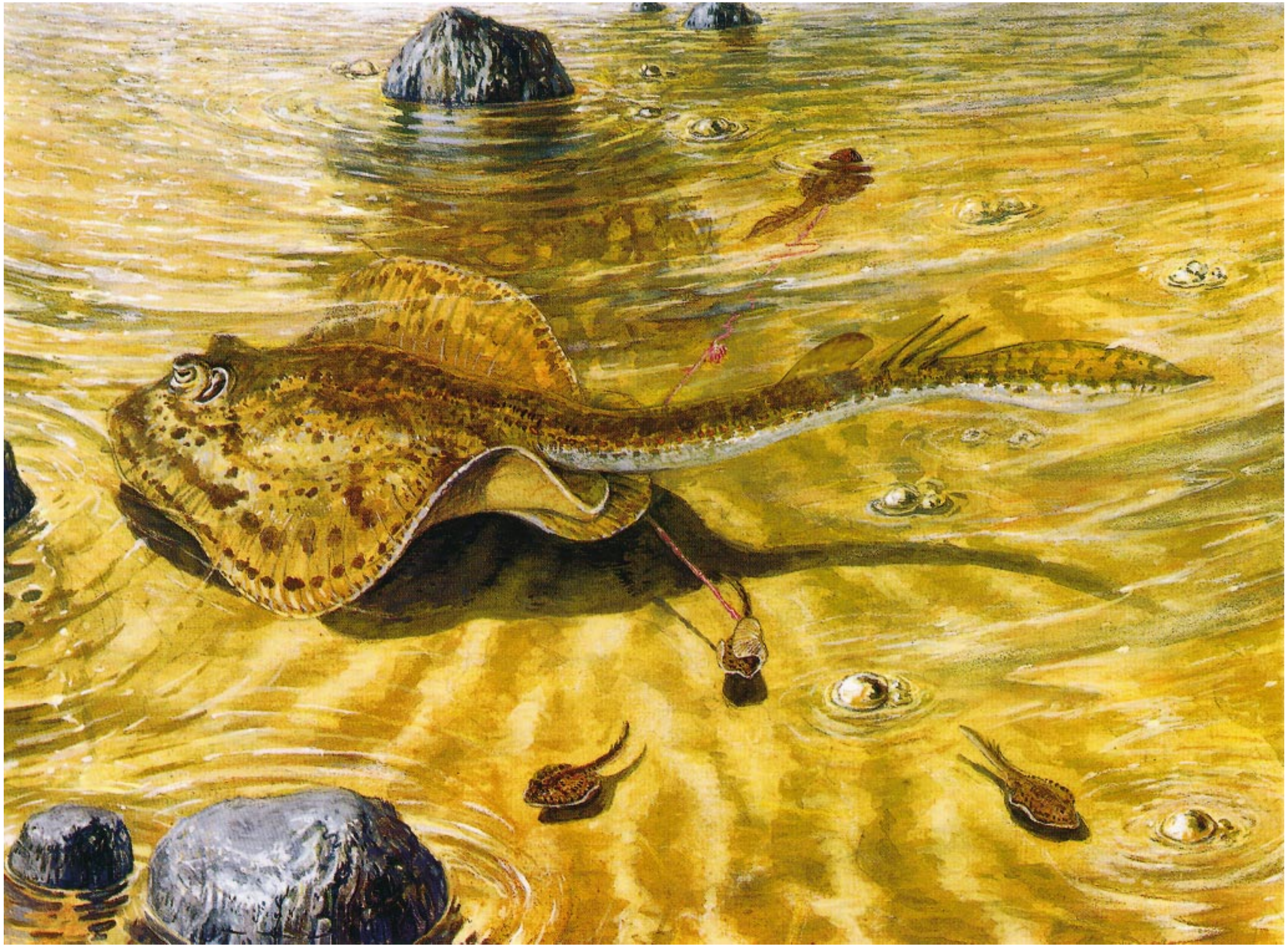
BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024

Number 284, 136 pp., 53 figures, 7 tables

Issued June 9, 2004

ISSN 0003-0090



Frontispiece. Artistic rendering of the new genus and species of stingray described in the present paper in its natural environment. This stingray taxon occurred in Fossil Lake, an extinct tropical to subtropical freshwater intermontane lake that formed as a consequence of the orogeny of the Rocky mountains (fig. 1). Sediments from Fossil Lake are exposed as the Fossil Butte Member of the Green River Formation in present-day Wyoming (some 52 million years before present). The adult female is giving birth through viviparity; this scene is inspired by specimen AMNH 11557, in which an adult female stingray is preserved alongside two small stingrays that are inferred to be her aborted late-term fetuses (fig. 3; see text for details). Based on an original painting by David W. Miller and modified from Maisey (1996: pl. 42).

CONTENTS

ABSTRACT

Freshwater stingrays from the Fossil Butte Member of the late early Eocene Green River Formation of Wyoming are reviewed, and a new genus and species of fossil stingray is described. †*Asterotrygon maloneyi*, n.gen., n.sp. is remarkably well preserved and is known from articulated skeletons of juveniles and adults, both males and females. It is distinguished from all Recent and fossil stingrays, including †*Heliobatis radians* from the same formation, by the unique presence of a dorsal fin covered with dermal denticles directly anterior to the caudal stings. Other characters that in combination distinguish the new fossil genus from all other stingrays include: retention of separate, individual vertebrae extending to the tail extremity instead of a cartilaginous rod posterior to caudal stings; dorsal surface of disc and tail covered by numerous, closely packed, minute denticles; tail relatively stout at base; and relative proportions of disc and tail. †*Asterotrygon*, n.gen. shares with certain stingray genera postorbital processes of neurocranium separated from a supraorbital process by a small notch in the supraorbital shelf, presence of both dorsal and ventral tail-folds posterior to caudal stings (and internally supported by rudimentary radial elements), and hyomandibulae separated from lower jaws by a gap that originally contained the hyomandibular-Meckelian ligament. A calcified angular cartilage between the hyomandibula and Meckel's cartilage is tentatively identified in †*Asterotrygon*, n.gen. as well. †*Asterotrygon*, n.gen. is unquestionably a stingray, presenting many myliobatiform synapomorphies including caudal stings on the dorsal aspect of tail, lack of jugal arches in neurocranium, a thoracolumbar synarcual cartilage posterior to scapulocoracoid, absence of thoracic ribs, and laterally expanded, shelflike postorbital processes. †*Asterotrygon*, n.gen. and †*Heliobatis* primitively retain a narrow and slightly arched puboischiadic girdle and primitively lack calcified rostral elements in adults.

A phylogenetic analysis of 23 stingray genera, two outgroups, and 44 informative morphological characters resulted in 35 equally most parsimonious trees. The strict consensus reveals the following hierarchical structure: *Hexatrygon* + (†*Asterotrygon*, n.gen., *Plesiobatis*, Urolophidae + (Urotrygonidae + (†*Heliobatis* + (Potamotrygonidae + (amphi-American *Himantura*, *Pteroplatytrygon*, *Himantura*, *Taeniura*, *Dasyatis* + (Gymnuridae + Myliobatidae)))))). Our resulting tree has nodes in common with previous phylogenetic analyses of stingrays (e.g., *Hexatrygon* is the most basal stingray genus; gymnurids and myliobatids [pelagic stingrays] are well-supported sister-groups), but includes novel components, such as a clade that includes all dasyatid genera (as a polytomy) and the component Gymnuridae + Myliobatidae. ''Dasyatidae'' is not monophyletic in any of the minimum-length trees obtained; Urolophidae (*Urolophus* and *Trygonoptera*) and Urotrygonidae (*Urobatis* and *Urotrygon*) are both monophyletic, but are not sister-groups. †*Asterotrygon*, n.gen. forms a clade with urolophids in 21 of the 35 equally most parsimonious trees. Successive approximations weighting adds only one additional node in relation to the strict consensus, which unites *Pteroplatytrygon*, *Dasyatis*, and *Himantura* sensu stricto (in a polytomy) with Gymnuridae + Myliobatidae. The resulting stingray phylogeny is at odds with previous phylogenies mostly regarding the affinities of amphi-American *Himantura* and *Taeniura*, which do not form a monophyletic group with the South American freshwater stingrays (Potamotrygonidae) in any of the minimum-length trees obtained. Similar to most elasmobranch groups, stingrays display much character conflict, and cladogram topologies are very sensitive to changes in character coding. Due to a high degree of character variation present in certain generic-level terminal taxa, a more fully representative species-level phylogeny is necessary to clarify the systematic importance of tail-fold configuration, ceratobranchial fusion patterns, and other characters discussed in our study. Three additional synapomorphies of stingrays were uncovered by our study, pertaining to the configuration of the basihyal, first pair of hypobranchial cartilages, and to the forward extension of the basibranchial copula. Our phylogenetic results imply the following biogeographic patterns: the relationships of †*Asterotrygon*, n.gen. demonstrate a strong Indo-west Pacific historical correlation, while †*Heliobatis* displays an affinity with the Americas; the node containing the greatest diversity of modern stingrays (''Dasyatidae'' + (Gymnuridae + Myliobatidae)) evolved only after an American stingray lineage was established sometime earlier than the early Eocene; and potamotrygonids date at least from the late early Eocene, and not the Miocene, as previous studies have implied. The mechanism responsible for the invasion of the potamotrygonid ancestor into South America could indeed have been a marine transgression as advocated by other authors, albeit a much earlier (pre-Miocene) one, during either the Late Cretaceous or the late Paleocene to early Eocene.

INTRODUCTION

Fossilized remains of stingrays (Myliobatiformes) are not uncommon components of Tertiary strata and are known from many widespread localities, both freshwater and marine. These occurrences, summarized in table 1, include the Paleocene of Africa, North America, and Europe (Arambourg, 1952; Estes, 1976; Halter, 1989); Eocene of Europe, Asia, and Africa (Casier, 1966; Chang and Zhou, 1993; Cappetta, 1984); Oligocene of Japan and Europe (Yabumoto and Uyeno, 1994; Bor, 1990); Miocene of South America, Cuba, Europe, and Asia (e.g., Hatai and Kotaka, 1962; Sahni and Mehrotra, 1981; Arratia and Cione, 1996; Schultz, 1998); and Pliocene of Europe, Japan, and North America (Landini, 1977; Yabumoto and Uyeno, 1994; Purdy et al., 2001). Even more recent (Quaternary) stingray remains have been found in Japan (reviewed in Yabumoto and Uyeno, 1994). The oldest stingray fossils that have been reported to date, however, are from the Early Cretaceous (Hauterivian) of northeastern England (Underwood et al., 1999). Other Mesozoic stingray records are from the early Late Cretaceous (Cenomanian) of Texas (Meyer, 1974; Cappetta and Case, 1999) and Egypt (Stromer, 1927; Werner, 1989), and upper Late Cretaceous of Wyoming (Estes, 1964), Texas (Maastrichtian: Welton and Farish, 1993; Case and Cappetta, 1997; see also Cappetta and Case, 1999), New Jersey (Cappetta and Case, 1975), South America (Bolivia: Schaeffer, 1963; Cappetta, 1975, 1992; Gayet et al., 1992; Arratia and Cione, 1996; Chile: Wetzel, 1930), Africa (Arambourg, 1952; Dartevelle and Casier, 1943, 1949, 1959; Cappetta, 1987; Noubhani and Cappetta, 1997), Jordan (Zalmout and Mustafa, 2001), and Europe (e.g., Albers and Weiler, 1964; Cappetta, 1987; Soler-Gijón and López-Martínez, 1998), but Mesozoic stingray remains are not as abundant as those from the Tertiary (for a stratigraphical review, see Cappetta et al., 1993). The vast majority of stingray fossils, however, including all of the occurrences listed above, consist of isolated teeth, dermal denticles, and occasionally serrated caudal spines (caudal ‘‘stings’’).

In contrast, more complete, articulated fossil stingray specimens are relatively rare in the fossil record and are presently known from only two localities, both of early Eocene age: the Monte Bolca Formation of northeastern Italy and the Green River Formation of Wyoming. Both localities are almost contemporaneous but represent very different paleoenvironments. The Monte Bolca Formation was deposited in a shallow, tropical, marine coral back-reef lagoon (Landini and Sorbini, 1996), while the Green River Formation was deposited within a series of tropical to subtropical freshwater lakes (Schaeffer and Mangus, 1965; Grande, 1984, 2001). The Monte Bolca deposits contain a more diverse stingray (and batoid) fauna, and both formations have yielded many stingray specimens represented by somewhat complete articulated skeletons. The batoid fauna of Monte Bolca is presently under review; it contains guitarfishes (Rhinobatidae), thornback rays (Platyrhinidae), and electric rays (Torpediniformes) in addition to stingrays, similar to many modern coral reef faunas. The Green River Formation has yielded no batoids other than stingrays, but to some extent this is to be expected, given that South American potamotrygonid stingrays, and certain species of the stingray genera *Dasyatis* and *Himantura*, are the only obligate modern freshwater batoids.

Stingrays were first reported from the Green River Formation by Marsh (1877), who described †*Heliobatis radians* on the basis of a single specimen from the Fossil Butte Member of Fossil Lake. Marsh’s description is rather brief and his specimen was not illustrated. Cope may have overlooked Marsh’s description, as shortly thereafter he erected †*Xiphotrygon acutidens* also from the Fossil Butte Member of Fossil Lake (Cope, 1879). Cope later provided a more complete description of his species accompanied by a remarkable illustration of a specimen which is now lost (Cope, 1884). Since then many

TABLE 1
Some Tertiary Records of Stingrays (Myliobatiformes)
All occurrences are of isolated teeth, dermal denticles or caudal stings. This compilation is not exhaustive, but additional records (for India and Africa in particular) are listed in the reference below (see also Cappetta, 1987).

Location	References
	Paleocene
Cabinda (Angola)	Dartevelle and Casier (1959)
Morocco	Arambourg (1952) Cappetta (1987) Noubhani and Cappetta (1997)
Niger	Cappetta (1972, 1987)
Belgium	Halter (1989)
Montana (U.S.A.)	Estes (1976)
New Jersey (U.S.A.)	Case (1996)
North and South Dakota (U.S.A.)	Cvancara and Hoganson (1993) Best (1987)
	Eocene
England	White (1931) Casier (1966) Ward (1979)
Belgium	Casier (1946) Herman et al. (1989)
France	Cappetta and Nolf (1981)
Germany	Stromer (1904)
China	Chang and Zhou (1993)
Georgia (U.S.A.)	Case (1981)
Morocco	Cappetta (1984, 1987) Noubhani and Cappetta (1997)
Egypt	Stromer (1905)
Jordan	Mustafa and Zalmout (2002)
	Oligocene
Japan	Yabumoto and Uyeno (1994)
Belgium	Bor (1990)
	Miocene
Brazil	Larrazet (1886) Richter (1984) Deynat and Brito (1994)
Argentina	Cione (1978) Cione and Expósito (1980) Arratia and Cione (1996)
Uruguay	Perea and Ubilla (1989)
Colombia	Lundberg (1997)
Peru	Frailey (1986) Lundberg (1998)
Cuba	Carvalho (unpubl.)
Austria	Schultz (1998)
India	Sahni and Mehrotra (1981)
Japan	Hatai and Kotaka (1962) Itoigawa et al. (1985) Yabumoto and Uyeno (1994)
North Carolina (U.S.A.)	Case (1980)
	Pliocene
Italy	Landini (1977)
Japan	Yabumoto and Uyeno (1994)

fossil stingray specimens have appeared from Fossil Lake, compelling Fowler (1947) to describe †*Palaeodasybatis discus* to accommodate what was thought to be a more diverse extinct stingray fauna. Fowler (1947) distinguished his new taxon from Cope's nominal species on the basis of minor differences in disc shape, apparently also unaware of Marsh's (1877) earlier account. Both nominal taxa of Cope (1879) and Fowler (1947) have been synonymized with †*Heliobatis radians* (Grande, 1980, 1984), a decision we further corroborate in this study.

The next indication of a more diverse Green River stingray fauna was provided by Grande (1980, 1984), who documented and illustrated an adult female specimen significantly distinct from typical †*Heliobatis radians*. The limestone matrix on which this specimen is preserved (AMNH P 11557) is remarkable because it also contains two small specimens which we infer to be aborted late-term fetuses. Another large female specimen, which is also markedly different from †*Heliobatis radians*, is just as noteworthy due to the presence of a small embryo preserved inside its pleuroperitoneal cavity. This adult female, recently obtained by the Field Museum of Natural History (Chicago), is designated the holotype of a new genus and species of stingray from Fossil Lake, which is described below. A total of 15 specimens of this new form have now been collected and identified, and form the basis of the present paper.

Stingrays (order Myliobatiformes) collectively form a monophyletic group within batoids, sharing numerous synapomorphies including the presence of a caudal sting (serrated caudal spine), lack of thoracic ribs and presence of a second (thoracolumbar) synarcual cartilage, among other features. Recent stingrays presently include about 185 species in 24 genera, mostly inhabiting tropical to subtropical shallow marine areas. Phylogenetic relationships among component stingray taxa have been the subject of a reinvigorated recent debate which has led to the understanding that some of the more common living stingray genera may not be monophyletic, most notably *Dasyatis* and *Himantura* (Rosa, 1985; Miyake, 1988; Nishida, 1990; Lovejoy, 1996; McEachran et al.

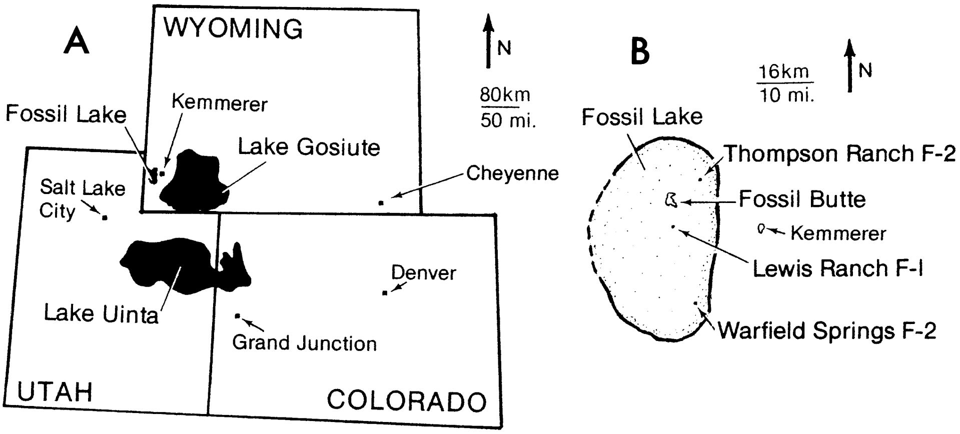


Fig. 1. **A.** Map of southwestern Wyoming, northeastern Utah, and northwestern Colorado showing the geographical extent of the intermontane lakes during their middle or late early Eocene phase. **B.** Fossil Lake during the deposition of the Fossil Butte Member of the Green River Formation, during the late early Eocene, showing a few prominent F-1 and F-2 localities where fossil stingrays have been found. From Grande and Buchheim (1994).

1996; see also Compagno and Roberts, 1982, 1984). In addition, these studies have corroborated that at least two monophyletic subgroups exist within stingrays: the Neotropical freshwater stingrays (Potamotrygonidae) and a clade containing pelagic stingray genera (Myliobatidae) plus the butterfly rays (Gymnuridae). The remaining stingray genera, which are primarily benthic in habitus, remain poorly resolved phylogenetically. Morphological features of systematic significance are preserved in the new fossil stingray taxon from the Green River Formation, and we have therefore included it in a matrix coding morphological characters of representative stingray genera. The evolutionary study presented here is not intended to resolve all persisting problems in myliobatiform systematics, although it is the most comprehensive morphological phylogenetic analysis of stingrays to date. Our systematic survey was conducted to reveal phylogenetic implications of salient anatomical features of the Green River stingrays, allowing for their placement in a more inclusive framework of stingray systematics and historical biogeography.

MATERIALS AND METHODS

The new genus and species of stingray reported here from the Green River Formation is known from 15 specimens (in addition to two tentatively identified specimens), some of which are well preserved and fairly complete (listed below is the systematic section), including juveniles and adults and specimens of both sexes. The only other described stingray from this formation (†*Heliobatis radians* Marsh, 1877) is known from hundreds of specimens in public and private collections, of which we were able to examine many (some of these are listed below in the systematic section). Both Green River stingray taxa are dorsoventrally flattened and are preserved in laminated limestone slabs of varying thickness and lithology. Specimens are readily prepared with the aid of a pinevise and other matrix-removing tools with sharp tips and an abrasive machine. All preparation of fossils was done with the aid of a dissecting microscope.

Fossil stingrays, and fossil batoids in general, are usually dorsoventrally exposed and two-dimensional, a constraint imposed by their enlarged pectoral fins that are continuous with the head (forming the disc). This renders working with fossil stingrays similar to working with radiographs of extant specimens, and many anatomical details (those observed in lateral view) are consequently obscured. This contrasts with three-dimentional shark fossils embedded in matrices amenable to acid or mechanical preparation (Schaeffer, 1981; Maisey and Carvalho, 1997). It is therefore difficult to achieve the same level of anatomical comprehension with fossil batoids (the only fully three-dimensional fossil batoid is †*Iansan*, a rhinobatoid from the Late Cretaceous of Brazil; Maisey, 1991; Brito and Séret, 1996).

MEASUREMENTS AND TERMINOLOGY

Measurements conducted on specimens were taken in a straight line, point-to-point, modified from Bigelow and Schroeder (1953), Rosa (1985), and Miyake (1988), and are as follows: TL, total length (snout tip to posterior tip of tail); DL, disc length (from anterior disc margin at snout region to posterior disc margin at disc axil); DW, disc width (distance between lateral disc margins at greatest width, i.e., at level of scapulocoracoid; width may be underestimated in some specimens because of broken distal tips of pectoral radials); TAL, tail length (from puboischiadic bar to posterior tip of tail); TAW, tail width (greatest width of tail as exposed, just posterior to pelvic fins); POL, preoral snout length (snout length from mouth opening to anterior margin of disc); MSC, distance between mouth and scapulocoracoid (from mouth opening to anterior margin of scapulocoracoid); SCW, scapular width (greatest width of scapulocoracoid, not including pectoral basal cartilages); PGW, pelvic girdle width (greatest width of pelvic girdle); STL, sting length (from sting base to posterior sting tip); PGT, distance between pelvics and tip of tail; CL, clasper length (from posterior margin of pelvic girdle and posterior tip of clasper); NCL, neurocranial length (from anterior contour of neurocranium at nasal capsule confluence to occipital region); NCW, neurocranial width (greatest width at level of nasal capsules). The following meristic counts were taken: PRO, propterygial radials; MES, mesopterygial radials; MET, metapterygial radials; TPR, total pectoral radials (= PRO + MES + MET); PVR, pelvic radials; VSP, vertebral centra from scapulacoracoid to pelvic girdle; VPS, vertebral centra from pelvic girdle to caudal sting; VST, vertebral centra posterior to sting; TV, total vertebral centra (= VSP + VPS + VST). The number of toothrows could not be inferred with accuracy, as teeth are not preserved in discrete rows but are scattered in the vicinity of the jaws and neurocranium. Many measurements traditionally taken on extant specimens could not be made on the fossils due to preservational imperfections (e.g., measurements involving the cloaca). The measurements above were taken to provide a general notion of size and proportions of the fossils, but because their accuracy depends on the preservation of the material, which varies significantly, they should not be accepted as strictly as if taken from extant specimens; the counts provided should be interpreted in a similar fashion. Measurements and counts are summarized in tables 2 and 3 for the new stingray taxon and table 4 for †*Heliobatis*.

Anatomical terminology is according to Daniel (1934), Miyake (1988), and Miyake and McEachran (1991) unless otherwise noted. We follow Rosa (1985) in using ‘‘sting’’ (as opposed to ‘‘spine’’) to refer to the elongated and serrated dermal derivative on the dorsal surface of the tail (usually more than one sting is present, and sometimes more than two). ‘‘Sting’’ and ‘‘serrated caudal sting’’ are used interchangeably. The term ‘‘stingray’’ is used here as equivalent to ‘‘myliobatiform rays’’. There are many different groups of myliobatiform rays, and most of these have a corresponding trivial name (e.g., eagle, cownose, whiptail, manta rays). ‘‘Stingray’’ is an all-encompassing term used for the entire order (Myliobatiformes) and does not include here platyrhinids (thornback rays) and *Zanobatus*, considered to be successive sister-groups to stingrays by McEachran et al. (1996). In the descriptive sections below the composition of the different myliobatiform families is based on Compagno (1973, 1977, 1999) and on the phylogenetic analysis presented after the descriptive accounts. The terms ‘‘benthic stingrays’’, ‘‘non-myliobatid stingrays’’, or ‘‘nonpelagic stingrays’’ apply to Recent and/or fossil stingrays that have a mostly benthic niche, excluding the morphologically specialized pelagic stingrays (which are here lumped into a single family, Myliobatidae; the exception is the monotypic *Pteroplatytrygon*, which is a ‘‘dasyatid’’ but is also pelagic). Benthic stingrays include *Hexatrygon*, gymnurids, urolophids, *Plesiobatis*, urotrygonids, potamotrygonids, almost all dasyatids, and the fossil taxa from the Green River and Monte Bolca Formations (except †*Promyliobatis*, a myliobatid from Monte Bolca). Consequently, we do not refer to a monophyletic group when making reference to ‘‘benthic stingrays’’, because they are not monophyletic without myliobatids (see our phylogenetic analysis below); these terms are used only for convenience. Synonymies are in abbreviated form, with the full citation included only in the references. The synonymy for †*Heliobatis radians* is not exhaustive.

The procedures employed in the phylogenetic analyses are described in Phylogenetic Procedures and Coding, after the morphological characterization of †*Heliobatis*.

COMPARATIVE STINGRAY MATERIAL

Recent stingray materials examined for this study are listed below, and include cleared-and-double-stained specimens (C&S), dry skeletons (SD), skeletons preserved in alcohol (SW), X-ray radiographs (XR), and dissected specimens (D). Dry and ‘‘wet’’ skeletons were prepared by subjecting dissected specimens to dermestid beetles (prepared by the staff of the Department of Ichthyology, AMNH). Cleared-and-stained specimens were prepared according to Dingerkus and Uhler (1977). Additional specimens of many stingray taxa were examined for external morphology, but only a few of these are included in the list below (belonging to species in which available specimens are more rare). Anatomical information extracted from the literature was confirmed by examining specimens whenever possible. Stingray classification in this list follows Compagno (1999).

Hexatrygonidae

Hexatrygon bickelli: BPBM 27761 (XR), CSIRO H 2543–07 (XR), CSIRO H 2226–01 (XR); MNHN uncataloged (2 specimens from New Caledonia).

Plesiobatidae

Plesiobatis daviesi: RUSI 11157 (XR; on file at CSIRO); MNHN uncataloged (2 specimens, from Fiji and New Caledonia).

Urolophidae

Urolophus aurantiacus: AMNH 26690 (D, XR), FUMT P 10502 (XR; on file at CSIRO).
Urolophus cruciatus: AMNH 59890 (C&S), AMNH 98247 (C&S), CSIRO H 20 (XR), CSIRO H 21 (XR), CSIRO CA 152 (XR), CSIRO CA 162 (XR).
Urolophus expansus: CSIRO T 293 (XR), CSIRO H 327 (XR), CSIRO H 343 (XR).
Urolophus flavomosaicus: CSIRO H 718–19 (XR), CSIRO H 718.22 (XR).
Urolophus gigas: CSIRO H 50 (XR).
Urolophus lobatus: CSIRO P 8197 (XR), CSIRO 28346–002 (XR).
Urolophus mitosis: CSIRO CA 2874 (XR), CSIRO CA 2875 (XR), CSIRO CA 2877 (XR).
Urolophus orarius: AMS I 20194–043 (XR), SAM uncataloged (XR; on file at CSIRO).
Urolophus paucimaculatus: CSIRO H 9 (XR), CSIRO C 4757 (XR), AMNH 99735 (SW), AMNH 95342 (SW), AMNH 216702 (SW), AMNH 217079 (SW), AMNH 217080 (SW), AMNH 217081 (SW), AMNH 217082 (SW) AMNH 217083 (SW), AMNH 217084 (SW), AMNH 217085 (SW).
Urolophus viridis: CSIRO CA 527 (XR), CSIRO H 779–01 (XR), CSIRO A 3355 (XR), USNM 222681 (XR).
Urolophus sp.: USNM 131105 (XR).
Urolophus sp.: AMNH 214469 (SW).
Trygonoptera mucosa: CSIRO H 898–02 (XR), CSIRO H 898–03 (XR), CSIRO H 898–06 (XR), CSIRO H 3499 (XR), CSIRO CA 3521 (XR), CSIRO P 27217–001 (XR), CSIRO P 27737–001 (XR).
Trygonoptera ovalis: CSIRO A 2817 (XR), CSIRO P 27958–001 (XR).
Trygonoptera personata: CSIRO H 894–01 (XR), CSIRO H 901–01 (XR).
Trygonoptera testacea: CSIRO H 33 (XR), CSIRO H 837–02 (XR), CSIRO H 837–06 (XR), CSIRO H 838–05 (XR), CSIRO H 874–07 (XR), CSIRO H 929–01 (XR), USNM 39993 (XR).
Trygonoptera sp.: CSIRO H 43 (XR), CSIRO P 14839 (XR), NMV A 1827 (XR), WAM P 14151 (XR).

Urotrygonidae

Urobatis concentricus: AMNH 15692 (XR).
Urobatis halleri: AMNH 15692 (XR), 44102 (XR), FMNH 42601 (C&S).
Urobatis jamaicensis: AMNH 18195 (XR), AMNH 25049 (XR), AMNH 28649 (D),

AMNH 44102 (D), AMNH 30385 (C&S), USNM 144075 (XR).
Urobatis maculatus: AMNH 44144 (XR).
Urobatis tumbesensis: AMNH 44021 (XR).
Urotrygon aspidura: CAS 48271 (XR).
Urotrygon chilensis: AMNH 44014 (XR), CAS 48271 (XR), FMNH 62371 (C&S), FMNH 93737 (C&S).
Urotrygon microphthalmum: NHM 1985.6.21.4–7 (D, XR).
Urotrygon nana: FMNH 72281 (C&S).
Urotrygon venezuelae: AMNH 55623 (C&S).

Dasyatidae

Dasyatis akajei: AMNH 44065 (XR).
Dasyatis americana: AMNH 30607 (C&S), AMNH P uncataloged (SD).
Dasyatis annotata: CSIRO T 449 (holotype; XR), CSIRO T 694 (XR), CSIRO T 696 (XR), CSIRO CA 697 (paratype; XR).
Dasyatis geijskesi: NNM 20487 (holotype), USNM 158726.
Dasyatis kuhlii: AMNH 44080 (XR), CSIRO CA 4309 (XR), CSIRO CA 1241 (XR).
Dasyatis leylandi: CSIRO CA 2806 (holotype; XR).
Dasyatis margarita: AMNH 41512 (XR), CU 53996 (XR), IRSNB 8497 (XR; on file at CSIRO).
Dasyatis pastinaca: AMNH 1511 (XR), AMNH 32796 (XR).
Dasyatis sabina: AMNH 16356 (XR), AMNH 51483 (D), AMNH 211610 (SW).
Dasyatis thetidis: CSIRO CA 4125 (syntype; XR), CSIRO H 1036–15 (syntype; XR).
Dasyatis ukpam: MNHN 1979–244 (XR).
Dasyatis zugei: AMNH 44056 (XR), OSU 1512 (XR, 4 specimens).
Dasyatis sp.: AMNH 41515 (XR).
Himantura chaophraya: QM I 11928 (XR).
Himantura gerrardi: NHM 1868.08.26.01.1 (XR).
Himantura granulata: SMF 4747 (XR; on file at CSIRO).
Himantura imbricata: AMNH 32501 (XR), CAS 41680 (XR), CSIRO I 1449 (XR), MNHN 2269 (XR), MNHN 1985–211 (D, XR).
Himantura krempfi: AMNH 41567 (XR).
‘‘*Himantura*’’ *pacifica*: AMNH 15661, 15662, 15663, 15710 (SD).
‘‘*Himantura*’’ *schmardae*: NHM 1908.5.28.2–3 (D, XR), USNM 33719, USNM 86071, USNM 128388.
Himantura toshi: CSIRO H 312 (XR), CSIRO H 959–01 (XR), CSIRO H 964–01 (XR), QM I 22355 (XR).
Himantura uarnak: CSIRO CA 2405 (XR).
Himantura walga: OSU 1506 (XR).
Pastinachus sephen: AMNH 44057 (XR), USNM 39982, USNM 147420.
Pteroplatytrygon violacea: MZUSP 49061 (D).
Taeniura grabata: MNHN 1989–1793 (D).
Taeniura lymma: AMNH 44076 (XR), AMNH 44076 (D), AMNH 44079 (C&S).

Potamotrygonidae

Paratrygon aiereba: MZUSP 14772 (XR), AMNH uncataloged (D).
Plesiotrygon iwamae: MZUSP 42848 (D, XR), MNHN uncataloged (XR).
Potamotrygon brachyura: MZUSP 14819 (XR).
Potamotrygon falkneri: UERJ 718.1 (D).
Potamotrygon henlei: MZUSP 14768 (XR).
Potamotrygon leopoldi: UERJ 719 (D, XR), MZUSP 35986 (XR).
Potamotrygon magdalenae: AMNH 55620 (C&S), MNHN 2368 (holotype; XR).
Potamotrygon motoro: AMNH 44034 (SW, C&S), MZUSP 19190 (D), FMNH 94503 (C&S).
Potamotrygon cf. *motoro*: AMNH 38138 (C&S, 4 specimens), AMNH 44032 (XR), AMNH 44034 (SW).
Potamotrygon cf. *ocellata*: MNRJ 10620 (XR).
Potamotrygon orbignyi: AMNH uncataloged (D, XR), MZUSP 14794 (XR).
Potamotrygon signata: MCZ 600 (syntype; XR).
Potamotrygon sp. (Rio Negro): MNRJ 3532 (D).
Potamotrygon sp. (Rio Taquari): MZUSP 25663 (XR).
Potamotrygon sp. nov. (Rio Tapajós): MZUSP 25489 (XR), MZUSP 25580 (XR).
Potamotrygon sp. nov. (Río Corantijn): USNM 225574 (XR).

Gymnuridae

Gymnura australis: CSIRO H 37 (XR), CSIRO H 323 (XR), CSIRO C 3584 (XR).
Gymnura japonica: AMNH 26691 (XR).
Gymnura marmorata: AMNH 18599 (XR).
Gymnura micrura: FMNH 89990 (C&S).

Myliobatidae

Aetomylaeus maculatus: AMNH 32500 (XR).
Aetobatus narinari: AMNH 44142 (XR, dorsal fin and caudal stings only), AMNH 53029 (C&S, gill arches only), AMNH 222833 (SW).
Mobula kuhlii: AMNH 15319 (C&S).
Mobula sp.: AMNH P 123 (SD).
Myliobatis californica: AMNH uncataloged (XR).
Myliobatis freminvillii: AMNH 15333 (XR).
Rhinoptera bonasus: AMNH 3728 (XR).

Fossil stingrays examined for this study, in addition to specimens from the Green River Formation, are listed below. This material is from the Eocene Monte Bolca Formation of northeastern Italy; the entire Monte Bolca batoid fauna is currently under review (Carvalho, in prep.). Familial, generic, and some specific assignments below are regarded as provisional.

Dasyatidae

†“*Dasyatis*” *dezignoi*: MCSNV VII B 86 and 87 (part and counterpart); UP 150 Z and 151 Z (part and counterpart).

†“*Dasyatis*” *muricata*: MCSNV VII B 92 and 93 (part and counterpart); MCSNV T 1020 and 1021 (part and counterpart); MCSNV IG 186653 and 186654 (part and counterpart); UP 159 Z and 160 Z (part and counterpart).

†“*Dasyatis*” sp.: MCSNV IG 23193 and 23194 (part and counterpart); MCSNV IG 129652; MCSNV IG 129653.

Urolophidae

†“*Urolophus*” *crassicaudatus*: MCSNV VII B 82 and 83 (part and counterpart); MCSNV VII B 84 and 85 (part and counterpart); MCSNV T 317 and 318 (part and counterpart); MCSNV VR 26607 and 26608 (part and counterpart).

†“*Urolophus*” sp.: MCSNV IG 174554; UP 8875 and 8876 (part and counterpart); UP 26227.

Myliobatidae

†*Promyliobatis gazolae*: MCSNV VII B 90 and 91 (part and counterpart).

ABBREVIATIONS

Institutional

AMNH	Department of Ichthyology (Division of Vertebrate Zoology), American Museum of Natural History
AMNH P	Fossil Fish Collection (Division of Paleontology), American Museum of Natural History
AMS	Australian Museum (Sydney)
ANSP	Academy of Natural Sciences (Philadelphia)
CAS	California Academy of Sciences (San Francisco)
CSIRO	Commonwealth Scientific and Research Organization (Hobart)
CU	Cornell University (Ithaca)
DMNH	Denver Museum of Natural History (Denver)
FMNH	Department of Zoology (Division of Fishes), Field Museum of Natural History (Chicago)
FMNH PF	Department of Geology (Fossil Fish Collection), Field Museum of Natural History (Chicago)
FUMT	University Museum, University of Tokyo (Tokyo)
IRSNB	Institut Royal des Sciences Naturales de Belgique (Brussels)
MCSNV	Museo Civico di Storia Naturale di Verona (Verona)
MNHN	Muséum National d’Histoire Naturelle (Paris)
MNRJ	Museu Nacional (Rio de Janeiro)
MZUSP	Museu de Zoologia da Universidade de São Paulo (São Paulo)
NHM	The Natural History Museum (London) (formerly BMNH)
NMV	National Museum of Victoria (Melbourne)
NNM	Nationaal Natuurhistorisch Museum (Leiden) (formerly RMNH)
OSU	Oregon State University (Corvallis)
QM	Queensland Museum (Brisbane)
RUSI	J.L.B. Smith Institute of Ichthyology, Rhodes University (Grahamstown) (presently South African Institute of Aquatic Biodiversity, SAIAB)
SAM	South African Museum (Cape Town)
SMF	Senckenberg Museum (Frankfurt)
SMMP	Science Museum of Minnesota (St. Paul)
TCWC	Texas A&M University, Department of Wildlife and Fisheries (College Station)
UERJ	Universidade do Estado do Rio de Janeiro, Departamento de Biologia (Rio de Janeiro)
USNM	National Museum of Natural History, Smithsonian Institution (Washington, DC)
UP	Universitá di Padova (Padova)
UW	Geological Museum, University of Wyoming (Laramie)
WAM	Western Australian Museum (Perth)
YPM	Peabody Museum of Natural History, Yale University (New Haven)
ZMB	Institut für Systematische Zoologie der Humboldt Universität (Berlin)
ZMH	Zoologisches Institut und Museum, Universität Hamburg (Hamburg)

Anatomical

aac	anterior angular cartilage
ac	angular cartilage
avf	anteroventral foramen
aoc	antorbital cartilage

ax	axial cartilage
b	beta cartilage
bb	basibranchial copula (medial plate)
bh	basihyal
bp	basipterygium
bpl	basal (trabecular) plate
cal	irregular calcification within hyomandibular-Meckelian ligament
cb1	ceratobranchial 1
cb2	ceratobranchial 2
cb5	ceratobranchial 5
cl	clasper
cr	cartilaginous rod
cst	caudal sting
ct syn	cervicothoracic synarcual
da	denticle apex
db	denticle base
df	dorsal fin
dm	dorsal marginal cartilage
dph	dorsal pseudohyoid bar
dr	dorsal radial element
dtf	dorsal tail-fold
e	eye
eb5	epibranchial 5
efr	enlarged first radial element of pelvic fin
epb	epiphysial bar
fica	foramen for internal carotid artery
fpf	frontoparietal fontanelle
ga	gill arches (with asscociated gill rays)
gr	gill rays
ha	hemal arch
hb1	hypobranchial 1
hyo	hyomandibula
ilp	iliac process
is	intermediate segment
isp	ischial process
lpp	lateral prepelvic process
ls	lateral stay of cervicothoracic synarcual
Mc	Meckel's cartilage
mdc	medial crest of cervicothoracic synarcual
mes	mesopterygium
met	metapterygium
mt	median (expanded) tooth and toothrow
n	neurocranium
na	nasal aperture
nc	nasal capsule
ncr	nasal cartilage(s)
ns	neural spine
oc	olfactory canal
of	obturator foramen
on	optic (II) nerve
onc	orbitonasal canal (posterior foramen)
pac	posterior angular cartilage
pec r	pectoral radial
pel r	pelvic radial
paf	parietal fossa
pb1	pharyngobranchial 1
pb5	pharyngobranchial 5
pcf	precerebral fontanelle (also pc or pf)
pib	puboischiadic bar
poc	preorbital canal
pop	postorbital process
pp	(median) prepelvic process
pq	palatoquadrate
pro	propterygium
prp	preorbital process
psc	prespiracular cartilage
re	rostral extremity
ro	rostral cartilage (rostrum)
sc	scapulocoracoid
scp	scapular process
se	sensory canal (junction of prenasal and subrostral canals)
sp	supraorbital process
spo	spiracular opening
ssc	suprascapula
t	teeth
tc	terminal cartilages of clasper
tl syn	thoracolumbar synarcual cartilage
vc	vertebral centrum
vm	ventral marginal cartilage
vph	ventral pseudohyoid bar
vr	ventral radial element
vt	ventral terminal cartilage (ventral covering piece of other authors)
vtf	ventral tail-fold

GEOLOGICAL SETTING

The Green River Formation represents an extinct great lake system (comprising Fossil Lake, Lake Uinta, and Lake Gosiute), that was formed as a result of the orogeny of the Rocky Mountains in what is now southwestern Wyoming, northeastern Utah, and northwestern Colorado (fig. 1). These intermontane lakes were of extremely long duration, especially if compared to modern lake sys-

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Fig. 2. Holotype of †*Asterotrygon maloneyi*, n. gen., n.sp. (FMNH PF 15166), an exceptionally well-preserved adult female in ventral view (ca. 625 mm TL), with an unborn, late-term fetus visible in the pleuroperitoneal region (magnified in fig. 13), indicated by arrowhead. Specimen is from fresh

water F-2 deposits of the early Eocene Fossil Butte Member of the Green River Formation. The teleosts preserved at the top of the slab are of the clupeid †*Knightia eocaena*. Anterior to top.

tems. For example, Lake Uinta is thought to have lasted for approximately 15 million years, ranging from late Paleocene to middle or late Eocene times, which is older than the present-day east African great lakes (considered to be among the oldest extant lakes known). Of the east African great lakes, Lake Tanganyika is thought to have formed between 9 and 12 million years ago, and Lake Malawi may be younger than 2 million years old (Delvaux, 1995). Lake Victoria, the largest of the African great lakes, may have been dry as recently as 15,000 years ago (Johnson et al., 1996), but both lakes Malawi and Victoria contain a much greater ichthyological species diversity compared to the older Lake Tanganyika (Turner, 1999; Turner et al., 2001; see also references in Grande, 1994; Grande and Buchheim, 1994).

Throughout their history, the extinct Green River lakes fluctuated in size as a result of both climactic and tectonic changes (Sullivan, 1980; Grande, 1985, 1989, 2001, presents rough outlines of the lakes throughout their history). Furthermore, each of the three lakes differed according to their duration, size, and sedimentology. The shortest-lived and smallest of the three lakes was Fossil Lake, which lasted for less than 5 million years, all within the North American Wasatchian stage. Within the Green River Formation, the Fossil Butte Member of Fossil Lake (exposed near Kemmerer, Wyoming), of late early Eocene age (approximately 52 million years before present), has yielded the greatest diversity of fossils to date (Grande, 1984, 2001), including all of the stingrays known.

There is a vast amount of evidence indicating that Fossil Lake comprised a freshwater system for the period in which the highly fossiliferous layer of the Fossil Butte Member was deposited. This evidence derives mainly from fossil organisms that have been collected from localities within Fossil Lake: freshwater plants (†*Ceratophyllum*, lily-pads, palms, cattails), insects and insect larvae, freshwater molluscs and crustaceans (e.g., crayfishes), freshwater-inhabiting tetrapods, as well as an extensive freshwater fish fauna (Grande, 1994). Recent work by sedimentologists, however, suggests that for a good part of their history the lakes of the Green River Formation may have been somewhat saline (review and references in Grande, 1994). We follow Grande (1984, 1989, 1994, 2001) and Grande and Buchheim (1994) in viewing the overwhelming amount of paleontological data as indicative of a freshwater system, at least during deposition of the main fossil-containing strata of the Fossil Butte Member. The climate of the lakes is estimated to have been from subtropical to tropical, perhaps similar to the climate of the present-day Gulf Coast and southern Atlantic regions of the United States (Bradley, 1948; Grande, 1984). McGrew and Casilliano (1975) provided thorough accounts of the geological history and depositional environment of Fossil Butte, and McGrew (1975) discussed taphonomic implications of its fossil fishes.

Both fossil stingray taxa have been extracted from two ‘‘groups’’ of localities within the Fossil Butte Member of Fossil Lake, both dated as late early Eocene. These ‘‘groups’’ of localities are designated ‘‘F-1’’ and ‘‘F-2’’ here, following the conventions of Grande (1994) and Grande and Buchheim (1994). Both groups of localities were deposited almost contemporaneously, but differ slightly with respect to their sedimentology and paleoenvironment, and also according to the fossil organisms they contain.

The F-1 localities (also known as the ‘‘18-inch layer’’) refer to a 30–40-cm-thick layer, representing probably only a few hundred years of deposition. The lithofacies contain finely laminated limestones representing the upper part of the Fossil Butte Member, and they are comprised of light-colored, kerogen-rich shales (Grande, 1989). The F-1 localities represent midlake deposits (fig. 1B) with deeper waters than F-2, and some 10 localities have been mined to date, all contemporaneous with each other (Grande and Buchheim, 1994). The F-1 localities are thought to represent a more anoxic paleoenvironment with a slower rate of deposition, compared to the F-2 localities.

The F-2 localities (sometimes referred to as ‘‘split-fish’’) are also contemporaneous with each other and represent near-shore paleoenvironments located primarily on the north- and southeastern shores of Fossil Lake at the time of deposition (fig. 1B). The F-2

Fig. 3. Paratype of †*Asterotrygon maloneyi*, n. gen., n.sp. (AMNH P 11557, ca. 378 mm TL adult female) in ventral view. Specimen is from freshwater F-2 deposits of the early Eocene Fossil Butte Member of the Green River Formation. Arrowheads indicate position of two small stingray specimens on limestone slab (these are inferred to be aborted late-term fetuses of the larger female; see ‘‘Remarks’’ under species account for further comment). Anterior to top. This specimen was generously donated by the late Thomas Maloney.

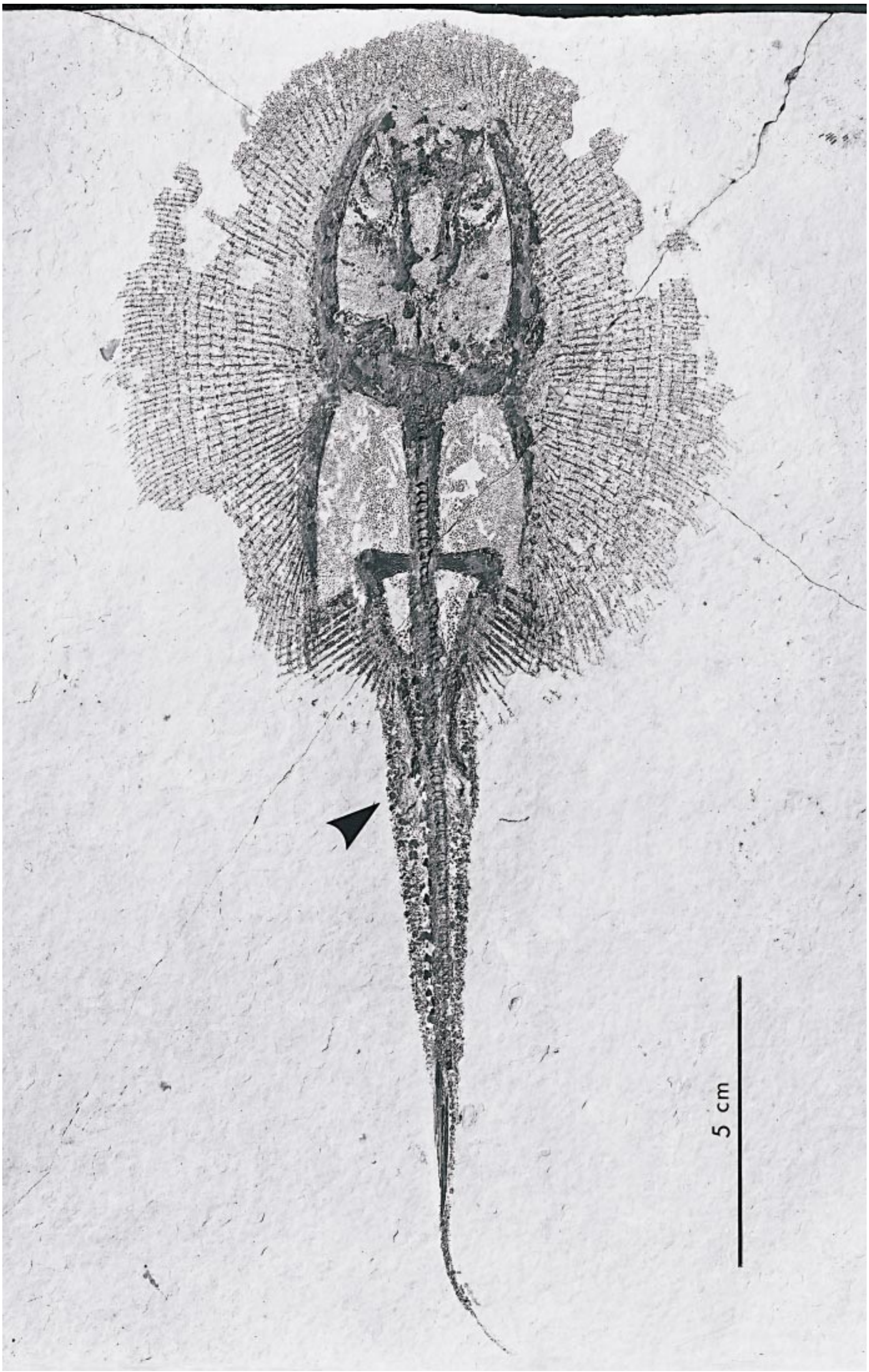

Fig. 4. Paratype of †*Asterotrygon maloneyi*, n.gen., n.sp. (FMNH PF 12989, ca. 238 mm TL adult male) in ventral view. Specimen is from freshwater F-2 deposits of the early Eocene Fossil Butte Member of the Green River Formation. Note elongated and developed claspers overlapping base of tail

horizon is almost 4 m thick, and is the result of greater sedimentation rates compared to the F-1 horizon. These deposits are inferred to represent a few hundred to a few thousand years of deposition (Buchheim, 1994). The F-2 localities are less abundant but are also heavily mined. It is thought that the F-2 lithofacies represented a more oxygen-rich habitat, with a higher dilution of organic materials and higher bioturbation rates. The F-2 deposits are of a slightly older age than those of F-1.

Grande and Buchheim (1994) summarized much data concerning the paleoenvironments of both F-1 and F-2 localities. They presented stratigraphic sections and maps indicating precise locations of mines and compared both F-1 and F-2 horizons in detail from geological and paleontological perspectives.

SYSTEMATIC PALEONTOLOGY

CLASS CHONDRICHTHYES HUXLEY, 1880

SUBCLASS ELASMOBRANCHII BONAPARTE, 1832

DIVISION SQUALEA sensu SHIRAI, 1992

SUPERORDER HYPNOSQUALEA CARVALHO AND MAISEY, 1996

SERIES BATOIDEA sensu COMPAGNO, 1973

ORDER MYLIOBATIFORMES sensu COMPAGNO, 1973

SUBORDER MYLIOBATOIDEI insertae sedis

†***Asterotrygon***, new genus

DIAGNOSIS: The presence of a dorsal fin covered by dermal denticles, just anterior to the caudal stings, is autapomorphic for †*Asterotrygon*, n.gen. The following unique combination of characters further distinguishes †*Asterotrygon*, n.gen. from both fossil and Recent stingray genera: dorsal surface of disc, snout, and tail, as well as base and sides of tail, covered by closely packed denticulation; denticles minute, with posteriorly pointed hooklike crowns and stellate bases, not forming discrete bucklers (also with distinct series of enlarged spines forming rows over tail and part of dorsal disc surface); individual vertebral centra extending to distal tip of tail, posterior to caudal stings (instead of an unsegmented cartilaginous or notochordal rod extending to distal tip of tail, posterior to caudal stings); disc and tail length almost equal; tail stout at base, tapering distally but not continuing caudally as a slender ‘‘whip’’; disc circular to oval in outline (disc length and width almost equal, except in FMNH 14567).

REMARKS: Fossil stingrays that are morphologically similar to †*Asterotrygon*, n.gen. and known from more-or-less complete skeletons include the monotypic †*Heliobatis* Marsh, 1877, occurring in the same localities and horizon as †*Asterotrygon*, n.gen., and †‘‘*Dasyatis*’’ *muricata* and †‘‘*Dasyatis*’’ *dezignoi*, both from the Eocene (Lutetian) of Monte Bolca, Italy (Jaekel, 1894). The new genus differs from all three taxa by the presence of a conspicuous dorsal fin (located just anterior to caudal stings, absent in all three taxa), a more rounded and smaller disc (disc trapezoidal or rhomboidal in the Monte Bolca taxa and many specimens of †*Heliobatis*), a shorter and much stouter tail at base (in all three taxa tail is slender at base, not tapering greatly, and is whiplike in †‘‘*Dasyatis*’’ *muricata*), and the presence of heavy denticulation over dorsal surface of disc, dorsal fin, snout, and over almost entire tail region (sparse denticles, if present, occur as enlarged spines in generally a single row over middisc and tail regions in all three taxa). †*Asterotrygon*, n.gen. further differs from †‘‘*Dasyatis*’’ *muricata* in having a much shorter tail (less than or equal to disc length in †*Asterotrygon*, n.gen., much greater than disc length in †‘‘*D.*’’ *muricata*; Jaekel, 1894: 143, fig. 32).

†*Asterotrygon*, n.gen. can be distinguished from the Recent genera *Potamotrygon* Garman, 1877, *Paratrygon* Duméril, 1852, and *Plesiotrygon* Rosa, Castello, and Thorson, 1987 (Potamotrygonidae) by the absence of the median prepelvic process. The combina-

←

region (axial cartilage dark, impressions of terminal cartilages are indicated by arrowhead). Some sections of pectoral disc are missing. Anterior to top.

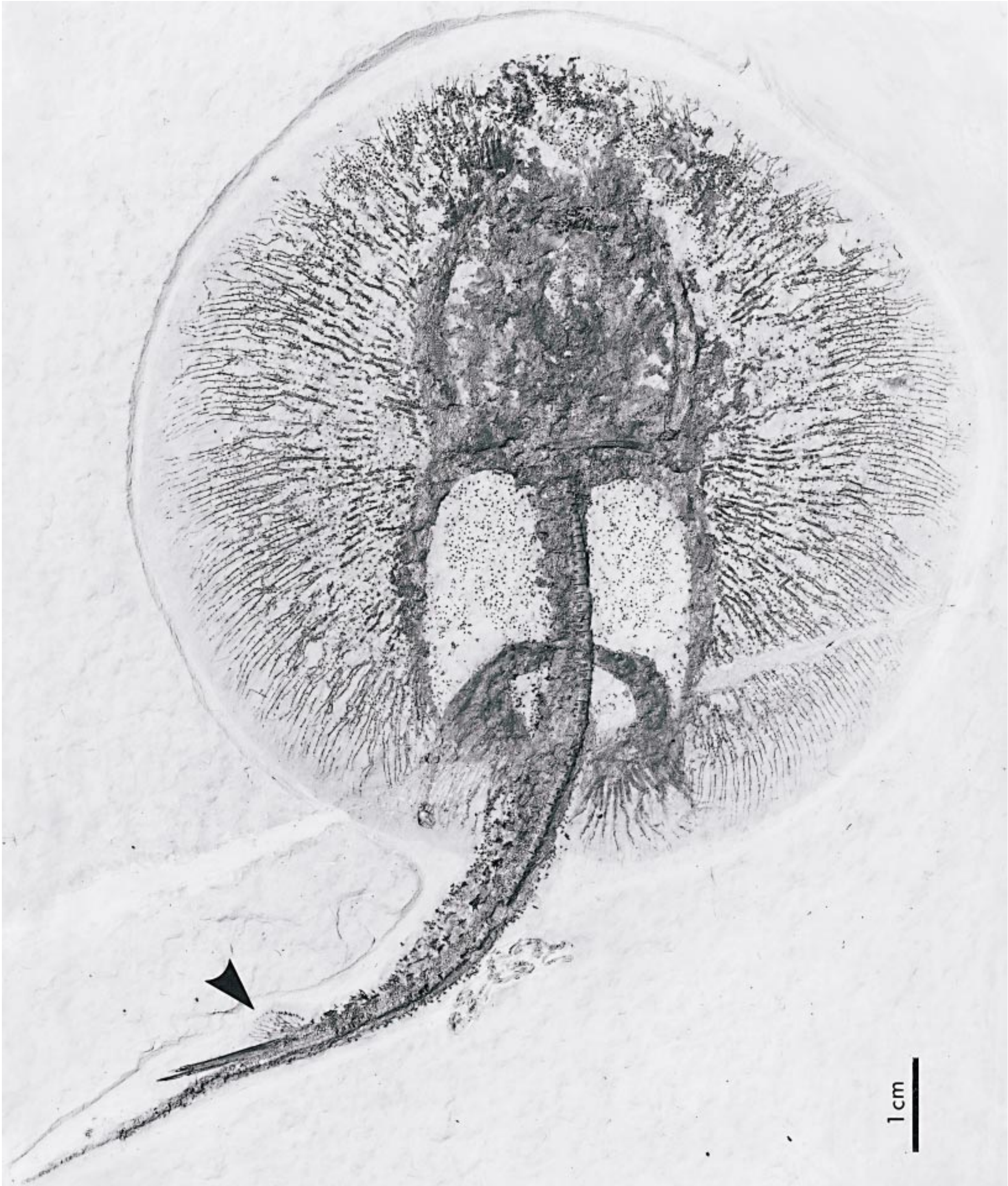

Fig. 5. Relatively complete paratype of †*Asterotrygon maloneyi*, n.gen., n.sp. (FMNH PF 14069, ca. 149 mm TL, presumably an immature female) in ventral view. Specimen is from freshwater F-2 deposits of the early Eocene Fossil Butte Member of the Green River Formation. Arrowhead depicts well-exposed dorsal fin at origin of caudal stings. Anterior to top.

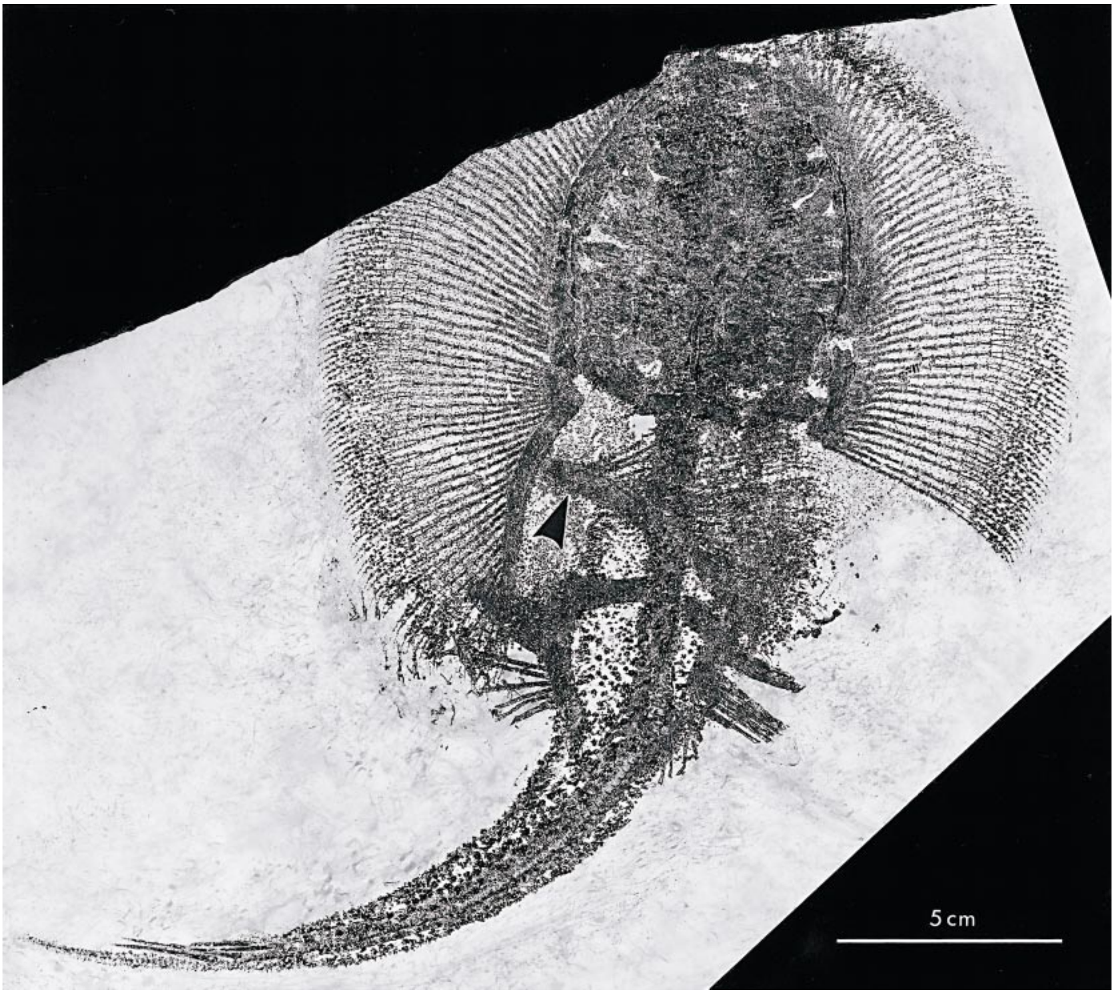

Fig. 6. †*Asterotrygon maloneyi*, n.gen., n.sp. (FMNH PF 12914, ca. 205 mm TL, presumably adult female) in dorsal view. Specimen is from freshwater F-1 deposits of the early Eocene Fossil Butte Member of the Green River Formation. Anterior left side of disc is missing, along with slab; arrowhead indicates posterior right portion of pectoral radials and metapterygium that have been disarticulated and overlap disc. Anterior to top.

tion of external features used to separate the new genus from fossil stingrays also separates it from all Recent myliobatiform genera as well. From potamotrygonids, *Dasyatis* Rafinesque, 1810, *Pastinachus* Rüppell, 1828, *Himantura* Müller and Henle, 1837, *Taeniura* Müller and Henle, 1837, *Pteroplatytrygon* Fowler, 1910, and *Urogymnus* Müller and Henle, 1837 (Dasyatidae), †*Asterotrygon*, n.gen. is distinguished by the presence of the dorsal fin (absent in all above genera), presence of individual vertebrae extending beyond caudal sting to posterior tip of tail (implying the absence of the cartilaginous notochordal rod at level of caudal stings, present in the above genera), circular to slightly oval disc shape (as opposed to a more trapezoidal or rhomboidal disc in most species, except *Urogymnus*), and a conspicuously thicker tail at base that is not whiplike (large specimens of *Potamotrygon* may have a thick, not whiplike, tail as well). The questionable dasyatid *Urolophoides giganteus* Lindberg, 1930 (*Urolophoides* Lindberg, 1930 is most likely a junior synonym of *Dasyatis* Rafinesque, 1810) has a short, stout tail, but lacks the dorsal fin and intense shagreen, as well as having a strongly rhomboidal disc (Lindberg and Legeza, 1959; Nishida and Nakaya, 1990). *Urogymnus* is further distinguished from †*Asterotrygon*, n.gen. by its lack of stings and proportionally shorter distance between eyes and anterior tip of disc (Compagno and Roberts, 1984; Last and Stevens, 1994).

†*Asterotrygon*, n.gen. differs from *Plesiobatis* Nishida, 1990 (Plesiobatidae) in its moderate snout length and anterior disc contour (snout very long and anterior disc pointed in *Plesiobatis*), presence of dorsal fin (absent in *Plesiobatis*), and greater proximity of eyes to anterior margin of disc (eyes very reduced and located far from snout tip in *Plesiobatis*; Last and Stevens, 1994). †*Asterotrygon*, n.gen. is distinct from urotrygonids (*Urobatis* Garman, 1913 and *Urotrygon* Gill, 1863) and urolophids (*Urolophus* Müller and Henle, 1837 and *Trygonoptera* Müller and Henle, 1841) by having a dorsal fin covered by denticles (dorsal fin completely absent in the former two genera and present in some species of the latter two genera, but never coated with denticles), intense covering of dermal denticles over dorsal surface (dorsal disc and tail surface generally with sparse denticulation in the former two genera, and mostly naked in the latter two genera), and lack of elongated caudal fin (invariably present in all four genera, with conspicuous dorsal and ventral lobes that are internally supported by radial cartilages).

†*Asterotrygon*, n.gen. is easily separated from *Hexatrygon* Heemstra and Smith, 1980 (Hexatrygonidae) by the presence of dorsal fin (absent in *Hexatrygon*) and by snout and disc shape (snout extremely elongated, triangular, and somewhat demarked from disc in *Hexatrygon*). From butterfly rays (Gymnuridae, *Gymnura* Kuhl, 1823, and *Aetoplatea* Valenciennes, 1841), †*Asterotrygon*, n.gen. is distinguished by disc shape (much broader than long in gymnurids, but disc width and length are about equal in †*Asterotrygon*, n.gen.), stout tail that is about equal to disc length (tail slender and short in gymnurids), and covering of dermal denticles (disc mostly naked in gymnurids). Eagle, cownose, and manta rays (Myliobatidae), including †*Promyliobatis gazolae* from Monte Bolca, are easily separated from †*Asterotrygon*, n.gen. by disc shape (invariably broader than long in these groups), head anterior to and separated from disc (pectoral disc projects anterior to head in †*Asterotrygon*, n.gen.), less intense dorsal denticulation (usually naked dorsal surface in pelagic stingrays), length of tail (usually long and whiplike in myliobatids, but shorter and stout in †*Asterotrygon*, n.gen.), naked dorsal fin (dorsal fin covered in denticles in †*Asterotrygon*, n.gen.), presence of cartilaginous rod extending posteriorly from region of caudal stings instead of individual vertebrae as in †*Asterotrygon*, n.gen., presence of cephalic extensions (''cephalic fins'') in *Mobula* Rafinesque, 1810 and *Manta* Bancroft, 1828 (absent in †*Asterotrygon*, n.gen.), and by differences in dentition (teeth numerous, small, and closely packed, with subtriangular cusps in †*Asterotrygon*, n.gen., as in most nonmyliobatid stingrays; teeth in all myliobatids except manta rays are arranged in broad toothplates). Anatomical features that further distinguish †*Asterotrygon*, n.gen. from some or all of the above genera are discussed in the skeletal description below.

Many Recent genera assigned to the Dasyatidae and Urolophidae are based on external characters not readily available in fossils (e.g., lack of tail-folds on both upper and lower surfaces of tail in *Himantura*; lack of dorsal tail-fold, but tall and long ventral tail-fold extending to distal tip of tail in *Taeniura*, etc.). Skeletal characters unique to most nonmyliobatid genera have not been found, and the skeleton is generally very conservative in both Recent and fossil nonmyliobatid genera. The definition given here to the new genus †*Asterotrygon*, n.gen. is nevertheless consistent with generic diagnoses of Recent stingrays, allowing for a quick and straightforward identification of all †*Asterotrygon*, n.gen. specimens examined. No other fossil or Recent stingray genus has a dorsal fin covered with hooklike denticles and the unique combination of individual vertebrae extending posteriorly to distal tip of tail, closely packed denticulation over disc, snout and tail, and stout tail at base.

ETYMOLOGY: The new generic name is de-

Fig. 7. †*Asterotrygon maloneyi*, n.gen., n.sp. (FMNH PF 14567, ca. 469 mm TL adult female), in dorsal view. Specimen is from freshwater F-1 deposits of the early Eocene Fossil Butte Member of the Green River Formation. Some left pectoral radials and anteriormost tip of disc are missing. Anterior to top.

Fig. 8. †*Asterotrygon maloneyi*, n.gen., n.sp. (FMNH PF 14098, ca. 344 mm TL adult female) in dorsal view. Specimen is from freshwater F-2 deposits of the early Eocene Fossil Butte Member of the Green River Formation (currently on exhibit in the FMNH). Some pectoral radials and anterior region of neurocranium missing, gill arches disarticulated. Anterior to top.

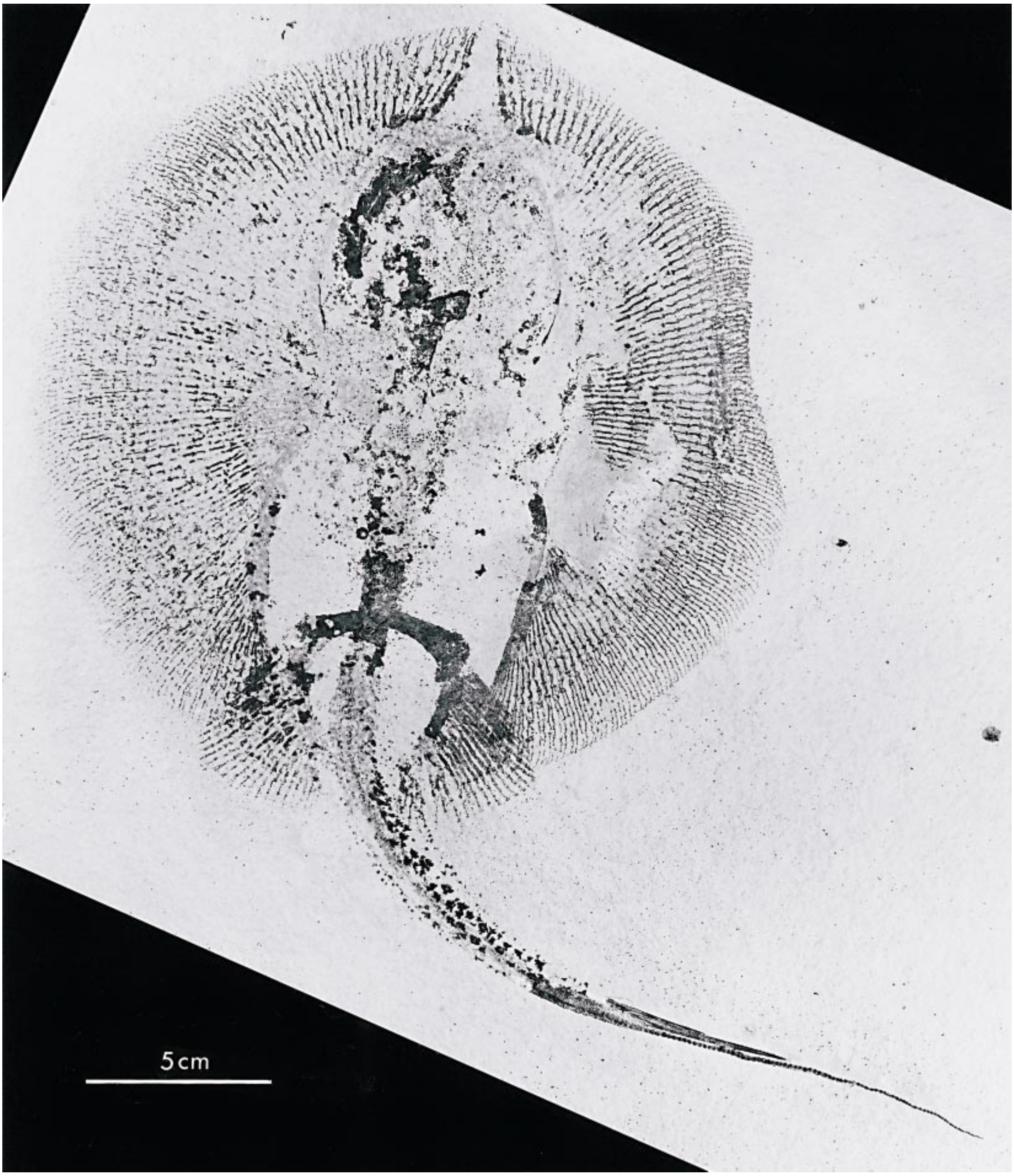

Fig. 9. †*Asterotrygon maloneyi*, n.gen., n.sp. (FMNH PF 14097, ca. 402 mm TL adult female) in dorsal view. Specimen is from freshwater F-2 deposits of the early Eocene Fossil Butte Member of the Green River Formation. Portions of neurocranium, jaws, visceral arches, pectoral basals and radials, and vertebrae are missing. Anterior to top.

TABLE 2

Measurements and Counts Conducted on Specimens of †*Asterotrygon maloneyi*, n.gen., n.sp.

Values are expressed as mm/percentage of disc width, except for total length (TL) and disc length (DL), which are shown in mm. See Measurements and Terminology for abbreviations of parameters. All specimens are female except FMNH PF 12989.

	FMNH 15166 holotype	AMNH 11557 paratype	FMNH 12989 paratype	FMNH 14069 paratype	FMNH 12914	FMNH 14567	FMNH 12990	FMNH 14097	FMNH 14098
TL	650.0	378.3	238.3	149.0	205.2	469.0	243.3	401.8	343.8
DL	334.0	190.5	119.9	86.2	173.6[a]	226.3	130.0[a]	206.8	200.1
DW	328.1	190.1	115.0	89.2	173.6	242.4	135.0[a]	202.1	199.6
TAL	352/107.3	187.8/98.8	118.4/103.0	62.8/70.4	160.7/92.6	242.7/100.1	113.3/83.9	195.0/96.5	143.7/72.0
TAW	36.1/11.0	34.4/18.1	17.5/15.2	7.5/8.4	31.6/18.2	21.9/9.0	16.5/12.2	19.5/9.6	17.2/8.6
POL	81.3/24.8	35.4/18.6	21.9/19.0	17.8/20.0	36.5[a]/21.0	—	—	—	—
MSC	102.2/31.1	62.0/32.6	34.9/30.3	22.3/25.0	58.6/33.8	—	—	—	73.9[a]/37.0
SCW	83.1/25.3	43.1/22.7	32.0/27.8	21.0/23.5	57.9/33.4	62.7/25.9	40.0[a]/29.6	47.0/23.3	47.0/23.5
PGW	70.1/21.4	40.6/21.4	26.1/22.7	16.8/18.8	41.0/23.6	52.2/21.5	32.0/23.7	44.4/22.0	44.4[a]/22.2
STL	56.4/17.2	45.9/24.1	21.4/18.6	12.7/14.2	28.8/16.6	42.6/17.6	27.7/20.5	46.0/22.8	41.1/20.6
PGT	273.2/83.3	213.6/112.4	143.9/125.1	86.6/97.1	187.7/108.1	247.9/102.3	126.1[a]/93.4	241.4/119.4	176.8/88.6
CL	—	—	30.1/26.2	—	—	—	—	—	—
NCL	78.1/23.8	—	33.2/28.9	24.3[a]/27.2	43.5[a]/25.1	67.3/27.8	—	—	—
NCW	49.2/15.0	—	21.0/18.3	16.4[a]/18.4	25.3/14.6	43.0/17.7	—	—	—
PRO	44	43	43[a]	28[a]	45	45	—	46[a]	—
MES	15	8	7[a]	13[a]	9	14	12[a]	—	—
MET	31	26	27[a]	30[a]	23[a]	33	27[a]	32[a]	34[a]
TPR	90	77	77[a]	71[a]	77	92	—	—	—
PVR	15[a]	15	17	19	—	22	16[a]	22	—
VSP	19	—	19	21	14[a]	21	—	—	—
VPS	79	69	69[a]	66	73	76[a]	63[a]	81	66[a]
VST	71[a]	47[a]	37[a]	30[a]	35[a]	56[a]	—	86	49
TV	169[a]	—	105[a]	117[a]	122[a]	153[a]	—	—	—

[a] Approximate value only due to preservational imperfection. In FMNH PF 14069, tail width (TAW) actually represents tail height because tail is partially exposed on its side.

rived from the Greek *asteros*, meaning "star", and *trygon*, the Greek word for stingray, in reference to the star-shaped bases of the dermal denticles scattered over dorsal disc and tail regions (see description of denticles below; also fig. 25). Gender feminine.

TYPE-SPECIES: †*Asterotrygon maloneyi*, new species.

INCLUDED SPECIES: Presently considered to be monotypic.

†*Asterotrygon maloneyi*, new species

Figures 2–13, 18–26a, c, d, 27; tables 2, 3

"undescribed ray": Grande, 1980, 1984 (pp. 23, 25, 28–30; figs. II.6a, II.6b, II.7a, II.7b; partial description).

"undescribed [genus]": Grande, 1989 (p. 25; brief mention).

"undescribed species and genus": Grande and Buchheim, 1994 (pp. 42–43, 52–53; fig. 9a; photograph, brief mention).

†*Heliobatis*: Maisey, 1996 (pp. 108, 112–114, pls. 42, 43; brief account) (not of Marsh, 1877; misidentification).

"female stingray": Grande, 1998 (p. 69; photograph of AMNH P 11557 only); Grande, 2002 (p. 16; photograph of FMNH PF 15166 only).

"undescribed genus and species": Grande, 2001 (pp. 6–8, fig. 3b; table 1; brief mention).

DIAGNOSIS: As for genus (see above).

MATERIALS: All specimens of the new genus and species of stingray are from the late early Eocene Fossil Butte Member of the Green River Formation. Specimens are either from the nearshore deposits (F-2) or from the midlake deposits (F-1). The quarries from where specimens were excavated are given here when available (refer to fig. 1), along

TABLE 3

Measurements and Counts Conducted on Juvenile Specimens of †*Asterotrygon maloneyi*, n.gen., n.sp.

Values are expressed as mm/percentage of disc width, except for total length (TL) and disc length (DL), which are shown in mm. See Measurements and Terminology for abbreviations of parameters. All specimens are female.

	FMNH 15180	NHM 61244	SMMP 83.25
TL	106.2	86.5	79.7
DL	54.4	43.0	41.7
DW	54.3	42.1	38.8
TAL	65.3/120.3	43.5/103.3	38.0/97.9
TAW	4.2/7.7	3.2/7.6	2.0/5.2
POL	11.4/21.0	9.2/21.9	8.1/20.9
MSC	18.1/33.3	12.3/29.2	14.1/36.3
SCW	14.2/26.2	12.0/28.5	11.7/30.2
PGW	13.2[a]/24.3	9.3/22.1	8.1/20.9
STL	9.5/17.5	6.8/16.2	5.5[a]/14.2
PGT	49.1/90.4	52.2/124.0	43.6/112.4
NCL	14.2[a]/26.2	12.8[a]/30.4	15.0[a]/38.7
NCW	9.1/16.8	9.8[a]/23.3	8.7[a]/22.4
PRO	39	43[a]	41[a]
MES	9	8[a]	8
MET	22	31[a]	22[a]
TPR	60	82[a]	71[a]
PVR	18	18	13
VSP	19	—	—
VPS	75	56	—
VST	53	23	—
TV	147	—	—

[a] Approximate value only due to preservational imperfection. In FMNH PF 15180, pelvic girdle width (PGW) is inferred as only one-half of girdle is present (value was doubled).

with information concerning how each specimen is exposed. **Holotype:** FMNH PF 15166, a well-preserved adult female (ca. 625 mm TL), in ventral view, with an unborn late-term fetus in the abdominal region (from an F-2 locality) (fig. 2); this slab has been previously figured in Grande and Buchheim (1994: 43, fig. 9a) and Grande (2001: 10, fig. 3b). **Paratypes:** AMNH P 11557, adult female (378 mm TL), preserved along with two small specimens (aborted late-term fetuses) on limestone slab, in ventral view (F-2) (fig. 3); FMNH PF 12989, adult male (238 mm TL), in ventral view exposed, from the Tynsky quarry (F-2; collected by L. Grande, 1984) (fig. 4); FMNH PF 14069, female (149 mm TL), presumably immature, in ventral view, from the Hebdon quarry (F-2) (fig. 5). **Additional specimens:** FMNH PF 12914, female (205 mm TL), in dorsal view, from Tynsky quarry (F-1) (fig. 6); FMNH PF 12990, adult (?) female (243 mm TL), in ventral view, from the Tynsky quarry (F-2) (fig. 10A); FMNH PF 14097, adult female, preserved in part and counterpart (402 mm TL), from Tynsky quarry (F-2) (fig. 9); FMNH PF 14098, adult female (344 mm TL), in ventral view (F-2; currently on exhibit in the FMNH) (fig. 8); FMNH PF 14567, adult female (469 mm TL), in dorsal view (F-1) (fig. 7); FMNH PF 15180 (106 mm TL), juvenile female (F-2), in ventral view (fig. 12); FMNH PF 15181 (ca. 122 mm TL, 14 mm in height; specimen is tail only), exposed in lateral view (F-2) (fig. 24F); NHM P 61244, juvenile or neonate (86 mm TL), apparently female, probably exposed in dorsal view (F-2) (fig. 11A); SMMP 83.25, neonate or aborted fetus (80 mm TL), sex difficult to determine, counterpart of specimen near tail region of paratype AMNH P 11557 (F-2) (fig. 11D); USNM 2028, adult female (about 450 mm TL), in dorsal view (F-2) (fig. 10B). **Tentatively identified material:** AMNH P 858, 2 small specimens, comparable to male paratype (FMNH PF 12989) in size, probably exposed in ventral view, with only anterior and lateral disc preserved (Twin Creek, probably F-1).

STRATIGRAPHIC HORIZON: Fossil Butte Member of the Green River Formation, Ypresian stage (corresponding to the North American Wasatchian stage), late early Eocene epoch (approximately 52 million years before present).

REMARKS: The first mention of the new stingray taxon described here from the Green River Formation is in Grande (1980, 1984). Grande (1980, 1984: 23) provided a brief characterization of †*Asterotrygon*, n.gen., noting that ‘‘the specimens in figures II.6 and II.7 have thick tails covered with a dense series of dermal denticles (placoid scales) bearing curved hooks . . . . These may represent a new species . . . ’’. (Note that Grande's figure II.7c depicts the holotype of †*Heliobatis radians* Marsh, 1877, and not a specimen of †*Asterotrygon maloneyi*, n.sp. as implied). It is difficult to precisely determine the number of stingray specimens extracted from the

Fig. 10. Preadult or small adult specimens of †*Asterotrygon maloneyi*, n.gen., n.sp. Both specimens are from freshwater F-2 deposits of the early Eocene Fossil Butte Member of the Green River Formation. **A.** FMNH PF 12990, approximately 243 mm TL female, in ventral view. Note that anterior, central and much of lateral disc region, and distal tip of tail are missing. **B.** USNM 2028, approximately 450 mm TL female, dorsally exposed. Visceral arches, pectoral basals, and pelvic girdle are dislocated in this specimen. Anterior to top.

Fig. 10. Continued.

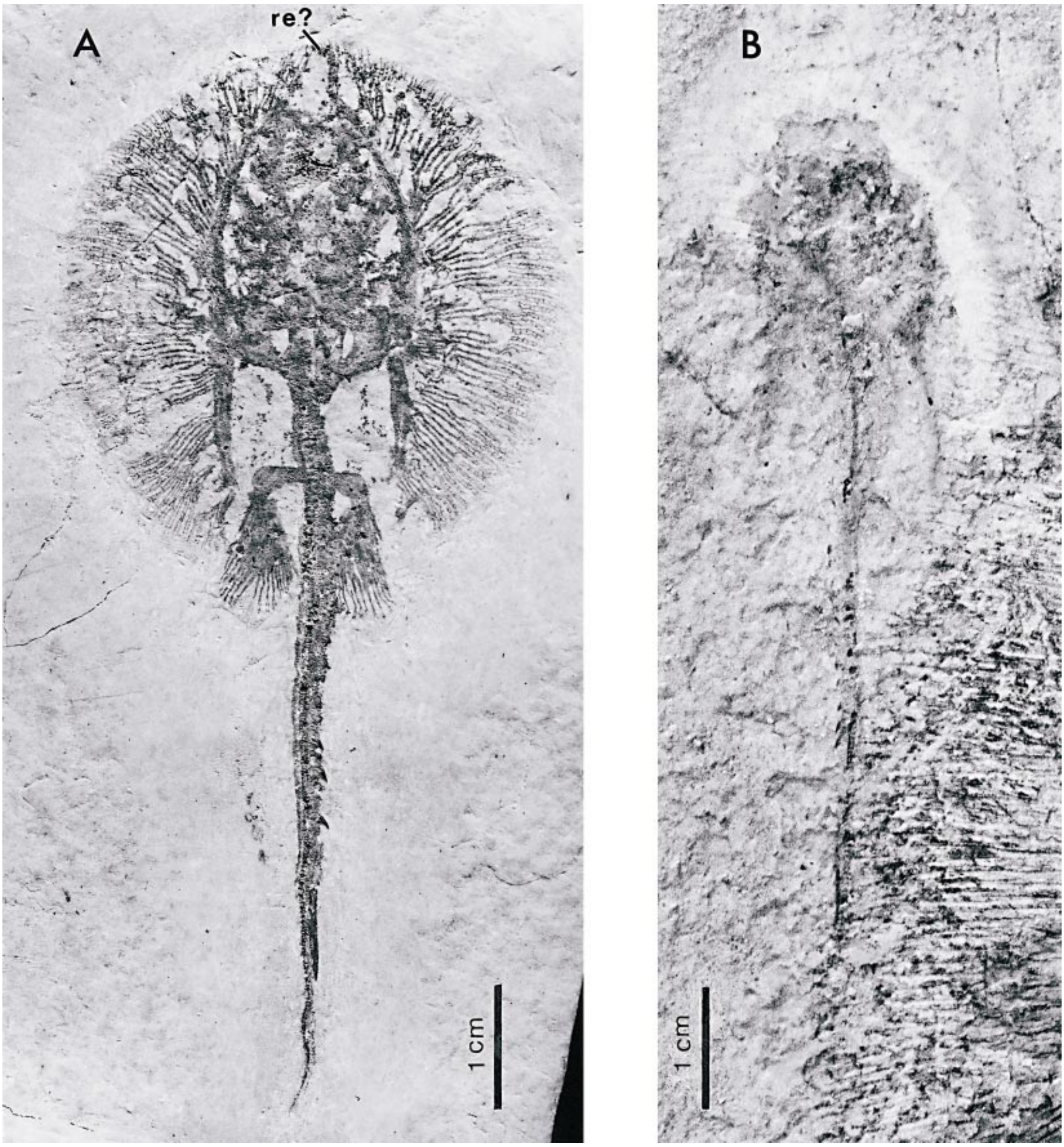

Fig. 11. Juveniles (and/or neonates) and fetuses of †*Asterotrygon maloneyi*, n.gen., n.sp. All specimens are from freshwater F-2 deposits of the early Eocene Fossil Butte Member of the Green River Formation. **A.** NHM P 61244, 86 mm TL juvenile, sex not determined, appears to be dorsally exposed. **B.** Late-term fetus preserved on left side of slab (adjacent to right side of disc) of paratype AMNH P 11557 (shown in fig. 3); much of the specimen is not preserved, such as pectoral and pelvic radials and pelvic girdle; radial elements of pectoral disc of AMNH P 11557 visible on right side. **C.** Late-term fetus (some 80 mm TL, sex not determined) preserved on the right side of slab (to the left of posterior tail region) of paratype AMNH P 11557 (see fig. 3); note that some features that are missing in this fossil are present in counterpart (D) to the right. **D.** SMMP 83.25, late-term fetus (counterpart of C). Anterior to top.

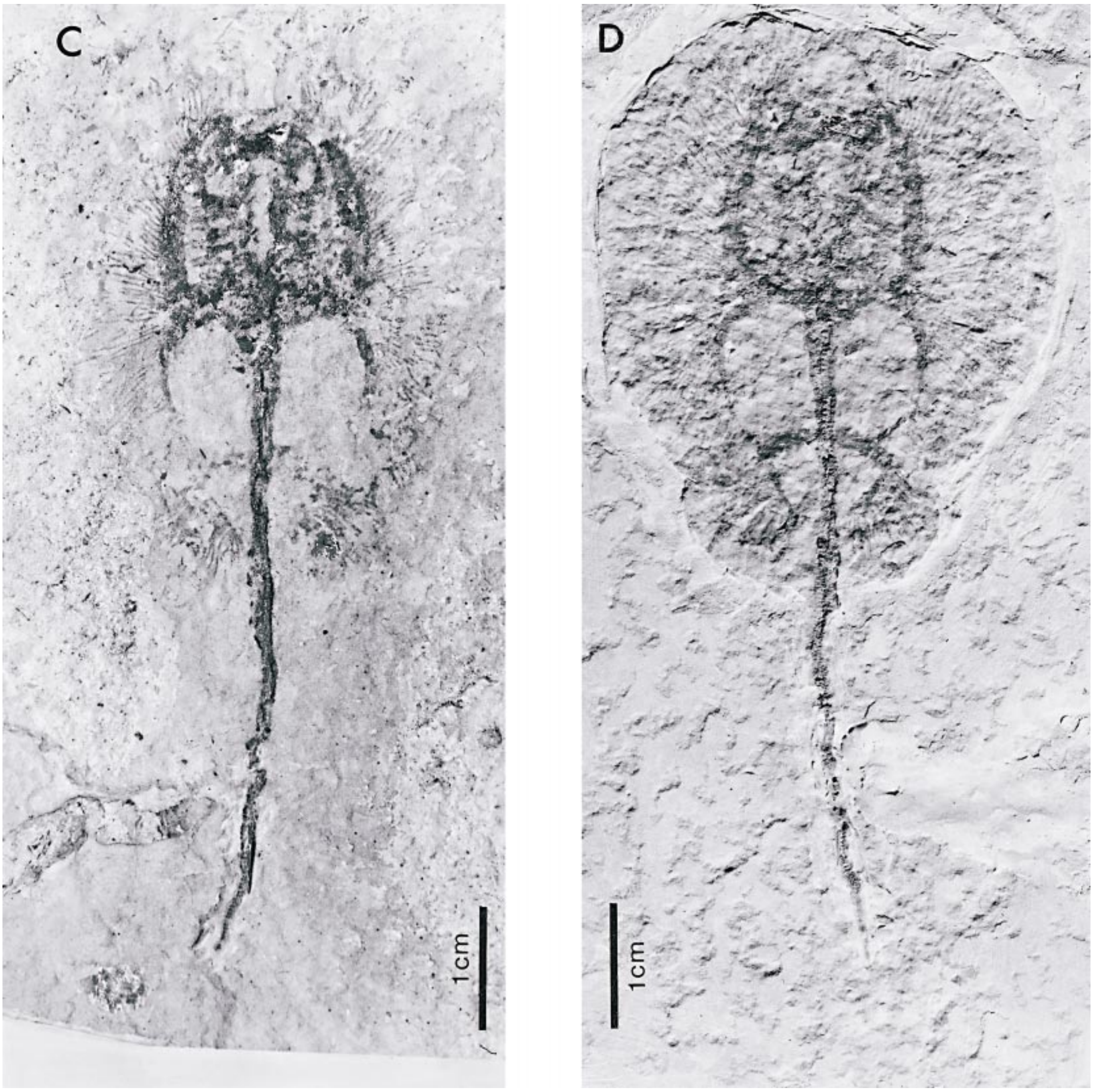

Fig. 11. Continued.

Green River Formation, but of the approximately 150 specimens of stingrays that we have seen in a period of some 20 years, only 15 are of †*Asterotrygon*, n.gen. (in addition to two more specimens that are only tentatively identified—AMNH P 858).

Presently, we describe only one species in the new genus †*Asterotrygon*, n.gen. However, the morphological variation observed among our specimens may indicate the presence of more than one species. †*Asterotrygon*, n.gen. specimens exhibit variation in spination that is concordant with that observed among species of living stingray genera, for example, *Dasyatis*, *Himantura*, *Urotrygon*, and *Potamotrygon*. Some specimens, including the type series, have a prominent covering of denticles over all or most of the dorsal disc region (e.g., figs. 3–6), while others appear to lack intense denticulation over outer disc margins (e.g., figs. 2, 7–9; AMNH P 858). This does not appear to be due to sexual dimorphism, as FMNH PF 12989 is the only definite male specimen examined.

Also, FMNH PF 12990 (fig. 10A) appears to have a somewhat more rounded, urolophid-like caudal fin, slightly distinct from the tail-folds present in all other specimens. However, this probably represents an elongated dorsal caudal tail-fold supported internally by radials as in *Potamotrygon* (fig. 37D), and not a discrete and conspicuously shaped caudal fin (see description of appendicular skeleton below). The distal portion of the tail is missing in this specimen, so we cannot be certain of its original condition. Consequently, we think that the Green River stingray fauna may have been more diverse than presently reported, but we deem it premature to erect further taxa until more material is available and details concerning the arrangement of denticles can be more fully understood. As pointed out by Grande (2001), underestimating the species diversity in the extinct Green River Lakes is mostly unavoidable, as important diagnostic features may not be preserved in the fossils (such as color patterns, crucial in identifying many species of living stingrays). A comparison between the fish assemblages of the extinct Green River Lakes and the modern eastern African Rift lakes reveals a much greater similarity in numbers of families than in numbers of species (ranging from 10 families in Lake Gosiute to 14 in Fossil Lake, compared to between 9 and 14 families in the African Rift lakes). This may be an indication that the species diversity of many different groups of fishes in the Green River Formation was originally greater than our current estimates based on their fossil remains (Grande, 2001).

A dorsal fin occurs in the following stingray groups, besides †*Asterotrygon*, n.gen.: Myliobatidae, some gymnurids (*Aetoplatea*), and in selected species of *Trygonoptera* (in three of the six species) and *Urolophus* (in about one-third of the species; 15 species are recognized as valid by Last and Stevens, 1994; Compagno, 1999). The occurrence of the dorsal fin in 2 of the approximately 12 species of gymnurids, and only in certain species of *Trygonoptera* and *Urolophus*, may indicate that the mere presence of the fin is not a reliable indicator of generic status, even though it is the primary character for distinguishing between *Aetoplatea* and *Gymnura*. However, the dorsal fin in †*Asterotrygon*, n.gen. occurs in conjunction with other characters indicative of its generic separation (e.g., covering of minute denticles over most of disc and tail, presence of individual vertebrae extending beyond caudal stings to posterior tail tip). Furthermore, the dorsal fin in †*Asterotrygon*, n.gen. is unique among stingrays in being thoroughly covered by denticles.

The onset of sexual maturity for males must occur at a relatively small size, just before or around 120 mm in disc length, as the male paratype has both claspers well preserved and calcified (FMNH PF 12989, ca. 240 mm in TL, 120 mm in DL, 115 mm in DW; figs. 3, 23A). The size at which females become sexually mature is more difficult to discern in fossils, as no reproductive organs are present. However, we can infer based on extant stingrays that female and male sizes at sexual maturity were probably similar to each other in †*Asterotrygon*, n.gen. We know with certainty that the holotype (measuring 625 mm in TL, 338 mm in DW) is an adult female because it contains an unborn fetal specimen (figs. 2, 13), and that one female paratype (fig. 3) is in all likelihood sexually mature as well (see following paragraph), as it measures 378 mm in TL and 190 mm in DL and DW; females probably became sexually mature at a much smaller size.

The two small specimens preserved alongside one of the paratypes (AMNH P 11557; fig. 3) are considered to be its aborted late-term fetuses (which we believe were probably very close to parturition) on the basis of the following evidence: they are unquestionably identified as †*Asterotrygon maloneyi*, n. sp.; their size in relation to their mother conforms very closely to maternal/late-term fetal proportions in Recent species of stingrays; stingrays are a relatively rare component of the Fossil Butte fish assemblage; and the probability of having two small fetuses preserved alongside the mother after birth is unlikely given that there is generally no rearing of the young or other forms of parental care in chondrichthyans (Breder and Rosen, 1966; Wourms, 1977), even though neonates of at least two species of *Potamotrygon* have been observed to remain on their mother's disc for a period of a few days after birth (Achenbach and Achenbach, 1976; Araújo, 1998). The fetuses contain small, scattered denticles over the dorsal surface of the disc, albeit not as intensely as seen in the type series, but this to be expected as fetuses generally have less intense denticulation compared to juveniles or adults. †*Heliobatis* specimens lack denticulation other than over the midline area close to the tail. Preservation of the two fetuses is not as complete as in the other specimens, but again this is not unusual given that their skeletons are less calcified. The tail region of these specimens is poorly preserved, as are their small dorsal fins (NHM 61244, a small neonate, nevertheless has a small dorsal fin remnant clearly preserved). Previous accounts of these specimens (AMNH P 11557) reported three fetuses on the slab alongside the adult female (Grande 1980, 1984), but one of these, situated close to the anterior disc margin, is actually a poorly preserved teleost (L. Meeker, personal obs.).

We have observed extant gravid female stingrays of different genera and species aborting fetuses upon capture. In particular, *Urobatis jamaicensis* from the Caribbean Sea (off Belize) agrees very closely in maternal/fetal (late-term) proportions to †*Asterotrygon*, n.gen. as inferred from AMNH P 11557. The relative rarity of †*Asterotrygon*, n.gen. specimens compared to †*Heliobatis*, coupled with the extreme rarity of fossilized neonates or small juveniles of stingrays in general, leads to the conclusion that paratype AMNH P 11557, an adult female, is maternally related to the two small specimens lying adjacently on the same slab.

The late-term embryo inside the holotype of †*Asterotrygon*, n.gen. (figs. 2, 13) appears to be situated in the left uterus (the specimen is preserved in ventral view). This does not preclude the possibility that a fetal specimen may have originally been present in the right uterus as well, which may have been aborted prior to death. Many extant stingrays have only the left oviduct functional (such as dasyatids; Bigelow and Schroeder, 1953; Snelson et al., 1988, 1989; H.F. Mollett and F.F. Snelson, Jr., personal commun.), while others have both uteri functional and sometimes synchronous (potamotrygonids, *Urobatis*, *Gymnura*; Babel, 1967; Thorson et al., 1983b; Carvalho, personal obs.), frequently with uneven development (such as having only one functional ovary, or one of the two ovaries or uteri more developed than the other; Bigelow and Schroeder, 1953; Capapé et al., 1992; Henningsen, 1996; W.D. Smith and N.K. Dulvy, personal commun.). The systematic relevance of reproductive tract symmetry must await the availability of more data for certain stingray genera (e.g., some pelagic stingrays, *Hexatrygon*, *Plesiobatis*). However, the presence of symmetrical reproductive tracts is probably the more general batoid condition (guitarfishes, electric rays, and pristids have both reproductive tracts functional, as do pristiophorids), and asymmetry may have evolved as a stingray synapomorphy (in this scenario, it would be reversed at least in potamotrygonids, gymnurids, and *Urobatis*). If this proves to be the case (i.e., asymmetry is derived for stingrays), then it is reasonable to assume that †*Asterotrygon*, n.gen. was asymmetrical as well, as †*Asterotrygon*, n.gen. is resolved as a basal stingray (see phylogenetic analysis below; however, this still depends on the condition in other basal stingrays such as *Hexatrygon* and *Plesiobatis*).

ETYMOLOGY: The specific epithet, *maloneyi*, is a patronym given in recognition of the generous donator of the largest paratype (AMNH P 11557; fig. 3), Thomas Maloney.

ANATOMICAL DESCRIPTION

The following anatomical description of †*Asterotrygon* roughly applies to †*Heliobatis* as well. Apart from diagnostic characters that distinguish both taxa, their skeleton is very generalized and similar, not differing greatly from the skeleton of extant nonpelagic stingrays in most details that can be directly compared. Extant dasyatid stingrays are also morphologically similar in many respects (Miyake, 1988; Nishida, 1990), a condition that has obscured their proper definition, which presently relies to a large degree on external characters. The fossil specimens studied here are two-dimensionally preserved in limestone slabs that are not readily acid-prepared and do not lend themselves to other matrix-removal methods (outside of manual work with needles). Therefore, much anatomical detail that might be of use in defining groups is not available (such as the

Fig. 12. Juvenile specimen of †*Asterotrygon maloneyi*, n.gen., n.sp. (FMNH PF 15180, ca. 106 mm TL female, ventrally exposed). Specimen is from freshwater F-2 deposits of the early Eocene Fossil Butte Member of the Green River Formation; preserved alongside a teleost, the percopsid †*Amphiplaga brachyptera*. Anterior to top.

distribution of foramina within the orbit, arrangement of condyles on scapulocoracoid). The descriptions below are based on many of the fossil specimens, especially the type series, as no single specimen provided all informative anatomical details. However, FMNH PF 15180 was particularly informative in relation to details of the ventral gill arches (figs. 12, 20), including the only basihyal reported from a fossil stingray.

To serve as guides for the anatomical description of the Green River stingrays, we

Fig. 13. Fetal specimen present in pleuroperitoneal cavity of holotype of †*Asterotrygon maloneyi*, n.gen., n.sp. (FMNH PF 15166; fig. 2), enlarged to show caudal sting (indicated by arrowhead).

provide images of entire cleared-and-stained stingrays (of a round ray, *Urotrygon chilensis* in fig. 14, and of a butterfly ray, *Gymnura micrura*, in fig. 15), along with an illustration of a complete potamotrygonid stingray skeleton (*Potamotrygon* sp. from the Rio Taquari, Rio Paraguai basin, Brazil; figs. 16, 17). Additional morphological details of these two cleared-and-stained specimens, and of other extant stingray taxa, are given in figs. 31–42 (note that abbreviations for anatomical structures given in the description below are depicted and labeled in figs. 16–26, 31–42).

Prismatic superficial calcification covers much of the skeleton and is particularly intense on the neurocranium, scapulocoracoid, pectoral basals, and puboischiadic bar. The prisms are small (less than 1 mm in diameter), generally polygonal but somewhat irregular in shape, and vary slightly in size. A single, thin layer of prismatic calcification is

Fig. 14. Dorsal view of cleared-and-stained specimen of *Urotrygon chilensis* (FMNH 93737) showing articulated skeleton; included to serve as a guide for the anatomical descriptions contained in this paper (ventral view of same specimen on opposing page). This specimen is further depicted (as close-ups) in figures 33, and 36–39. Anterior to top.

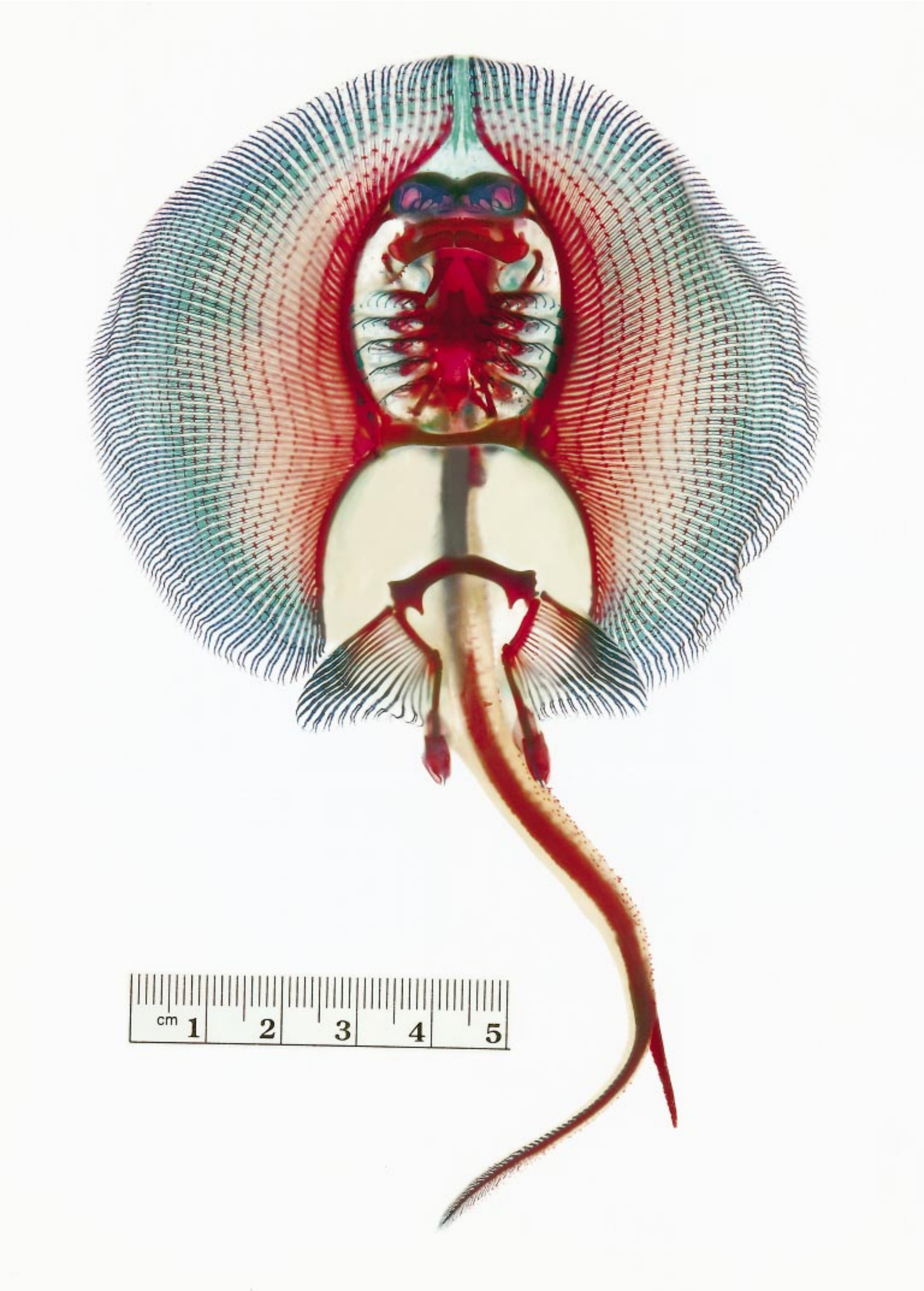

Fig. 14. Continued. Ventral view.

present, a widespread condition among neoselachians and most Mesozoic elasmobranchs, but unlike xenacanths and a few other Paleozoic sharks (Schaeffer, 1981; cf. Ørvig, 1951). The juvenile specimens examined (e.g., NHM P 61244, SMMP 83.25) have less prismatic calcification compared to the larger fossils.

NEUROCRANIUM

The neurocranium (n) is preserved at least partially in almost all specimens, but FMNH PF 12989 (paratype; fig. 4) was particularly informative. Specimens FMNH PF 15166 (holotype; fig. 2), FMNH PF 15180 (fig. 12), AMNH P 11557 (paratype; fig. 3), FMNH PF 14069 (paratype; fig. 5), FMNH PF 12914 (fig. 6), FMNH PF 14567 (fig. 7), FMNH PF 14098 (fig. 8), USNM 2028 (fig. 10B), and NHM P 61244 (fig. 11A) also provided structural details. In dorsal view, the neurocranium of †*Asterotrygon* has an outline generally indistinct from extant nonmyliobatid stingrays such as potamotrygonids, *Trygonoptera*, urotrygonids, and most dasyatids. The neurocranium is widest anteriorly at the level of the nasal capsules, where it is almost in contact with the propterygium on both sides. A keyhole-shaped dorsal fontanelle is present and can be seen in most specimens, even those that are exposed ventrally (e.g., fig. 4). Neurocranial features that can be observed are those that are prominent dorsoventrally. Prismatic calcification covers almost all of the neurocranium, including the nasal capsule area, and some specimens are heavily calcified (fig. 7). The intense shagreen of small to medium-sized denticles, covering much of the neurocranium, contributes to the difficulty of observing certain features, such as the shape of the postorbital processes in the male paratype (fig. 4).

A rostral cartilage (or rostrum; ro) is not present in our adult fossil specimens, and †*Asterotrygon* lacks any calcified neurocranial structure anterior to the nasal capsules, as do adult stingrays in general. This contrasts with the condition observed in embryonic or juvenile specimens of various extant stingray taxa (*Urobatis*, *Urotrygon*, *Urolophus*, *Trygonoptera*, *Potamotrygon*, *Plesiotrygon*), in which a small, detached subtriangular rostral extremity (not the rostral appendix of Miyake et al., 1992b) is present between the pectoral fin extremes (Holmgren, 1940; Rosa, 1985; Miyake, 1988; Miyake et al., 1992b; McEachran et al., 1996). The subtriangular rostral extremity of stingrays forms in connection with the anterior medial outgrouth of the trabecula; it is carried forward by the expanding neurocranium in conjunction with pectoral fin extension, but appears to be absent in pelagic stingrays (*Mobula kuhlii* [AMNH 15319]; however, more ontogenetic data are needed for pelagic stingrays). The rostral extremity is also absent in most small specimens of †*Asterotrygon* (e.g., fig. 11D), which is not surprising given that in extant stingrays it is a hyaline, uncalcified structure; its absence in †*Asterotrygon* may therefore be preservational. This conclusion is supported by specimen NHM P 61244 (40 mm in DW and DL, 86 mm in TL; fig. 11A), in which a small, wedgelike structure (re?) occurs between both anterior pectoral fin extremes; this structure is partially covered by denticles and may represent an impression of the rostrum. In juvenile stingray specimens in which it is present, the rostral extremity is usually not posteriorly elongated. This may be only an artifact of preparation, however, as the rostral extremity of *Urolophus cruciatus* (AMNH 98247) extends farther posteriorly, comprising about one-third of the distance between the anterior disc margin and the anterior neurocranial contour. Whether the rostral extremity continues all the way to the anterior neurocranial margin in this specimen, perhaps as a very slender and uncalcified rod, is not clear. In addition, stingrays are reported to have a vestigial medial outgrowth of the trabecula at the junction of the nasal capsules (Holmgren, 1940; Miyake et al., 1992b), which eventually disappears in fully formed individuals (there is no indication of this structure in *Urolophus cruciatus* [AMNH 98247]). This outgrowth, supposedly the rudimentary rostral base, is lacking in *Gymnura* (fig. 31), *Taeniura lymma* (fig. 32), *Urotrygon chilensis* (fig. 33), and potamotrygonids (fig. 34), but may be vestigially present in *Urobatis halleri* (fig. 38A, ro?); its arrangement and distribution among stingrays is yet to be determined. Among †*Asterotrygon* specimens, only FMNH PF 15180 appears to have a small, triangular outgrowth at the anterior margin of the neurocranium between the nasal capsules (fig. 20). However, this structure may be part of the nasal capsules, the rostral base per se, or the rostral extremity that has not been dislocated anteriorly with the anterior extension of the pectoral fin.

The nasal capsules (nc) in †*Asterotrygon* are wider than long and are oval in general outline. There is a slight notch or concavity anteriorly in between both nasal capsules, where they become confluent. This is more apparent in certain specimens (e.g., fig. 18), including the holotype, where the anterior cranial contour is well preserved, but is only faintly visible in paratype AMNH P 11557. It is also not possible to precisely determine the extent of the dorsal internasal septum in most specimens, but FMNH PF 12989 clearly has a slender prismatically calcified area between the closely set olfactory canals (oc), somewhat similar to *Urotrygon venezuelae* (Miyake, 1988: 163, fig. 35a). The dorsal internasal septum, considered to be the anterior segment of the trabecular cartilage (El-Toubi and Hamdy, 1959; Miyake et al., 1992b), separates the nasal sacs and capsules; its extent is determined by the trabecular contribution, nasal aperture size and position relative to each other, the arrangement of the olfactory canals, and by the forward and lateral expansions of the central nucleus and lateral pallium of the telencephalon (Northcutt, 1978). The olfactory canals in FMNH PF 12989 are visible through the precerebral fontanelle (seen in dorsoventral view), and the dorsal internasal septum appears to be relatively slender (fig. 18). In the holotype, however, the internasal septum is wider, with a greater distance between the olfactory canals. The width of the dorsal internasal septum varies among stingray taxa, being relatively wide in myliobatids, *Hexatrygon*, *Plesiobatis*, *Trygonoptera*, *Urobatis*, and some species of *Himantura* and *Dasyatis* (according to material examined). Species of potamotrygonids also vary in this character, and it is difficult at present to precisely quantify the width of the dorsal internasal septum in stingrays (more comparisons are presently being undertaken). The precerebral fossa (a perforation of the anterior cranial or ethmoidal wall) was presumably truncated, as in modern stingrays and batoids in which the rostral cartilages are reduced (Miyake, 1988). As it has not been excavated and is partially crushed, the depth of the precerebral fossa is not known in our fossils. Nasal cartilages (ncr) are not preserved in †*Asterotrygon*, even in FMNH PF 15180, a specimen with preserved olfactory canals (fig. 20).

The neurocranium is markedly curved anterolaterally at the level of the nasal capsules, and appears to abut the internal surface of the propterygium. A preorbital process (prp) was present on both sides of the neurocranium, as in extant stingrays. In Recent benthic stingrays the preorbital process is triangular, directed posterolaterally and situated behind the nasal capsules on the dorsal surface of the neurocranium. In our fossils, however, this region is obscured by massive jaw cartilages and perhaps also by the ventrally situated antorbital cartilages. The antorbital cartilages (aoc) are almost ventral topological counterparts of the dorsal preorbital processes in many extant and fossil stingrays. They are situated ventrolaterally on the nasal capsule just anterior to the level of the preorbital processes, and are generally more massive than the preorbital processes. Because fossil stingrays are dorsoventrally preserved, structures that are topologically on the same dorsoventral plane will usually be obliterated. The antorbital cartilages are subtriangular structures, usually curved and tapering caudally from the ventral posterolateral surface of the nasal capsule with which they articulate. They are anteroposteriorly flattened in stingrays. In FMNH PF 12989 the antorbitals are about one-fifth as long as the neurocranium (fig. 18), reaching to mid-neurocranial length, and are therefore proportionally larger than in many extant urolophid and potamotrygonid species. There is some variation in antorbital cartilage shape, as in FMNH PF 14567; the left antorbital, which remains articulated, is triangular but straighter than in other fossils (fig. 19; this structure is identified as the antorbital, as it appears to be articulated and is too large to be the angular cartilage, judging from the little space available for the hyomandibular-Meckelian ligament in this specimen). In many specimens the antorbitals remain artic-

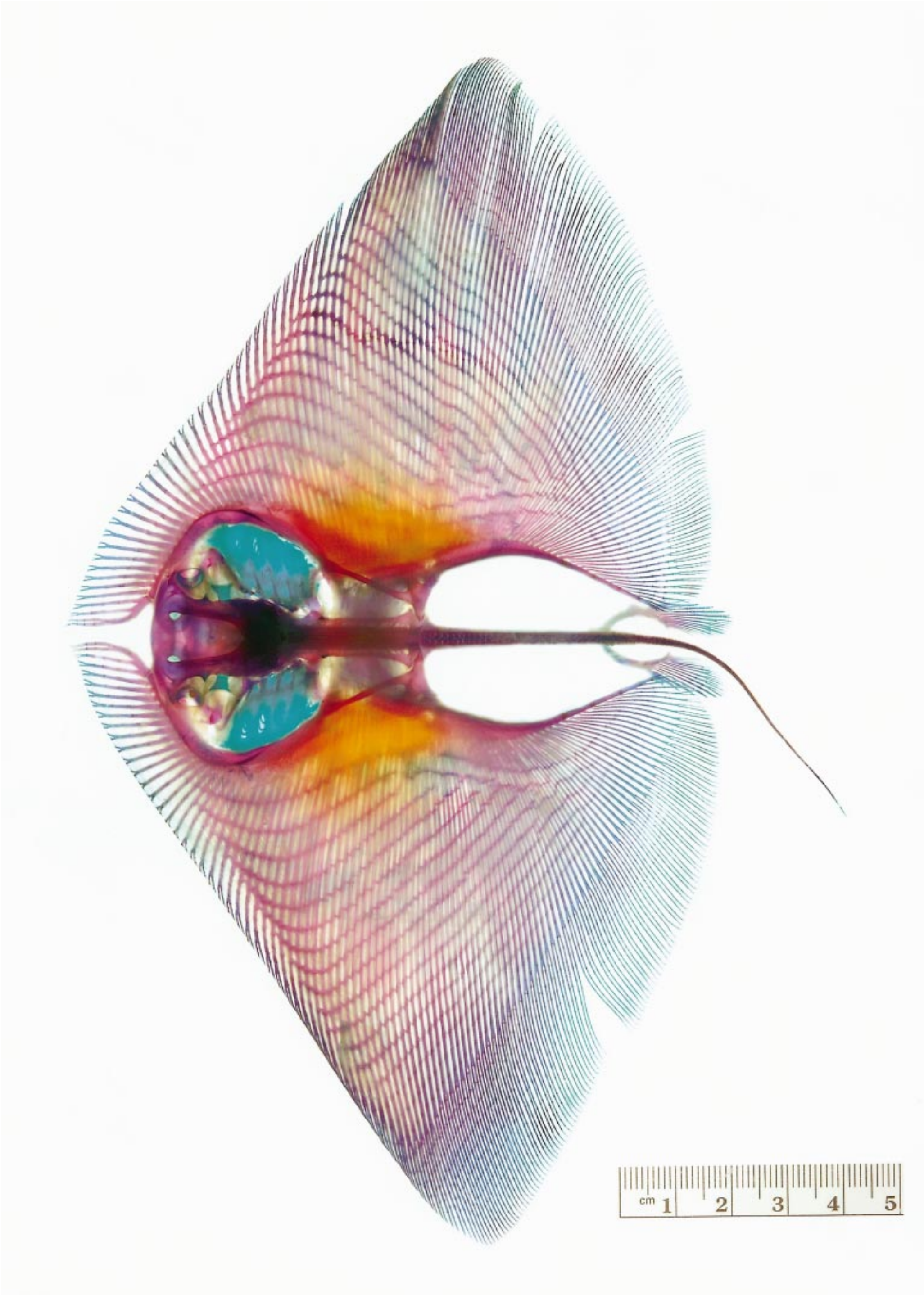

Fig. 15. Dorsal aspect of cleared-and-stained butterfly ray, *Gymnura micrura* (FMNH 89990) (ventral side of same specimen on opposing page). Anatomical details are further shown in figures 31, 35, 36, 38 and 39. Anterior to left.

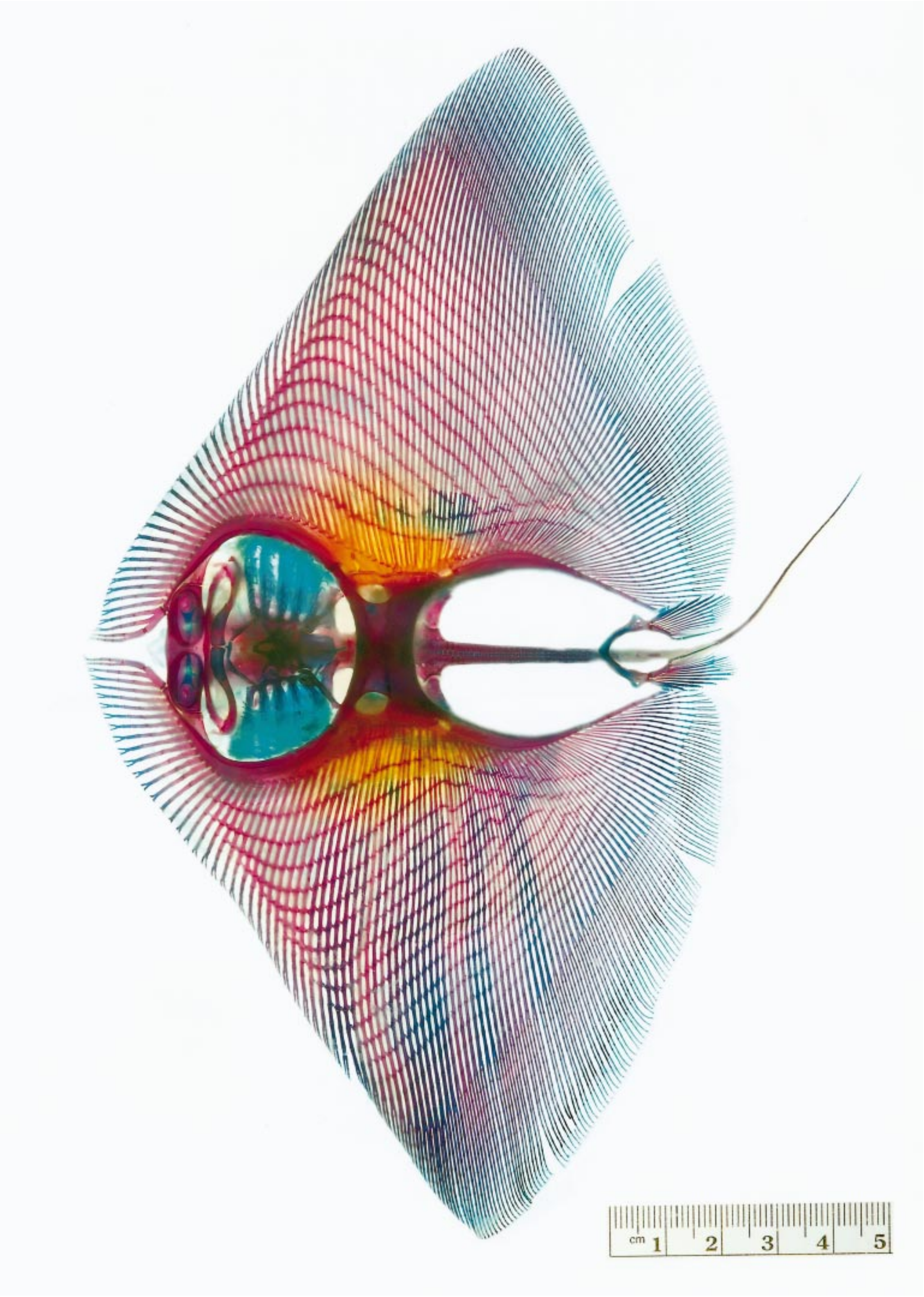

Fig. 15. Continued. Ventral view.

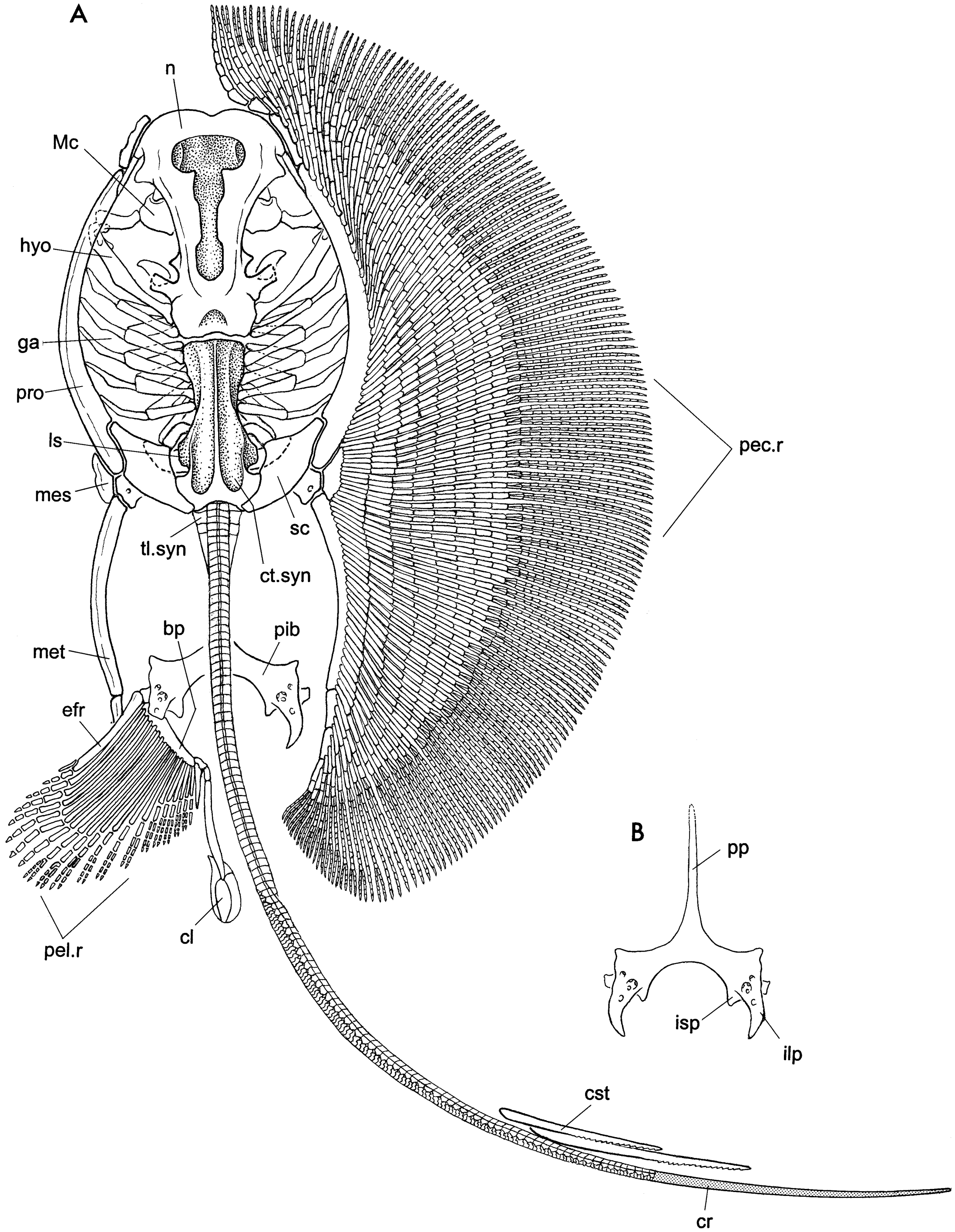

Fig. 16. Skeleton of *Potamotrygon* sp., an extant freshwater stingray (Potamotrygonidae) from the Rio Taquari, Rio Paraguai basin, Brazil (MZUSP 25663, 336 mm TL, subadult male). This illustration is provided to serve as a comparative basis and guide for the anatomical description of the Green River stingrays. **A.** Entire skeleton. **B.** Detail of pelvic girdle (to scale) showing the elongated median prepelvic process, characteristic of potamotrygonids. Note that in panel A the gill arches and gill rays are sche-

ulated in their original position, but in others they are displaced to fill the space between the orbits and internal margins of the propterygia. The left antorbital cartilage is partially preserved in paratype AMNH P 11557, and is relatively smaller than in FMNH PF 12989, appearing to taper less while being more blunt at its posterior tip. The preorbital canal (poc), through which pass branches of the trigeminal (V) and other nerves from the orbit to the ethmoid region, is not visible in specimens of †*Asterotrygon*, even though it is enlarged in Recent stingrays anterior to the preorbital process on the dorsal surface of the nasal capsule (figs. 31–34).

A single elongated dorsal fontanelle, representing the unchondrified anterior roof of the cranial cavity (de Beer, 1937), is present in stingrays and occupies over two-thirds of neurocranial length. However, some modern stingray taxa exhibit a median constriction, representing a remnant of the epiphysial bar (epb), partially separating an anterior precerebral fontanelle (pcf) from a posterior frontoparietal fontanelle (fpf) (Miyake, 1988). The epiphysial bar is more intact in juvenile stingray specimens, but is especially well developed in *Potamotrygon*, where it can be almost complete (numerous specimens; fig. 34A); it appears as an anteromedian constriction in the dorsal fontanelle in *Taeniura lymma* (separating the pcf and fpf in fig. 32A; also Garman, 1913: pl. 71, fig. 6). Two dorsally exposed (FMNH PF 14098 and USNM 2028) and one ventrally exposed specimen (FMNH PF 12989) support the presence of a median constriction in †*Asterotrygon*, and the dorsal fontanelle is faintly divided into anterior (precerebral fontanelle) and posterior (frontoparietal fontanelle) regions, as in species of *Urolophus*, potamotrygonids, *Pastinachus sephen*, *Pteroplatytrygon violacea*, *Plesiobatis daviesi*, and *Taeniura lymma*. Most ventrally exposed †*Asterotrygon* specimens (the majority of specimens, including the holotype) display a single unconstricted dorsal fontanelle (precerebral fontanelle + frontoparietal fontanelle), but this may be an artifact of preservation. The fontanelle is relatively wide in the holotype, where its internal borders are well delineated posteriorly. The posterior portion of the dorsal fontanelle displays no constriction in the fossils, and therefore the tectum orbitale is not visible. However, some stingrays may retain a posterior constriction as well, faintly dividing the dorsal fontanelle farther posteriorly (Meng, 1984). The frontoparietal fontanelle tapers posteriorly, ending in an oval curve, which is clearly visible in many †*Asterotrygon* specimens, including the holotype.

The orbital region of †*Asterotrygon* is longer than wide and occupies less than two-thirds of neurocranial length, being widest anteriorly at the level of the preorbital processes. The orbits are therefore relatively elongate, but this does not mean that the eye diameter was also large. The eyes in †*Asterotrygon* may have been large and bulging, as in some Recent stingray genera (*Potamotrygon*, *Dasyatis*, *Taeniura*, *Urobatis*, *Urolophus*), but orbit length does not necessarily correlate with eye diameter (*Plesiotrygon* has orbital proportions similar to *Potamotrygon*, even though it has significantly smaller eyes in comparison). The orbits are slightly concave in dorsal perspective. It is difficult to determine the width and extent of the supraorbital shelf in our two-dimensional fossils, but it appears to have been confluent anterioly with the preorbital process, which is largely obscured. The orbital region of †*Asterotrygon* was arranged as in most benthic stingrays, and not shortened as in gymnurids (fig. 31) and myliobatids.

Whether the supraorbital shelf was continuous with the postorbital process (pop), or if a notch separated both structures, is of some systematic significance. Species of *Urolophus*, *Plesiobatis daviesi*, *Pteroplatytrygon*, and pelagic stingrays (with the exception of *Myliobatis* and possibly *Aetomylaeus*) have the supraorbital crest continuous with the

←

matically depicted for clarity, but that pectoral radials, vertebral centra, and other features are accurately rendered; the iliac process on the left side and marginal cartilages of the clasper have been omitted; left pelvic fin skeleton is depicted dorsal to pectoral disc (metapterygium) for clarity.

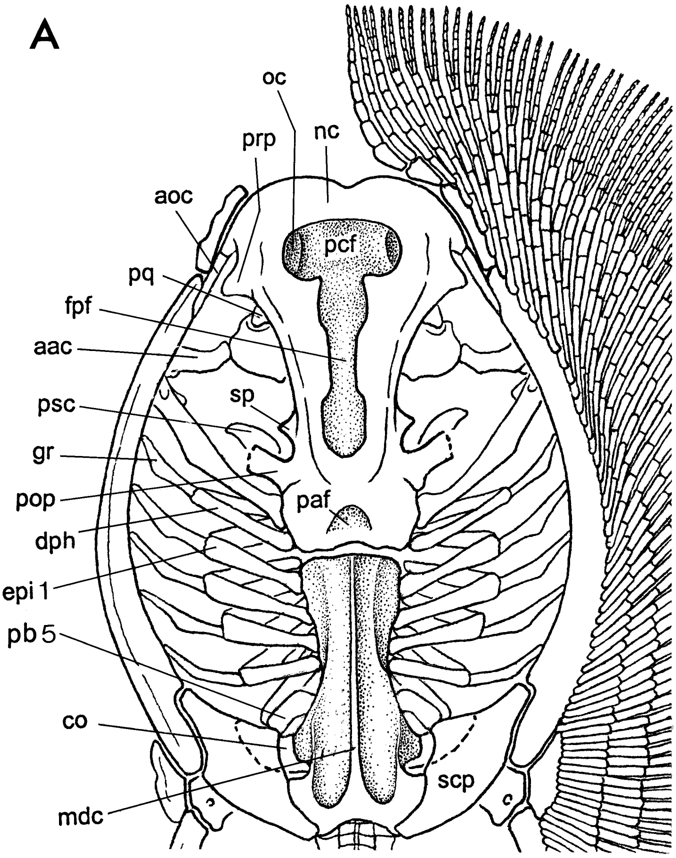

Fig. 17. **A.** Enlarged neurocranial region of *Potamotrygon* sp. from figure 16A, in dorsal view.

postorbital process, while dasyatids (except *Pteroplatytrygon*), potamotrygonids, *Urobatis* and *Urotrygon*, *Trygonoptera*, and *Hexatrygon* present a groove or notch between both structures. The postorbital groove allows for the passage of the infraorbital lateral line canal. Accordingly, the anterior margin of the postorbital process is at an oblique angle to the supraorbital crest in the taxa presenting a groove. In *Urolophus*, *Pteroplatytrygon*, *Plesiobatis*, and most pelagic stingrays, however, the canal passes through a dorsoventral opening in the postorbital process (Miyake, 1988), which also has a more transversely directed anterior profile. In †*Asterotrygon*, enlarged nuchal, orbital, and/or spiracular dermal denticles, along with the prominent hyomandibulae, obscure the postorbital process (e.g., in the holotype and in FMNH PF 12989; fig. 18), which is best preserved in FMNH PF 14567. The postorbital process of this specimen is slightly directed anteriorly, forming an angle in relation to the long axis of the neurocranium. In FMNH PF 15180 the anterior margin of the left postorbital process is preserved, which is obliquely oriented, reaching to about one-third of the length of the hyomandibula (situated directly behind it). A small triangular protuberance (the equivalent of the supraorbital process, sp; fig. 17A) is apparent anterior to the postorbital process of FMNH PF 14567 (fig. 19), separated from it by a slight indentation of the supraorbital crest. (Holmgren [1942: 179] referred to this protuberance as the ‘‘supraorbital process’’, a term we adopt, and used it to strengthen his presently unsupported view of the close relationship between certain petalichthyid placoderms, such as †*Macropetalichthys*, and rays; cf. Jarvik, 1980: 376–378). The supraorbital process is visible on both sides of the neu-

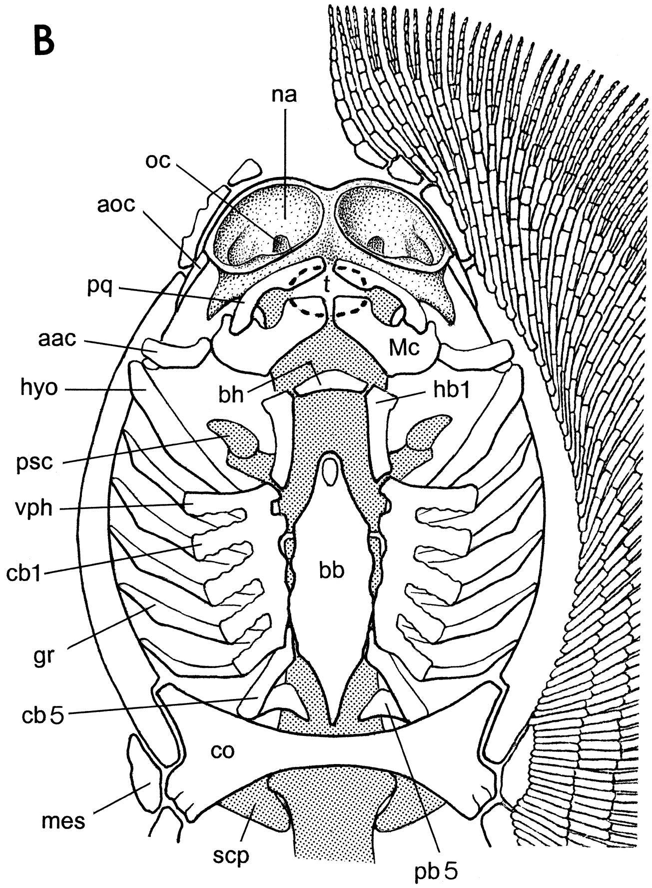

Fig. 17. Continued. **B.** Ventral view of same. Gill arches are somewhat diagramatically illustrated as in figure 16A.

rocranium, and †*Asterotrygon* therefore presents the condition seen in dasyatids, potamotrygonids, *Trygonoptera*, and urotrygonids among nonmyliobatid stingrays. The postorbital process is broad and shelflike in †*Asterotrygon*, as in all stingrays. Foramina through the supraorbital crest for rami of the superficial ophthalmic nerve are not discernible in any specimen of †*Asterotrygon*.

The parietal fossa (paf) in stingrays may contain both the endo- and perilymphatic formina, or only a single pair of endolymphatic openings, and it comprises the posterior one-fifth of the dorsal surface of the neurocranium. In †*Asterotrygon* the fossa is filled with matrix, and is similar to Recent stingrays in proportions, but whether both pairs of foramina are confluent or separate cannot be determined. A crest outlines the fossa along its margins. The hyomandibular facet is located laterally on the ventral aspect of the neurocranium, more or less between the frontoparietal fontanelle and parietal fossa, and posterior to the postorbital processes. In Recent stingrays there is also an articular facet for the anteroposteriorly compressed dorsal pseudohyoid element posterior to the hyomandibular articulation, but this cannot be observed in the fossils. The otic capsules at the posterior corners of the neurocranium are tumid, but along with the occipital condyles they are largely obscured or crushed in †*Asterotrygon* by elements of the pseudohyoid arch, gill arches, and possibly synarcual cartilage, and little anatomical detail remains. As in all stingrays, a jugal arch is absent from the posterolateral corners of the neurocranium.

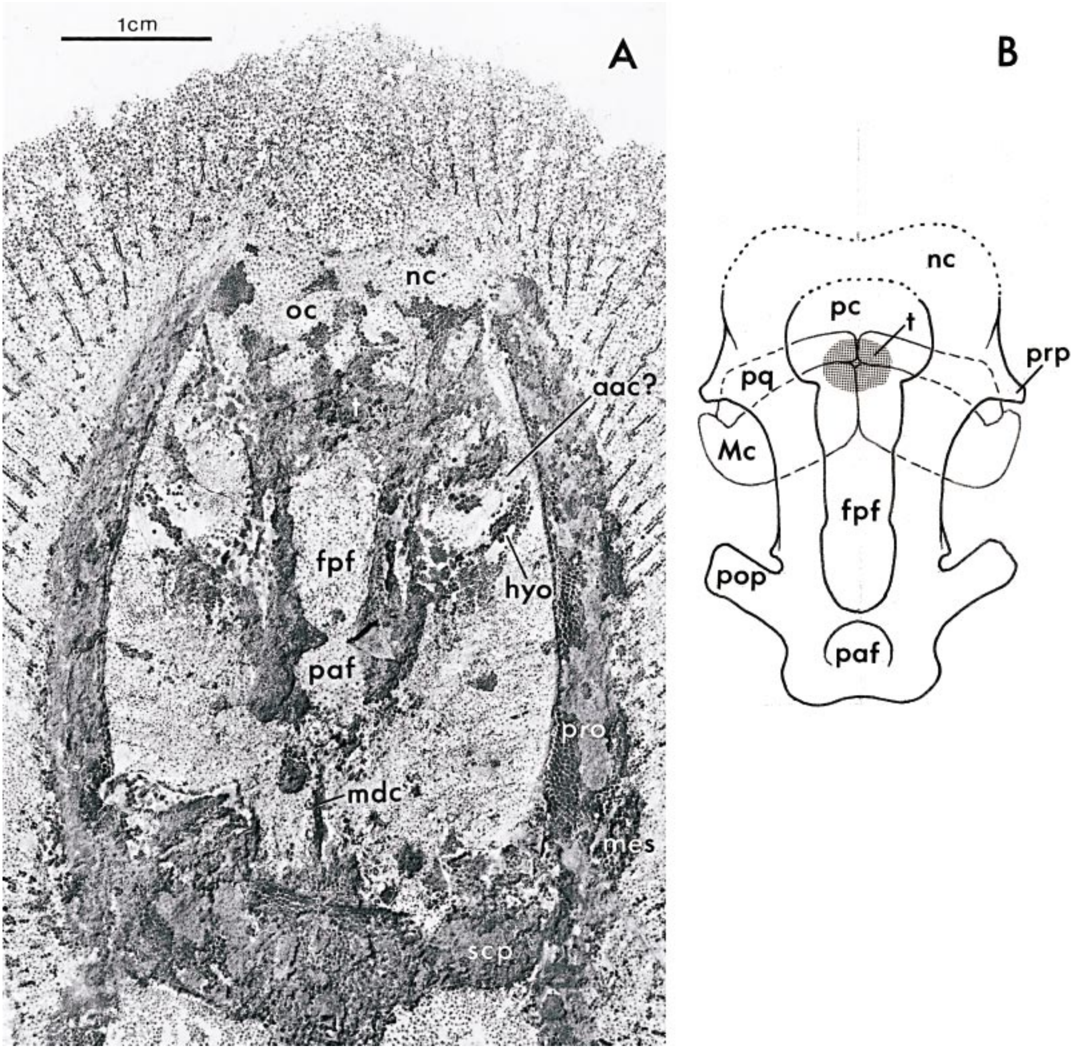

Fig. 18. Neurocranium and visceral arches of †*Asterotrygon maloneyi*, n.gen., n.sp. (FMNH PF 12989, adult male paratype; entire specimen in fig. 4). **A.** Ventrally exposed splanchnocranium. **B.** Schematic outline of neurocranium from same specimen. Note intense, almost uniform covering of closely packed and very small dermal denticles, which are more visible anterior to neurocranium between pectoral radials. Larger denticles are obliterating postorbital processes. Only impressions in the matrix of the putative angular cartilage(s) (aac?) remain, and they are not clearly visible in the photograph (A). Note that hyomandibula on right side lacks a large central section of prismatic calcification, and that portions of nasal capsules, jaws, neurocranium, and gill arches are missing. Anterior to top.

JAWS, HYOMANDIBULAE AND VISCERAL ARCHES

The jaws are well preserved in the female paratypes (fig. 21), but especially in the juvenile specimen FMNH PF 15180 (all of which are ventrally exposed; fig. 20). The jaws are dislocated, obscured, or even missing in other specimens. The jaws of †*Asterotrygon* are robust, massive structures as in most Recent stingrays (not slender as in *Paratrygon* and gymnurids), extending laterally to occupy almost the entire space between both propterygia. Both sets of jaws are strongly reinforced with prismatic calcification, and both upper and lower jaws are composed of mirror-image antimeres that meet

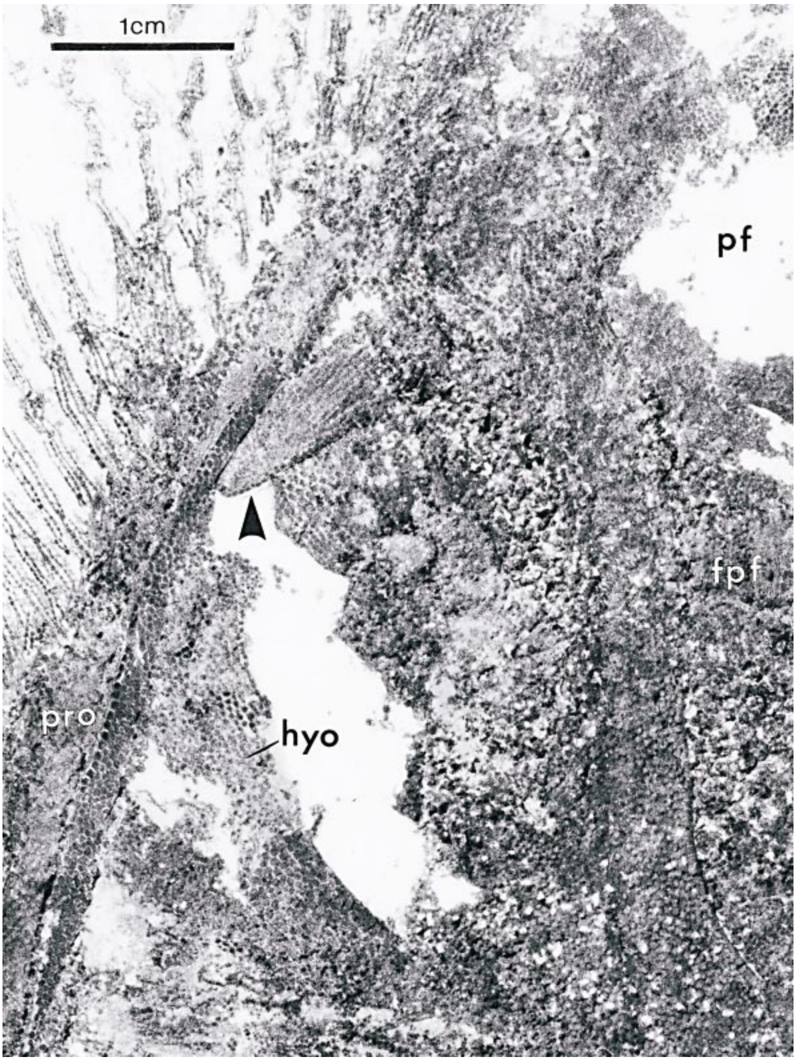

Fig. 19. Left aspect of neurocranium of †*Asterotrygon maloneyi,* n.gen., n.sp. (FMNH PF 14567; entire specimen in fig. 7), dorsally exposed, showing triangular shape of antorbital cartilage (indicated by arrowhead). Anterior to top.

mesially. The upper jaws (palatoquadrates; pq) are slightly thicker than the lower jaws (mandibular or Meckel's cartilages; Mc) in AMNH P 11557, but not so in FMNH PF 14069 or FMNH PF 15180, and this may be due to differences in the orientation of the jaws when preserved. The mandibular cartilages are more arched than the palatoquadrates and bear a widely rounded posterior margin (figs. 20, 21). Both antimeres of the mandibular cartilages and palatoquadrates are not fused symphysially (as in certain myliobatid stingrays), and are separated by a small space that originally contained strong horizontal ligaments attached to both antimeres. The arched appearance of the jaws varies among individuals and is also probably strongly correlated with jaw position when mineralized. Both mandibular and palatoquadrate cartilages taper slightly toward the midline, and both have pronounced outer corners that are curved in most specimens. The upper surface of the mandibular cartilage is relatively straight in AMNH P 11557

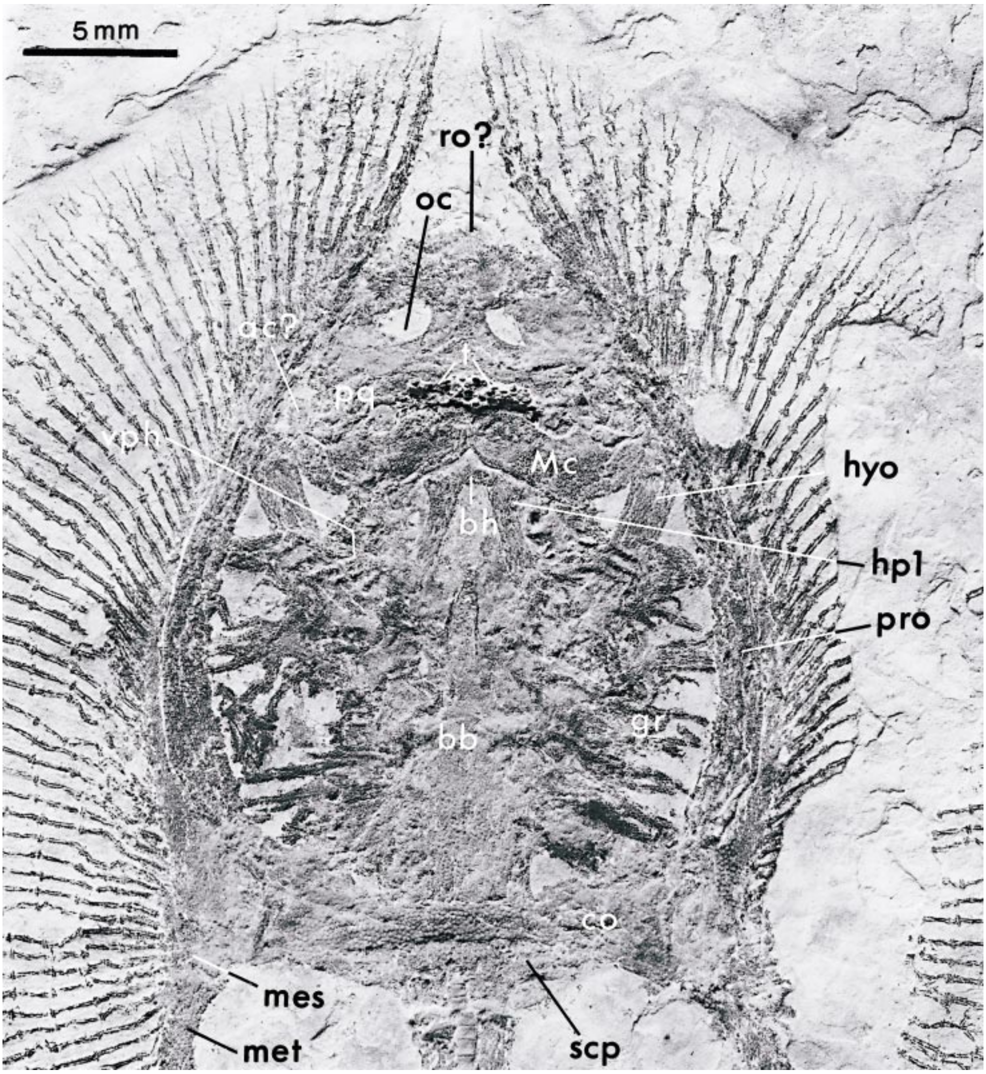

Fig. 20. Enlarged view of FMNH PF 15180 from figure 12, depicting extremely well-preserved jaws, ventral gill arches, and other features of a juvenile specimen of †*Asterotrygon maloneyi*, n.gen., n.sp. Note preservation of basihyal cartilage, first pair of hypobranchials, and gill rays of ventral pseudohyoid bar preserved in original positions.

and FMNH PF 14069, but in FMNH PF 15180 there is a circular opening between the lower surface of the palatoquadrate and the upper aspect of the lower jaw, as in most Recent nonmyliobatid stingrays. The palatoquadrate resembles the condition in potamotrygonids, *Dasyatis*, *Himantura*, *Taeniura*, and urolophids in being relatively straight on its dorsal flange. The mandibular cartilage contains a strong concavity at its laterointernal corner in which it articulates with the palatoquadrate in extant nonmyliobatid stingrays. There is also a pronounced curvature lateroexternally for the stout hyomandibular ligament. Both of these curved surfaces appear to be present in our fossils, along with the large fossa for the adductormandibulae musculature, but because of overlying structures and partial crushing of the jaws, the degree of development of these surfaces and the exact nature of the palatoquadrate-mandibular cartiage articulation

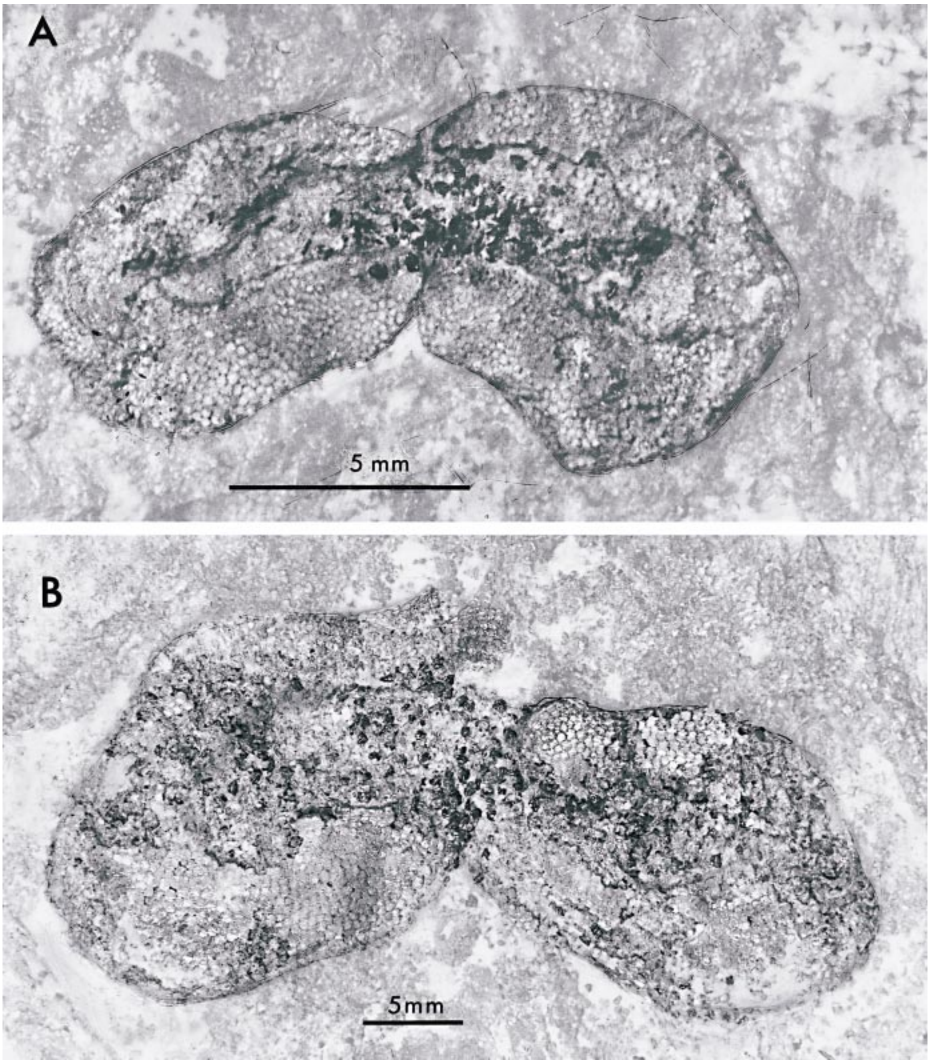

Fig. 21. Jaws of †*Asterotrygon maloneyi*, n.gen., n.sp., with scattered teeth visible between upper and lower jaws. **A.** FMNH PF 14069 (paratype; entire specimen in fig. 5). **B.** AMNH P 11557 (paratype; entire specimen in fig. 3). Jaw outlines have been reinforced.

cannot be further discerned, even though they appear to resemble that of extant stingrays (*Dasyatis*, *Potamotrygon*).

The ventrolateral processes of the mandibular cartilage are absent in all specimens of †*Asterotrygon* except FMNH PF 15180. The ventrolateral process is a triangular, posterior projection from both outer corners of the mandibular cartilage, and it is present in *Taeniura*, potamotrygonids, and many other nonmyliobatid stingrays. Its precise distribution and importance as a systematic character are still to be determined. The ventrolateral process of FMNH PF 15180 is more apparent on the right side, projecting past the palatoquadrate. This feature, along with any superficial feature of the external aspect of the lower jaw, was probably obliterated in other specimens. The winglike process (a stout, lateral or posterolateral projection of the lower jaw) appears to be restricted to pelagic stingrays (Nishida, 1990) and is clearly absent in †*Asterotrygon*.

The hyomandibulae of stingrays are elongate cartilages articulating with the braincase at its posterolateral surfaces, from which they extend anteroventrally to the level of the outer jaw corners. In †*Asterotrygon*, the hyomandibula (hyo) is strongly calcified and therefore relatively well preserved in most specimens. It projects not only anteroventrally but also slightly laterally, reaching the internal wall of the propterygium just posterior to the lower jaw corner, and almost reaching the jaw joint. The hyomandibula is stout when observed from a lateral perspective in extant stingrays, but it is more slender when observed in dorsoventral view. In †*Asterotrygon*, however, the hyomandibulae are relatively stout, especially in the holotype (where they are not very elongated), even though they are dorsoventrally preserved (the hyomandibulae are also fairly wide in the paratypes and in FMNH PF 12914 and PF 14567; fig. 19). The hyomandibula is generally more slender in smaller specimens (NHM 61244, FMNH PF 14069), but FMNH PF 15180 is an exception (fig. 20), as it presents relatively wide hyomandibulae that do not taper from their articulation toward the jaws (this may be due to its orientation when preserved). In most specimens, the hyomandibula is widest close to its attachment to the ventral otic region of the neurocranium (from a dorsoventral perspective), as in most extant benthic stingrays. The internal surface of the hyomandibula is slightly concave, especially close to the jaw corners. The proximal portion of the hyomandibula is also partially obscured by enlarged nuchal denticles in some specimens (e.g., fig. 18). The hyomandibula is devoid of rays, as in extant stingrays. Pre- and postspiracular cartilages and ‘‘hyomandibular accessory cartilages’’ (Nishida, 1990) are not preserved or cannot be identified in †*Asterotrygon*.

In stingrays, the articulation between the hyomandibular cartilage and the lower jaw can be either through a strong, stout hyomandibular-Meckelian ligament (*Taeniura*, *Dasyatis*, *Urolophus*, *Trygonoptera*, *Himantura*), through the ligament reinforced by separate cartilages formed within it (angular cartilages of *Potamotrygon* and *Plesiotrygon*; Garman, 1913), or through a more direct connection, without a stout ligament between the hyomandibulae and Meckelian cartilages (*Hexatrygon*). A very small and inconspicuous ligament is present in pelagic stingrays and gymnurids, and this is considered to be a more direct connection as in *Hexatrygon*. In †*Asterotrygon*, there is a small, slightly transverse element situated between the hyomandibula and lower jaw (more conspicuous in FMNH PF 15166, AMNH P 11557, FMNH PF 15180, FMNH PF 12989, NHM 61244). This element does not represent the recurved, medially directed distal tip of the hyomandibula. The distal (anterior) section of the hyomandibula can be oriented in this fashion even though the stout hyomandibular-Meckelian ligament is present (e.g., *Urobatis halleri* [fig. 38A], *Urotrygon chilensis* [fig. 33], *Himantura krempfi* [AMNH 41567]). This inflection of the hyomandibula, however, is usually small and does not extend to contact the lower jaw. The transverse element of †*Asterotrygon* contacts the lower jaw and is heavily covered by prismatic calcification (especially in FMNH PF 15180; however, the individual prisms are mostly missing or scattered, and usually only their impressions remain). This prismatic calcification supports the notion that a separate cartilage, similar to the angular cartilages (ac) of potamotrygonids, was present in the ligament uniting the hyomandibula and lower jaw in †*Asterotrygon* (best observed in FMNH PF 15180 and in NHM 61244, both juvenile specimens). Holmgren (1943: 74) considered the angular cartilages (his ‘‘mandibular rays’’) to be of mandibular arch origin.

Even though the hyomandibular-Meckelian ligament may become strengthened, slightly chondrified, and even reinforced with scattered internal calcification, actual prismatic calcification is absent from the ligament in specimens presenting these conditions (e.g., *Taeniura lymma* [fig. 32], *Trygonoptera testacea* [fig. 40B]). This condition may also vary intraspecifically (such as in *Trygonoptera testacea*) and does not appear in most radiographs. The angular cartilages of *Potamotrygon* and *Plesiotrygon*, however, are prismatically calcified and clearly visible in radiographs (fig. 40). These cartilages are stout, oval to rectangular in shape, and embedded within the strong hyomandibular ligament. As such, they are unique among Recent stingray taxa to potamotrygonids except *Paratrygon* according to our specimens (see also Garman, 1913; cf. Lovejoy, 1996). *Himantura schmardae* (NHM 1908.5.28:2–3) has very small calcified elements that are barely visible in radiographs (Lovejoy, 1996); they may be easily overlooked in dissections. The distal (anterior) extremity of the hyomandibula of potamotrygonids is not inflected medially to a large extent, where the hyomandibular-Meckelian ligament is present. Although somewhat tentative because of preservational issues, we conclude that the condition in †*Asterotrygon* resembles the discrete angular cartilages of *Potamotrygon* and *Plesiotrygon*, because these appear to be prismatically calcified, discrete cartilages. In turn, this suggests that the hyomandibular-Meckelian ligament was present in †*Asterotrygon* as well, even though impressions of the ligament are not clearly preserved in the fossils (which is to be expected). In FMNH PF 15180, the putative angulars appear to be composed of a single, relatively elongate element on each side, slightly directed posteriorly. A small separate cartilage located along the internal margin of the hyomandibula, and posterior to the attachment of the hyomandibular ligament, is present in numerous species of *Urolophus* (observed in many specimens) and pelagic stingrays (Garman, 1913). This cartilage (termed here the *secondary* hyomandibular cartilage), however, is considered functionally isolated and not homologous to the angular cartilages of potamotrygonids (Lovejoy, 1996; McEachran et al., 1996), but this remains to be elucidated. No such element is visible in specimens of †*Asterotrygon*.

Stingrays typically possess five gill arches (although there are six in *Hexatrygon*) in addition to the pseudohyoid arch located between the hyomandibular and first gill arch. Elements of the ventral gill arch skeleton have been studied in more detail (Miyake, 1988; Miyake and McEachran, 1991), and stingrays characteristically possess an enlarged medial plate (comprising posteriorly the basibranchial copula, considered to be the result of ontogenetic fusion of hypobranchial and basibranchial components; bb), ankylosis or slight overlapping of the proximal segments of the last two ceratobranchials (unconfirmed in *Hexatrygon*), anteriorly and obliquely directed short, separate hypobranchial 1 elements (hb1), and a small transverse and separate basihyal cartilage (bh). Additionally, the ceratobranchial and pseudohyoid cartilages are fused in stingrays (the number of fused ceratobranchial elements varies among taxa). Most pelagic stingrays lack the first hypobranchial along with the basihyal (Nishida, 1990), but whether this is primitive or secondary depends on the myliobatiform phylogeny adopted (derived in our phylogenetic study below; cf. appendix 2). Primitively in stingrays, the last pair of ceratobranchial and epibranchial elements articulate with the anteromedial aspect of the coracoid bar, and the basihyal and the medial plate are separated by a large gap (Nelson, 1969).

The pseudohyoid and gill arches are poorly preserved in †*Asterotrygon*. The most informative specimen is FMNH PF 15180 (figs. 12, 20), which has certain elements of the ventral gill skeleton intact. Five pairs of gill arches are present in addition to the pseudohyoid arch (also observed in FMNH PF 14567 and FMNH PF 12914). The basihyal cartilage (bh) in †*Asterotrygon* is a very small and separate element, slightly wider than long, and similar to the basihyal of *Urobatis jamaicensis* (AMNH 30385), *U. halleri* (fig. 38B), and *Dasyatis americana* (AMNH 30607), but stouter than the basihyal of gymnurids, and not fragmented as in potamotrygonids. It is situated just posterior to the lower jaw symphysis (fig. 20). Unfortunately, the pseudohyoid arch is mostly obscured in FMNH PF 15180, but the right ventral pseudohyoid (vph) is present as a very slender, prismatically calcified element that still articulates with its associated pseudohyoid rays (which are posteriorly directed). Lateral to the basihyal are the first hypobranchials (hb1), which in FMNH PF 15180 are exceptionally well preserved (fig. 20). The first hypobranchials are shaped as in potamotrygonids (especially *Potamotrygon magdalenae* [AMNH 55620]; see fig. 34B), urolophids, urotrygonids (fig. 33B), and other benthic stingrays, that is, tapering posteriorly only slightly from their articulation with the basihyal, but not as tapered as in *Gymnura* (fig.

35B). Both hypobranchial 1 elements are almost as long as one of the mandibular cartilages from symphysis to jaw corner. The hypobranchials are obliquely oriented and contact posteriorly the ventral pseudohyoid, lateral to the anterior extension of the basibranchial copula. The first hypobranchial elements in †*Asterotrygon* were not as broad anteriorly as in *Taeniura*, or even as much as in some species of *Dasyatis*. Posterior to the hypobranchials, and separated from them by a small gap, is the basibranchial copula (bb; medial plate). The copula bears a poorly preserved anterior projection, very similar to the condition seen in most benthic stingrays (*Urobatis*, *Urolophus*, *Urotrygon*, *Taeniura*, potamotrygonids), but absent in *Plesiobatis* and pelagic stingrays (Miyake and McEachran, 1991). This projection in †*Asterotrygon* appears to be more anteriorly extended than in *Gymnura* as well. The full posterior extent of the basibranchial copula is difficult to determine, but in stingrays it usually extends as a very slender projection to the level of the scapulocoracoid. In †*Asterotrygon*, the posterior extension of the copula is difficult to observe, but is present in FMNH PF 15180 as a sightly elevated, slender ridge of prismatic cartilage, similar to the basibranchial copula present in *Trygonoptera*, *Urobatis*, and potamotrygonids, and not as short as in gymnurids. The extent to which ceratobranchials are fused to each other (if at all) and to the ventral pseudohyoid bar cannot be determined in the fossils.

The articulation between the last pair of ceratobranchials and the scapulocoracoid can be seen in FMNH PF 12989 and FMNH PF 15180, where the ceratobranchials appear relatively straight and narrow. We consider these articulating elements to be ceratobranchials and not epibranchials, as both specimens are ventrally preserved and ceratobranchials are typically more slender and straight compared to the slightly curved epibranchials of nonmyliobatid stingrays. The preserved posterior portion of both ceratobranchial 5 elements are prismatically calcified and articulate with the coracoid lateral to its connection with the synarcual cartilage, at about one-third of synarcual length. The gill basket occupied almost the entire gill cavity between the pectoral propterygia in †*Asterotrygon*.

In specimens FMNH PF 15166 (fig. 2), FMNH PF 15180 (figs. 12, 20), FMNH PF 12989 (fig. 4), FMNH PF 14069 (fig. 5), FMNH PF 12914 (fig. 6) and FMNH PF 14567 (fig. 7) numerous disarticulated gill rays (gr) are scattered in the gill chamber, but some are preserved in their original positions in FMNH PF 15180 (fig. 20) and in FMNH PF 15166. In Recent stingrays, gill rays supporting the gill lamellae are present on the dorsal and ventral pseudohyoid arches and on cerato- and epibranchials 1–4. In our fossils it is generally not possible to associate the slender and fragmented gill rays with any particular arch, even though they occur throughout the entire gill chamber (but in FMNH PF 15180 the ventral pseudohyoid is associated with corresponding gill rays; fig. 20). The gill chamber is compacted anteroposteriorly in FMNH PF 12989 and in FMNH PF 14069. A large gap is visible between the basihyal and basibranchial anterior extension in FMNH PF 14069, even though the basihyal is not well preserved and its precise shape cannot be discerned (our identification of a patch of prismatic calcification just posterior to the mandibular cartilages as the basihyal in this specimen is tentative). There are no signs of extrabranchial cartilages in †*Asterotrygon* (these are formed from the fused distal tips of gill rays). The gap that separates the mandibular cartilages from the anterior limit of the basibranchial (which itself is usually not visible) contains disarticulated elements of the visceral arches and synarcual cartilage in some of the fossils.

SYNARCUAL AND VERTEBRAL SKELETON

Stingrays have two synarcual cartilages, an anterior cervicothoracic synarcual (ct syn) and a posterior thoracolumbar synarcual (tl syn) (Compagno, 1973, 1977). The thoracolumbar synarcual is unique to stingrays. The anterior synarcual articulates with the occipital region of the neurocranium and extends posteriorly to meet the scapular processes of the shoulder girdle. It is prismatically calcified and consists of a dorsal and ventral component, both formed ontogenetically by fusion of different vertebral (basidorsal and basiventral) elements (Miyake, 1988). The anterior synarcual is relatively well developed and prominent in stingrays. In †*Asterotrygon* the cervicothoracic synarcual is preserved in many specimens (e.g., figs. 6, 7, 22). The medial crest (mdc) of the synarcual is a dorsal ridge that runs anteroposteriorly along almost its entire length and is visible in dorsally exposed specimens, especially FMNH PF 14567 (fig. 22B) and FMNH PF 12914, where the ridge is markedly elevated. One ventrally exposed specimen (FMNH PF 12989) clearly displays a string of vertebrae running the entire length of the preserved synarcual (13 partially fused vertebrae along the synarcual midline are present). In most stingrays, vertebral centra occupy only the posterior one-half to one-third of synarcual length. Lateral stays (ls; supposedly formed by fused pleural ribs and basiventrals) are not visible in any specimen, even though they are prominent components of cervicothoracic synarcuals of stingrays. Dorsally, the posterior segment of the first synarcual is composed of the secondarily fused suprascapulae that articulate with the ascending lateral scapular processes of the shoulder girdle (FMNH PF 12989, FMNH PF 14567). The posterior, suprascapular portion of the synarcual appears rectangular in outline in almost every specimen, even those that are ventrally preserved. The suprascapular portion of the synarcual in †*Asterotrygon* is robust compared to extant nonmyliobatid stingrays, where it appears to be more slender (*Urotrygon*, *Urobatis*, *Potamotrygon*). The overall width of the synarcual anterior to the suprascapulae is similar to extant benthic taxa as seen in NHM P 61244, where the synarcual width is just less than neurocranial width at the occipital region. Spinal nerve foramina cannot be identified and counted in our fossils.

The posterior or thoracolumbar synarcual is less pronounced than the cervicothoracic synarcual, and is a relatively simple structure. This synarcual tapers posteriorly, ending at about midway between the scapulocoracoid and pelvic girdle, and has unfused individual vertebral centra along its entire length. The second synarcual in †*Asterotrygon* is very similar to extant nonmyliobatid stingrays. In FMNH PF 12989, where it is well preserved, the thoracolumbar synarcual is about five times the width of individual centra at its origin, where it attains its greatest lateral dimensions, and is prismatically calcified (fig. 22). Observation of the second synarcual requires the fossil specimen to have a dorsoventrally preserved tail region posterior to the shoulder girdle (e.g., FMNH PF 12989); in other words, the vertebral column cannot be dislocated and rest on its side, as is commonly the case. FMNH PF 14069 has the column preserved laterally, and only the very anterior portion of the second synarcual is present.

Vertebral centra do not articulate with pleural ribs in †*Asterotrygon*, and ribs associated with basiventrals are absent, as in all stingrays. Numbers of vertebral centra posterior to the first synarcual are given in tables 2 and 3. It is more difficult to determine transitions between mono- and diplospondyly in our fossils than in extant stingrays, because myomeres are not preserved and individual centra may be displaced. In stingrays, this transition usually occurs at the level of the pelvic girdle or just posterior to it, and that appears to be the case in NHM P 61244. In FMNH PF 14069, where the vertebral centra are exceptionally well preserved, the area of transition is not entirely clear but appears to be posterior to the pelvic girdle, close to the posterior edge of the pelvic fin. Specimens FMNH PF 15166 (holotype; fig. 2), AMNH P 11557 (paratype; fig. 3), FMNH PF 14069 (paratype; fig. 5), FMNH PF 12914 (fig. 6), and FMNH PF 14567 (fig. 7) have enlarged, laterally compressed neural spines (ns) or arches from just posterior to the scapulocoracoid to close to the caudal stings. The neural arches are obliquely oriented posteriorly in relation to the centra and are closely situated to each other. Ventral arches are also present in extant stingrays, but are much smaller in comparison to the neural arches at least until the level of caudal stings, and this was probably the case in †*Asterotrygon* as well. Individual basidorsals or interdorsals cannot be discerned in the fossils. Individual vertebrae are spool-shaped in lateral view and more elongated in the caudal region, even though they are much smaller compared to centra close to the second synarcual. Faint rings of calcification are present peripherally within

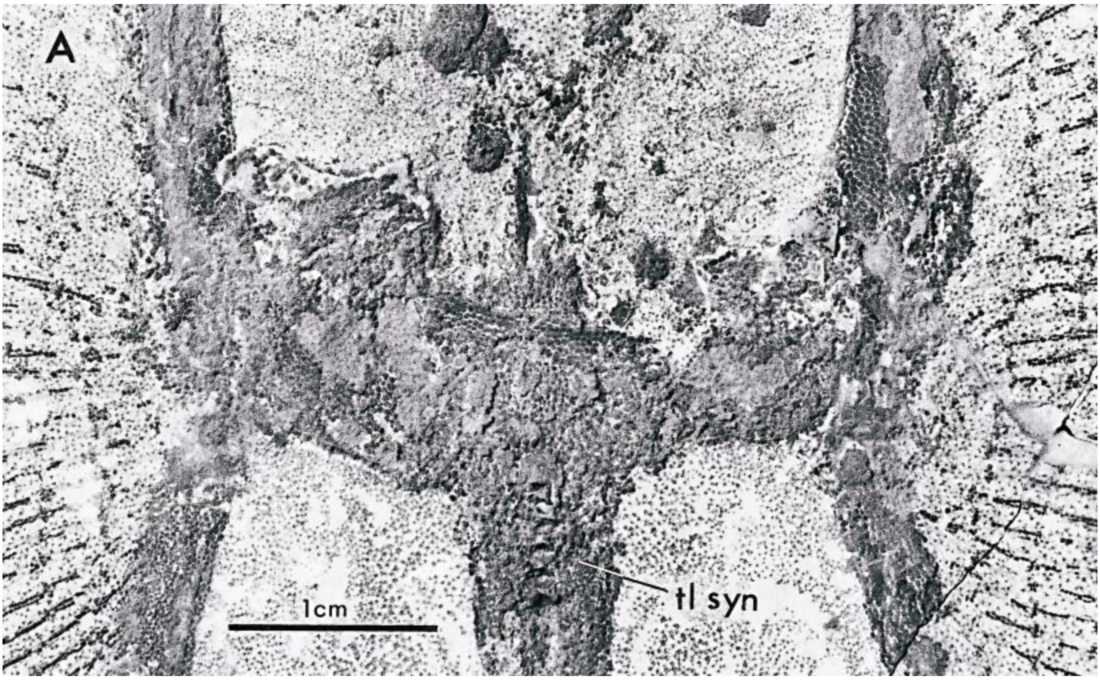

Fig. 22. Scapular region depicting scapulocoracoid and pectoral basals of †*Asterotrygon maloneyi*, n.gen., n.sp. **A.** FMNH PF 12989, ventrally exposed (paratype; entire specimen in fig. 4); note small dermal denticles distributed over entire surface. **B.** FMNH PF 14567, dorsally exposed (entire specimen in fig. 7); mesopterygium missing from left side. Anterior to top.

the centra and can be observed in specimens in which the centra are preserved, exposing their anterior or posterior surfaces (FMNH PF 14098, USNM 2028).

†*Asterotrygon*, unlike almost all extant stingrays that lack a caudal fin, has discrete vertebral centra continuing to the posterior tip of the tail, which can be observed in juveniles, small specimens, and adults. The unsegmented cartilaginous rod (cr), a notochordal extension that continues caudally beyond the caudal stings (instead of separate vertebral centra), is therefore absent in our fossils (cf. figs. 24, 26 to figs. 37C, D, and 40E). This rod is present in most stingray genera and is absent in taxa that have a caudal fin (urotrygonids and urolophids), *Plesiobatis* (Nishida, 1990), *Hexatrygon* (Heemstra and Smith, 1980), as well as in all other nonmyliobatiform batoids. However, this condition may vary slightly among species, as *Dasyatis annotatua* has individual vertebrae extending well beyond the caudal sting (CSIRO T 694, CSIRO T 697) and *Gymnura* has discrete vertebrae extending to the tip of the tail (we have confirmed this in four species of *Gymnura* so far), contrary to the findings of Lovejoy (1996) and McEachran et al. (1996).

Appendicular Skeleton

The entire shoulder girdle (scapulocoracoid) consists of a single, somewhat flattened U-shaped structure in †*Asterotrygon*. The scapulocoracoid (sc) is composed of a transverse ventral coracoid bar (co) and lateral, dorsally projecting scapular processes (scp) that articulate medially with the suprascapulae (ssc) which are fused to the posterior segment of the cervicothoracic synarcual. The coracoid bar is best preserved in ventrally exposed specimens (FMNH PF 15180 [fig. 20], FMNH PF 14069), but the entire shoulder girdle is easily recognized as a prominent transverse structure at mid disc in all specimens. The anteroposterior length of the coracoid bar varies slightly among specimens,

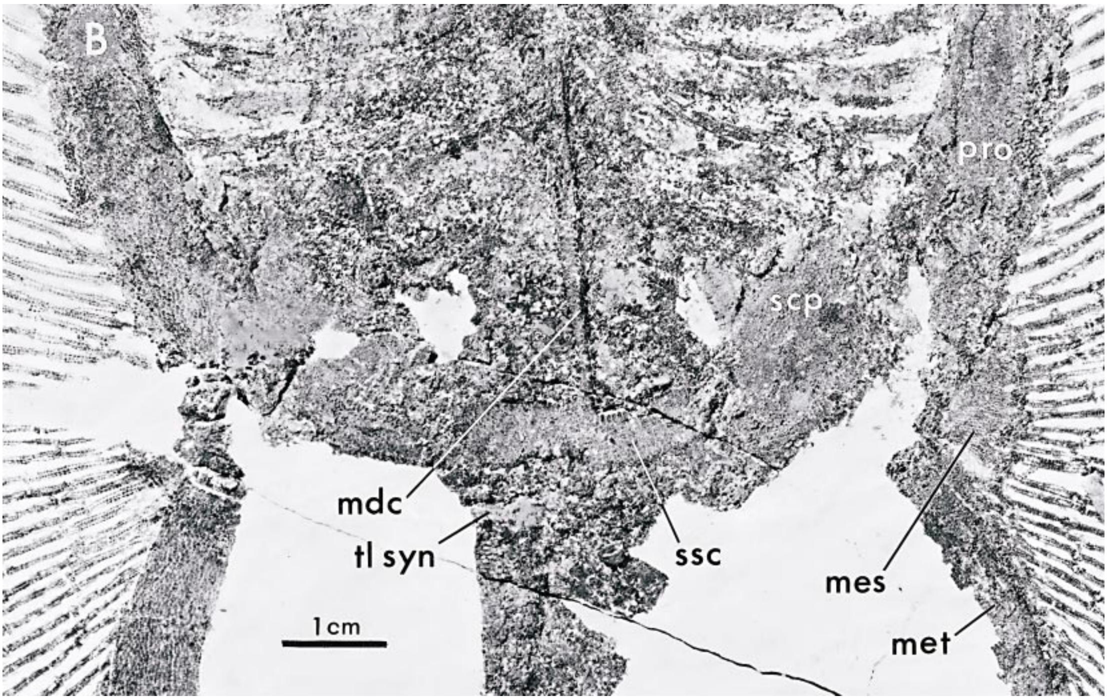

Fig. 22. Continued.

but how much of this variation is due to its orientation during preservation is unknown. In FMNH PF 14069 the coracoid resembles that of Recent *Potamotrygon* and other benthic genera in being slender transversally, but unlike *Potamotrygon* the anterior border of the coracoid is relatively straight across and not slightly concave. The scapular processes are best preserved in FMNH PF 14567 (fig. 22B) and FMNH PF 12914 (fig. 6), where they appear as large subtriangular pieces articulating with the synarcual by means of prominent articular surfaces. This articulation in stingrays is of the ball-and-socket type (Compagno, 1973, 1977), and we can infer on the basis of its position and appearance in dorsoventral view that this was the case in †*Asterotrygon* as well. The scapular processes are obliquely positioned in relation to the synarcual cartilage, as in modern stingrays (*Urotrygon*, *Urolophus*). The foramen present on the dorsal component of the scapular process of some stingray taxa (‘‘af’’ fenestra of Miyake, 1988; ‘‘foramen of the scapular process’’ of Lovejoy, 1996) cannot be identified in the fossil material.

The scapulocoracoid laterally joins the internal skeleton of the pectoral fins or disc, which is composed of basal cartilages (pro-, meso-, and metapterygium) articulating with numerous elongated and subdivided radial elements that extend to the outer margins of the disc (plesodic condition). The propterygium (pro) extends for slightly over one-half of disc length. In both †*Asterotrygon* and extant stingrays, the anteriormost portion of the propterygium becomes subdivided into three or more segments anterior to the level of the nasal capsules (even in *Mobula* [AMNH 15319], which bears an elongated propterygium that is anteriorly expanded to support the cephalic lobes, but in which there is also a small anterior segment). In some extant nonmyliobatid stingrays (*Urolophus*, *Trygonoptera*, *Dasyatis*, *Himatura*) the propterygium becomes subdivided at about midnasal capsule length (cf. Lovejoy, 1996), but in †*Asterotrygon* this division appears to be in front of the anterior cranial margin, even though this is difficult to determine in the fossils. The anterior segments of the propterygia bend medially toward the midline, leaving a prominent gap that was occupied by the small rostral cartilage (a rostral piece was presumably present—possible vestiges of it are found in NHM P 61244, see above). The anteriormost segment of the propterygium (or the first radial propterygial element anteriorly) is bifid, articulating with two rows of radials as in extant nonmyliobatid stingrays. The propterygium bears an elongated ridge and sulcus for the insertion of the pectoral fin muscles along almost its entire length.

In †*Asterotrygon*, the posterior section of the propterygium contacts the scapulocoracoid, as in various extant benthic taxa (*Dasyatis*, *Urolophus*, *Potamotrygon*), by means of an elongated articular surface with two distinct condyles (procondyles). The anterior procondyle is at the anterolateral corner of the shoulder girdle, and the posterior one is close to the mesocondyle (the articular surface of the mesopterygium). The pro- and mesocondyles are clearly separated from each other in stingrays (Miyake, 1988), and this is the case in †*Asterotrygon* (fig. 22A). The lateral aspect of the scapulocoracoid, however, is not visible in our two-dimensional fossils, but the articulation between the propterygium and scapulocoracoid can be discerned from a dorsoventral perspective, appearing very similar to Recent nonmyliobatid stingrays. The medial or internal surface of the posterior tip of the propterygium is slightly concave where it articulates with the scapular process (FMNH PF 12989), contacting it in at least two different places (presumably at the procondyles) but possibly throughout more of its length, as is common in many extant benthic stingrays. The lateral aspect of the scapular process is relatively straight, and consequently the propterygium is not separated from the mesopterygium by a small process in †*Asterotrygon*.

The mesopterygium (mes) is more difficult to observe in our fossils due to scattering of its prismatic calcification. It is slightly wedge-shaped and subtriangular in the holotype FMNH PF 15166 (right side), in FMNH PF 14567 (fig. 22B), and in the left side of paratype AMNH P 11557, as in many nonmyliobatid stingrays, but in FMNH PF 12989 (fig. 22A) the mesopterygium is more elongate, projecting anteriorly somewhat obliquely to the propterygium. This discrepancy is probably due to incomplete preservation in the latter specimen. The scapular process is situated at close to the posterior two-thirds of its length. Approximately 13 mesopterygial radials are present in FMNH PF 12989 (counted on both sides; table 2).

The metapterygium (met) is elongated and curved, tapering posteriorly and terminating close to the level of the pelvic girdle. In †*Asterotrygon*, the metapterygium appears as a single piece, unlike many nonmyliobatid stingrays where it can become subdivided posteriorly into smaller segments that also articulate with radials. The metapterygium also bears a pronounced groove for the insertion of the pectoral fin musculature; it is similar to the propterygium but is not as elongate or as wide.

The radial elements articulating with basal cartilages are identical in structure (numbers of radials for each basal are shown in tables 2 and 3). All radials are segmented from the basal cartilages to the outer disc margin. In FMNH PF 12989, FMNH PF 12914, and FMNH PF 14567, where radial segments are clearly preserved, there are at least 15 radial segments, but perhaps one or two additional segments were present distally. In the holotype (fig. 2), 17 radial segments are present at the level of greatest disc width. The individual segments of the radials are relatively short and reduce slightly in length in the direction of the outer disc margin. In specimens FMNH PF 15166 and FMNH PF 12914, radials of the ninth row (counting from basals to outer margin of disc) are bifid, but in FMNH PF 12989 and FMNH PF 14567 it is the eighth radial segment that bifurcates. Therefore, there are always twice as many radials at the outer disc margin than articulating with the basal cartilages. The derived condition of *Gymnura* and myliobatids

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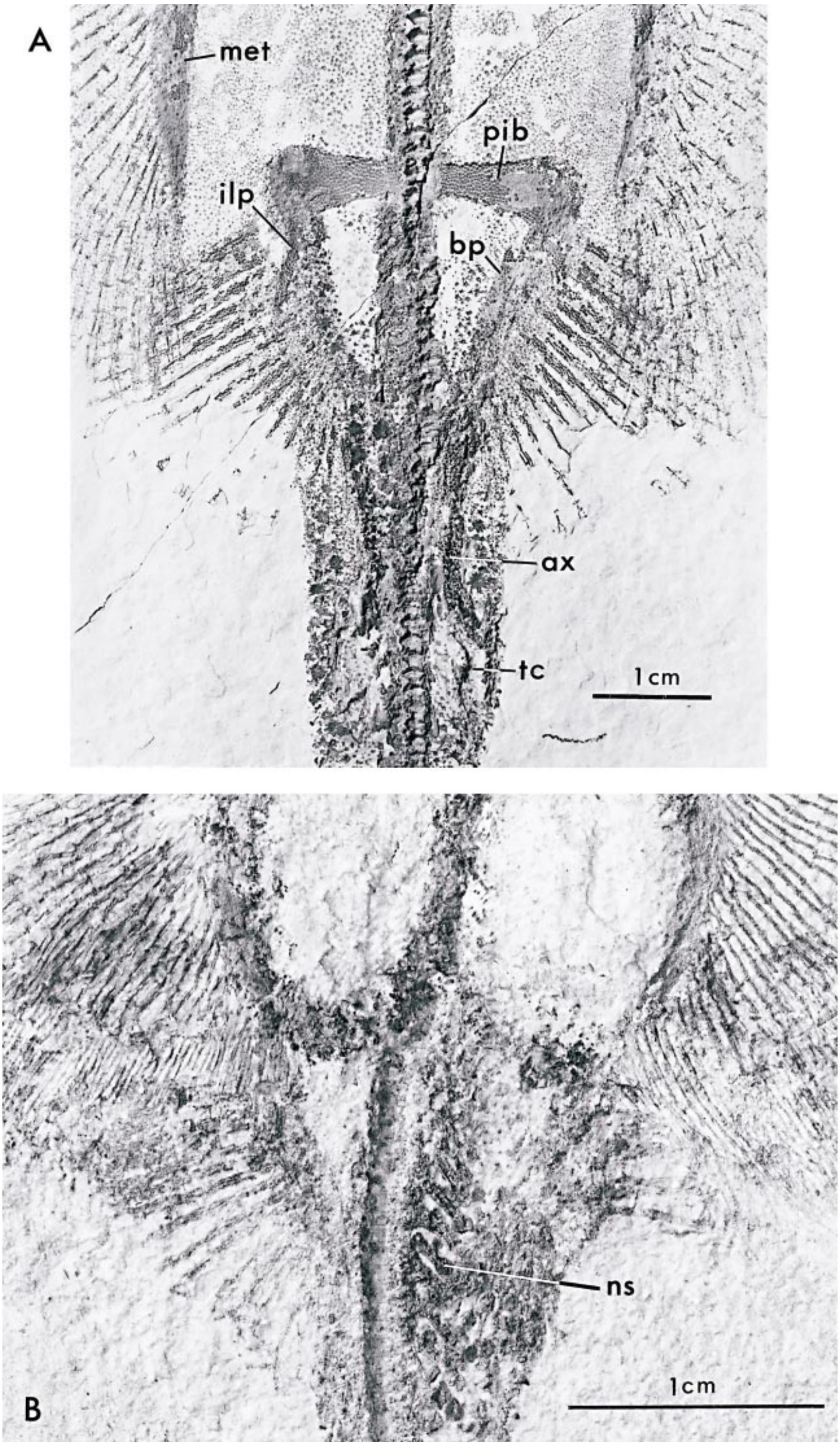
Fig. 23. Pelvic girdle of †*Asterotrygon maloneyi*, n.gen., n.sp. **A.** Male paratype (FMNH PF 12989) in ventral view (entire specimen in fig. 4), depicting claspers situated dorsal to tail base; note axial



cartilage and impressions of terminal cartilages. **B.** Paratype (AMNH P 11557), also in ventral view (complete specimen in fig. 3). Anterior to top.

(Nishida, 1990) in having laterally expanded radial elements that articulate with adjacent radials (fig. 39A, B) is not present in †*Asterotrygon*.

The puboischiadic bar (pib; pelvic girdle), being broad and dorsoventrally flattened, is well preserved in most specimens, but more so in FMNH PF 15166, FMNH PF 15180 (right side only), PF 12989 (fig. 23A), and PF 12990. The girdle is stoutest at its corners, where the basipterygia (bp) originate and extend posteriorly, tapering to a variable extent. Its anterior surface is roughly straight in most specimens, and is much less arched in comparison to the slightly concave posterior surface (FMNH PF 12989). In other specimens (FMNH PF 15166, FMNH PF 14567) the pelvic girdle is slightly arched at both anterior and posterior margins. Minor distortion and preservational differences may account for the observed variation among specimens.

The pelvic girdle resembles that of many stingrays in general aspects, excluding potamotrygonids. It is arched anteriorly but not as much as in *Gymnura* (fig. 36C, D) or pelagic stingrays (*Mobula*). It is difficult to determine if a median prepelvic projection is present due to crushing from vertebrae, but if one was present it would have been a short, triangular process similar to extant stingrays other than potamotrygonids (*Urotrygon chilensis* [fig. 36E], *Taeniura lymma* [fig. 36A, B], *Urobatis jamaicensis* [AMNH 30385], *Urolophus cruciatus* [AMNH 59890], species of *Dasyatis*). Also, no pronounced lateral prepelvic processes as in *Potamotrygon* can be seen in †*Asterotrygon*, but the pelvic girdle projects anterolaterally at its corners in some specimens (e.g., FMNH PF 12914, FMNH PF 12990), similar to the condition in *Urotrygon*, *Plesiobatis*, and other stingrays (Nishida, 1990).

There is some evidence of small ischial processes (isp) (Miyake, 1988) on the inner corners of the posterior margin of the pelvic girdle in †*Asterotrygon* (ischial processes are present in most stingrays, and are particularly well developed in potamotrygonids; fig. 16B). In FMNH PF 12989 (right side; fig. 23A), FMNH PF 12990, FMNH PF 14069, and NHM P 61244, these processes appear as ill-defined protuberances. In FMNH PF 14567 and FMNH PF 14097, however, the processes are more triangular and located where the posterior concavity of the pelvic girdle curves inward, as in *Urotrygon* and *Urobatis*. Other than the ischial processes, there are no distinct features of the posterior margin of the girdle, such as median postpelvic processes described and figured by Nishida (1990: fig. 36) for platyrhinids. (Nishida's ''post-pelvic processes'' [also McEachran et al., 1996] seem to amount to irregularities in the posterior surface of the puboischiadic bar, and not to distinct projections. This is corroborated by the apparent absence of any distinct process from *Platyrhina sinensis* [AMNH 26413, AMNH 44055] and from *Platyrhinoidis triseriata* [OSU 40]; Carvalho, in press.) The iliac process (ilp), which also projects posteriorly and medially from the corners of the puboischiadic bar in many stingrays and more basal batoids, may be present in our fossil specimens. However, because this process may overlie or be aligned with the basipterygium to some extent, its identification is difficult in the fossils (FMNH PF 14097). The iliac process is preserved in FMNH PF 12989 (fig. 23A), where it projects posteriorly in an oblique fashion from the pelvic girdle. It is elongated, more or less straight, and tapers posteriorly (extending to at least the sixth radial element in FMNH PF 12989). The iliac process of many extant stingrays may be slightly curved to project medially (and dorsally), and is not as tapered. The iliac process in extant stingrays is not as elongate as in FMNH PF 12989. The iliac process in †*Asterotrygon* may also have a posterodorsal orientation, but this is not evident in the fossils. Obturator foramina (of), through which pass diazonal nerves, are not well preserved, but can be observed in FMNH PF 15180 (one small foramen on right side; fig. 12).

The pelvic fin is also plesodic; the first pelvic radial element is characteristically enlarged (efr), as in many stingray groups, and articulates with the lateral aspect of the puboischiadic bar. Even though it has been called the pelvic propterygium (Nishida, 1990), this element should not be considered the serial homolog of the pectoral propterygium; it is formed by ontogenetic fusion of radials. The numbers of pelvic radials are given in tables 2 and 3, and they fall within the ranges observed in many extant stingrays, increasing slightly in relation to specimen size (cf. Nishida, 1990: 58, table 3). Each pelvic radial in FMNH PF 12989 has at least three segments (four in FMNH PF 14567), the most basal segment being much more elongate than the more distal segments. The most distal segment is bifurcated.

Claspers are present and well developed in only one specimen (figs. 4, 23A). Prismatic calcification is present over the entire axial cartilage (ax), further corroborating that this specimen is sexually mature. The claspers are relatively long and straight, with preserved axial cartilages extending along most of its length. The entire length of the claspers is roughly just under one-third of tail length as measured from posterior margins of pelvics. No beta cartilages can be seen, but this may be preservational. On the right clasper, running more or less parallel to the axial cartilage, there is a slightly curved piece that may be the beta cartilage (terminology from Miyake, 1988). The axial cartilage bends outward slightly at its posterior tip, and the entire clasper is spoon-shaped. Discrete cartilages of the terminal clasper components are not readily observed, but more than one is present. The largest element apparently is the ventral covering piece (ventral terminal cartilage; tc), but only its impression remains in the fossil. Anterior to the ventral terminal cartilage are impressions of the dorsal and/or ventral marginal cartilages.

The dorsal fin is present in most specimens of †*Asterotrygon* in which the distal portion of the tail is laterally preserved to some degree (fig. 24). The dorsal fin is more prominent and well preserved in one female paratype (FMNH PF 14069; fig. 24B) and in specimen FMNH PF 15181 (fig. 24F). NHM 61244, a small neonate, also has a weak impression of the dorsal fin present anterior to caudal stings. The holotype has a small dorsal fin preserved, covered by denticles, but no internal structure is apparent (fig. 24E). In specimens FMNH PF 14069 and FMNH PF 15181 the tail is markedly preserved on its side, accounting for the excellent exposure of the dorsal fin (also FMNH PF 14567; fig. 24D). The dorsal fin is located just anterior to the caudal stings, but its posterior lobe slightly overlaps the caudal stings. Presumably, the overlapping is due to the posterior lobe being free from the dorsal surface of the tail, with the fin inflecting a short distance anteriorly before inserting onto the dorsal tail surface. The fin is relatively small and rounded in outline. Small hooklike denticles are present over most of the fin in most specimens (FMNH PF 15166, FMNH PF 12914, AMNH P 11557), but in both FMNH PF 14069 and FMNH PF 15181 denticles are more apparent on the anterior margin or ridge of the fin. The presence of hooklike denticles covering the dorsal fin or at least its dorsal ridge is a unique feature for †*Asterotrygon*, not occurring in other stingrays where a dorsal fin is present.

The dorsal fin is clearly plesodic in FMNH PF 14069 and FMNH PF 15181, with internal skeletal support primarily composed of slender, elongated radial elements, which radiate from the fin base to the outer fin margin (less evident in FMNH PF 14567). In FMNH PF 15181 the radials bifurcate distally (less so than FMNH PF 14069). Basal components of the dorsal fin endoskeleton also appear to be present in FMNH PF 14069, but these are not present in FMNH PF 15181. These elements are slightly wider than the more distal radials and are organized into a poorly defined row from the fin base to about one-third of its height. The radial elements are very prominent in FMNH PF 14069, extending to the outer fin margin. In this respect the dorsal fin of †*Asterotrygon* resembles the dorsal fin of *Urolophus flavomosaicus* (CSIRO 718.22) and *Aetoplatea zonura* (Nishida, 1990; fig. 41A here), and even the dorsal fins of rajids (Nishida, 1990). The dorsal fins of Recent myliobatids have enlarged basal elements and occupy a greater portion of the dorsal fin base compared to FMNH PF 14069 (*Aetomylaeus maculatus* [AMNH 32500], *Aetobatus narinari* [fig. 41E]; *Myliobatis*, *Rhinoptera*, *Mobula*, *Manta*; Nishida, 1990). The ‘‘basal elements’’ in FMNH PF 14069 are probably not enlarged basal cartilages as in myliobatids, but just small radial segments horizontally arranged (as in *Aetoplatea zonura*; fig. 41A). The height of the dorsal fin is just greater than tail height at the level of the dorsal fin in FMNH PF 14069 and FMNH PF 14567, but in AMNH

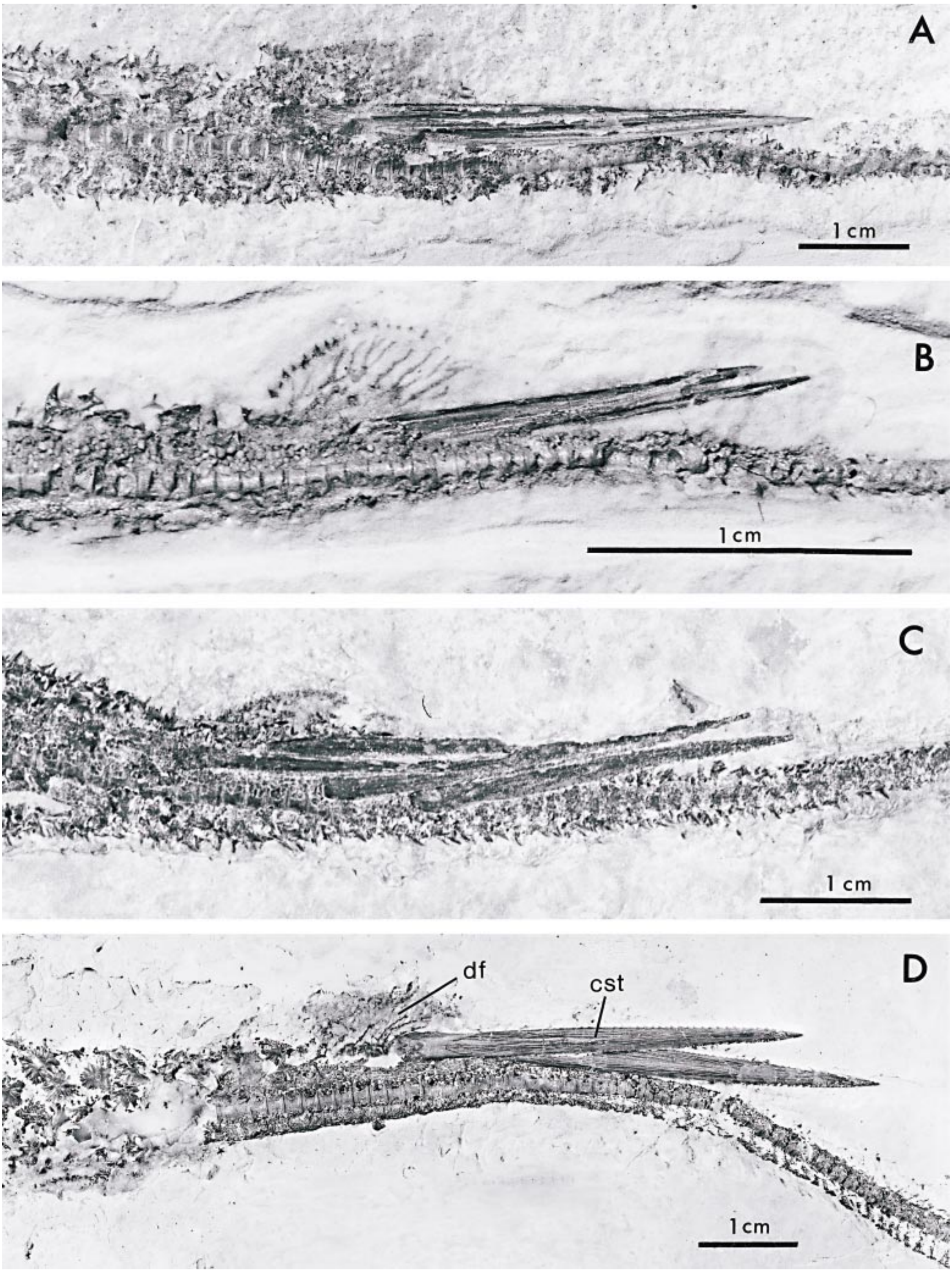


Fig. 24. Dorsal fin and caudal stings of †*Asterotrygon maloneyi*, n.gen., n.sp. **A.** Paratype AMNH P 11557 (specimen in fig. 3). **B.** Paratype FMNH PF 14069 (specimen in fig. 5). **C.** FMNH PF 12914 (specimen in fig. 6). **D.** FMNH PF 14567 (specimen in fig. 7). **E.** Holotype FMNH PF 15166 (specimen in fig. 2; arrowhead showing poorly preserved dorsal fin). **F.** FMNH PF 15181 (specimen is tail only). Morphology of internal skeletal support of dorsal fin is more clearly preserved in panels B and F. Anterior to left.

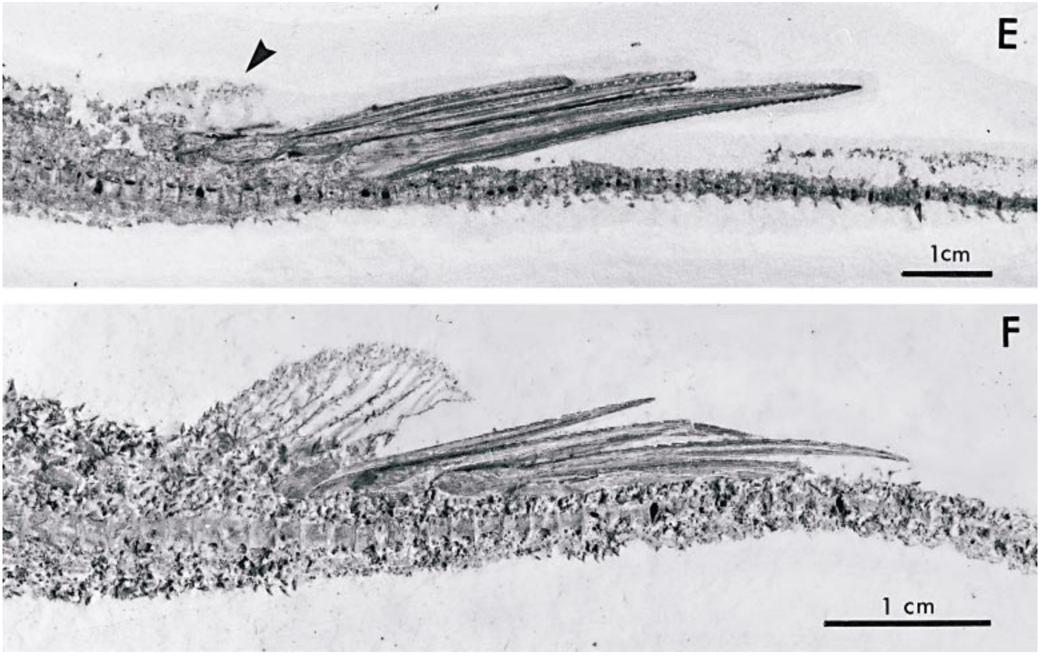


Fig. 24. Continued.

P 11557 and FMNH PF 12914 the dorsal fin is not as tall as the tail at its insertion (fig. 24). This may be due to different orientation of the fin and tail in the specimens. Although the dorsal fin is not apparent in all specimens (usually not in those in which the tail is preserved dorsoventrally), a small cluster of denticles is sometimes observed anterior to the caudal stings, indicating that the fin was originally present (e.g., FMNH PF 12989).

Specimen FMNH PF 12990 is unique in having an impression of a putative caudal fin posterior to the caudal sting (fig. 10A). The fin is incompletely preserved but was apparently rounded dorsally and posteriorly, with a more prominent dorsal lobe and a smaller ventral lobe. If this interpretation is correct, then the caudal fin is similar to some species of *Urobatis*, *Urolophus*, and *Trygonoptera* in being taller than long. Alternatively, the caudal fin in FMNH PF 12990 may represent incompletely preserved tail-folds, as only a small portion of the tail posterior to the caudal sting is present. We cannot be sure because the posterior extent of this ‘‘fin’’ is not known. The tail region posterior to the caudal stings in FMNH PF 14567 (figs. 7, 24D) has small dorsal and ventral elements (rudimentary radials according to Nishida, 1990), reminiscent of dorsal and ventral tail-folds of some *Potamotrygon* species. Rudimentary radials, both dorsal and ventral, are also present in the holotype (fig. 24E), FMNH PF 12989, and to a lesser extent in FMNH PF 14069 (not visible in fig. 24B). In FMNH PF 12989, rudimentary radials occur only on one side of the vertebral column, but it is not possible to discern which side, as the tail is preserved laterally. Low tail-folds were therefore present in †*Asterotrygon*, and it probably extended to the posterior tip of the tail and originated shortly after the caudal stings. The height of the tail-fold both dorsally and ventrally was slightly greater than the height of the tail where the tail-folds originated.

DERMAL SKELETON

DERMAL DENTICLES: In †*Asterotrygon*, the dermal skeleton is composed of numerous small denticles scattered over most of the dorsal surface of the disc, dorsal fin, and tail region, as well as the lateral aspects of the tail. These small denticles are interspersed with larger denticles (or spines) primarily over dorsal middisc and midtail regions. Denticles and spines are preserved in ventral, dorsal, and lateral view, and both ventrally and dorsally preserved specimens display denticles in lateral aspect. The smaller denticles and larger spines are similar in morphology, differing only in size. As in other myliobatiforms, the denticles lack peduncles between the crowns and basal plates. Terminology for dermal denticles is mostly from Deynat and Séret (1996).

Specimens FMNH PF 12989 (fig. 4), FMNH PF 14069 (fig. 5), FMNH PF 12914 (fig. 6), and AMNH P 11557 (figs. 3, 25A) have the densest shagreen. Small denticles are easily observed in most specimens, without the aid of magnification, in the region lateral to the vertebral column between the pectoral and pelvic girdles (offering a convenient way to distinguish †*Asterotrygon* from †*Heliobatis*). The small dorsal denticles are smaller than individual teeth, are present anterior to the snout, and cover the entire dorsal disc region almost to disc margins (figs. 4, 5). In FMNH PF 12989, an adult male specimen (238 mm TL), the denticulation is particularly dense, but this is not a secondary sexual feature, as FMNH PF 12914 (female, 204 mm TL) is also very densely covered, particularly on disc margins (cf. figs. 4 and 6). Paratype AMNH P 11557 has a particularly dense denticulation, especially toward lateral disc surfaces (fig. 25A, B). Small denticles are also present anterior to the neurocranium in a juvenile specimen, but these are barely exposed (FMNH PF 15180; fig. 20). The smaller, more numerous denticles surround larger individual denticles (spines) over mid disc and over much of the dorsal tail region. The holotype (fig. 2) has small denticles scattered on its disc (not as much as in the paratypes), as well as larger denticles over the neurocranium and tail region. Small denticles continue posteriorly to the very tip of the tail and cover the dorsal fin in the holotype and other specimens (e.g., FMNH PF 12914). The shape of the smaller denticles varies according to how worn or eroded they are, but generally the denticles are posteriorly curved, slender and hooklike, and may be very apically pointed (cf. figs. 25D and 38E). The basal plates of the denticles are star-shaped (fig. 25C, D), with three to five or more corners, similar to many potamotrygonids (e.g. Castex, 1967), *Taeniura meyeni* (Smith, 1952), and stingrays in general; the stellate denticle bases (db) are even comparable to some of the denticles of the astraspid *Pycnaspis* from the Ordovician Harding Sandstone of Colorado (Ørvig, 1958; Jarvik, 1980). In †*Asterotrygon*, the corners of the stellate denticle bases are basal ridges that are continuous with the longitudinal crown ridges that project toward the apex of the denticle (da), similar to the denticles of *Manta* described by Gohar and Bayoumi (1959: 198, text-fig. 4). The small denticles generally have very slender crowns compared to the diameter of the basal plates.

The larger spines are similar to the smaller denticles and vary in size as judged from the diameter of their basal plates and the height of their crowns in laterally preserved denticles. The basal plates of these spines can be star- or asterisk-shaped, and many larger spines have irregularly shaped bases, but some of this variation is preservational, as many of the spines are obliquely embedded in the matrix. The longitudinal basal ridges determine the shapes of the spine bases, as in the smaller denticles. The bases are best observed in ventrally exposed specimens (e.g., FMNH PF 15166, FMNH PF 12989, FMNH PF 14069; see also fig. 25). The crowns are posteriorly curved, with relatively sharp apexes on some denticles, while others are more worn. In FMNH PF 12989, where some spines are laterally preserved on the tail region, the width of the crowns at midheight is about equal to that of the basal plates, meaning that the enlarged spines did not have very thin crowns, at least on the dorsal tail surface, as did the smaller denticles. The adult male specimen (FMNH PF 12989) has enlarged nuchal or spiracular spines partially obliterating the postorbital processes and hyomandibulae. This may be an indication of secondary sexual dimorphism, as enlarged spines as such are not present in FMNH PF 14069 (female) or the larger paratype (AMNH P 11557, also female), but this is contradicted by FMNH PF 12914 (female), which also has enlarged spines over lateral and posterior portions of the neurocranium at the level of postorbital processes (as does the holotype, FMNH PF 15166, a large female). The enlarged spines or tubercles occur in more than one row over the tail, as evidenced by FMNH PF 12989, FMNH PF 12914, FMNH PF 14069, FMNH PF 14567, and AMNH P 11557, but whether these were organized in strict rows cannot be determined. Enlarged spines are also present over the middisc region at least at the level of the pelvic girdle (FMNH PF 12989), but possibly extending more anteriorly. These spines are difficult to assess in many specimens because they may be obliterated or dislocated by the vertebral column over the middisc region. FMNH PF 12914 has spines over much of its midline, and these are slightly smaller than the nuchal spines over the neurocranium.

Specimens FMNH PF 14567 (fig. 7) and FMNH PF 14097 have less or no denticulation over lateral disc margins and the anterior snout region. Denticles are present over the middisc region and posteriorly all over the tail as in all other specimens of †*Asterotrygon*. These specimens are from both F-1 and F-2 localities, and both are adult females. They may represent a distinct variety or species of stingray, but are here included in †*Asterotrygon maloneyi* (see above, p. 29). FMNH PF 14097 has small denticles scattered on the slab in which it is preserved, lateral to the tail, which may represent denticles originally present on the dorsal disc or tail region that were dislodged postmortem.

There is no indication in any specimen of †*Asterotrygon* of denticles with enormously enlarged basal plates (tubercles), or of dermal disc bucklers formed by fusion of enlarged denticle bases, as in some extant species of *Potamotrygon* (*P. constellata* and *P. motoro*) and isolated potamotrygonid fossils from South American Miocene deposits (Deynat and Brito, 1994; Lundberg, 1998; Carvalho, Lundberg and Maisey, in prep.). Also absent are denticles with symmetrically arranged crown dichotomies, as in *Potamotrygon yepezi*, *P. motoro*, *P. falkneri*, and *P. schuehmacheri* according to our specimens (see also Castex, 1967; Deynat and Séret, 1996).

CAUDAL STINGS: Caudal stings (cst) are elongated, dorsoventrally flattened, tapering dermal structures, with posteriorly directed serrations on both sides and a very acute extremity (Bigelow and Schroeder, 1953). Caudal stings are hypertrophied dermal denticles (Daniel, 1934) and occur in all extant stingray genera except *Urogymnus*, and in almost all stingray species; their presence is indicative of stingray monophyly. The caudal stings are enveloped in an epidermal sheath in extant stingrays. This sheath contains blood vessels ventrally, adjacent to the longitudinal ridges of the stings, and glandular epithelium towards its periphery, which is responsible for the production of venom (Halstead and Modglin, 1950; Halstead, 1970). The caudal sting is already formed by parturition in extant stingrays (although present, it is slightly less acute in embryos), and this was the case in †*Asterotrygon* as the fetus preserved inside the holotype has a small (13 mm in length) sting that is fully formed (fig. 13).

The caudal stings of †*Asterotrygon* are easily observed in all specimens except USNM 2028; they occur at more or less the posterior one-third of the tail on its dorsal surface (figs. 24, 26). Usually more than one sting is present, but FMNH PF 15181 (fig. 24F), FMNH PF 15166 (fig. 24E), and FMNH PF 12914 (fig. 24C) have four, which is uncommon even among extant stingrays. The lateral serrations along one side of the sting are separated by a space almost as wide as the caudal sting itself in FMNH PF 12989, but in FMNH PF 14069 the lateral serrations are more closely packed together. In FMNH PF 14069, the lateral margins of the caudal sting superficially appear to be smooth, but under greater magnification (25×) lateral serrations are visible at least posteriorly on the caudal sting, and they probably occurred from at least midsting length. The serrations are very small, numerous, and directed almost transversely to the main axis of the caudal sting in FMNH PF 14069 (fig. 24B), but in FMNH PF 12989 the serrations are more slanted posteriorly and are fewer in number (resembling the serrations of the caudal sting of *Plesiotrygon iwamae*). In the holotype (FMNH PF 15166; fig. 24E), the stings are somewhat slanted as well, but not as much as in the male paratype (FMNH PF 12989), and the tip of the dorsalmost sting is broken off and vertically lodged in the tail extremity. The stings are best preserved in FMNH PF

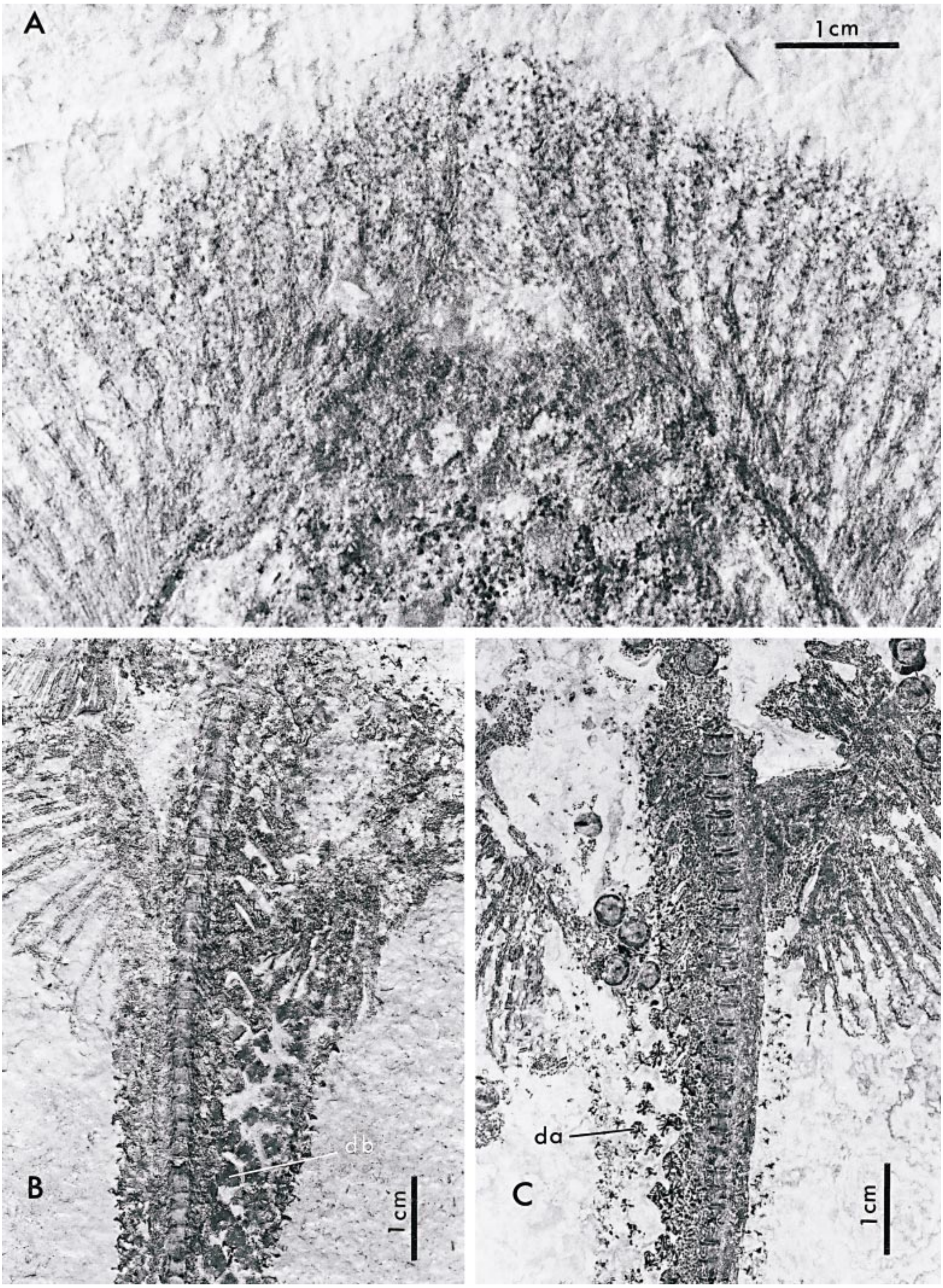


Fig. 25. Denticles of †*Asterotrygon maloneyi*, n.gen., n.sp. **A.** Anterior snout region of paratype AMNH P 11557 in ventral view (specimen in fig. 3). **B.** Base of tail region of paratype AMNH P 11557 (ventral view). **C.** Tail-base area of USNM 2028 (female), in dorsal view (specimen in fig. 10B). **D.** Enlarged view of denticles at base of tail of USNM 2028 from panel C (also figured in Grande 1984:

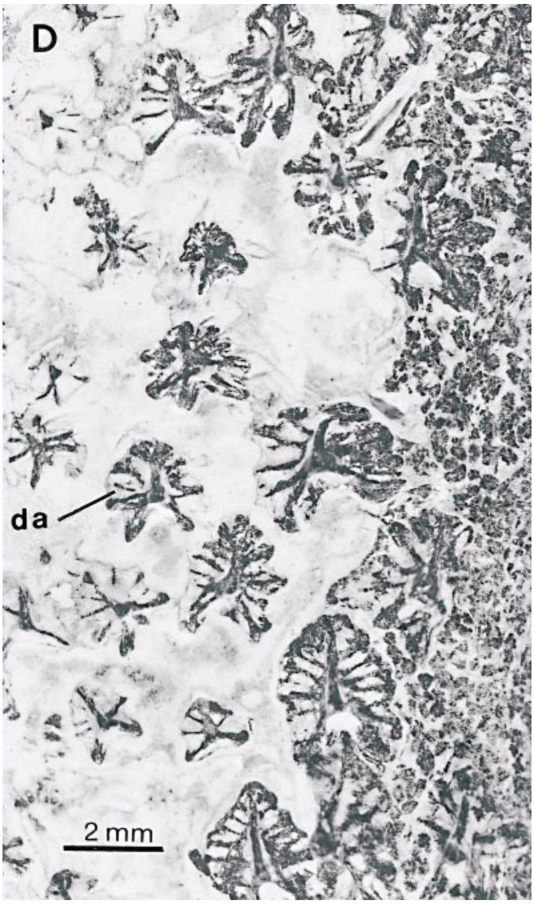


Fig. 25. Continued.

14567 (fig. 24D), where two stings are present and serrations are clearly visible beginning at about midsting and continuing caudally. In FMNH PF 14098 the serrations are shaped as posteriorly curved hooks (fig. 26D), especially close to apex, and are more pronounced compared to other specimens, resembling the stings of species of *Dasyatis*, *Gymnura*, and *Myliobatis* (Bigelow and Schroeder, 1953). All specimens appear to have more numerous, hooklike, and smaller serrations compared to FMNH PF 12989 (an adult male), and the low-angled, slanting serrations of this specimen may be a secondary sexual character.

In cross section, the stings are convex and broadly rounded dorsally, without a median longitudinal dorsal groove that is present in extant stingrays (e.g., *Dasyatis*, *Myliobatis*; Halstead and Modglin, 1950). Ventrally, the two longitudinal grooves extend almost the entire length of the sting on both sides of the elevated ventral median ridge (these are particularly pronounced in the holotype, where the stings are ventrally exposed). These grooves accommodated the elongated venom-producing glandular epithelium as in living stingrays (Halstead and Modglin, 1950; Halstead, 1970). The ventral median ridge is also rounded, but not as broadly rounded as the dorsal surface. The sting itself is made of bonelike dentine, covered by a thin layer of enamel, and penetrated by numerous canals forming a network within the dentine (vasodentine). The canals are visible in cross section in FMNH PF 12989, and in this regard the caudal stings of †*Asterotrygon* are similar to extant stingrays. In FMNH PF 12989, where three stings are present, the dorsalmost sting has a very worn outer surface, with blunt, barely noticeable serrations. The sting underlying the dorsalmost sting has more pronounced and less worn serrations, indicating that †*Asterotrygon* replaced stings as in extant stingrays, that is, from underneath, by shedding the dorsalmost sting. The underlying stings appear longer because of their more posterior attachment on the tail (also in the holotype, FMNH PF 15166). In the fossils (such as the holotype), the basal end of the sting bears two small knobs that help to attach the sting in the dermis as in extant stingrays.

TEETH: The teeth in †*Asterotrygon* were originally in a quincunx arrangement but are now usually scattered between upper and lower jaws, being sometimes displaced as far as the pectoral propterygia. Numerous teeth are present but their rows cannot be counted

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29, fig. II.7a). Note that in panels A and B only ventral aspect of denticle bases are exposed as specimen is ventrally preserved, while in panels C and D dorsal extremities (apexes) of denticles are visible (specimen is dorsally exposed). Anterior to top.

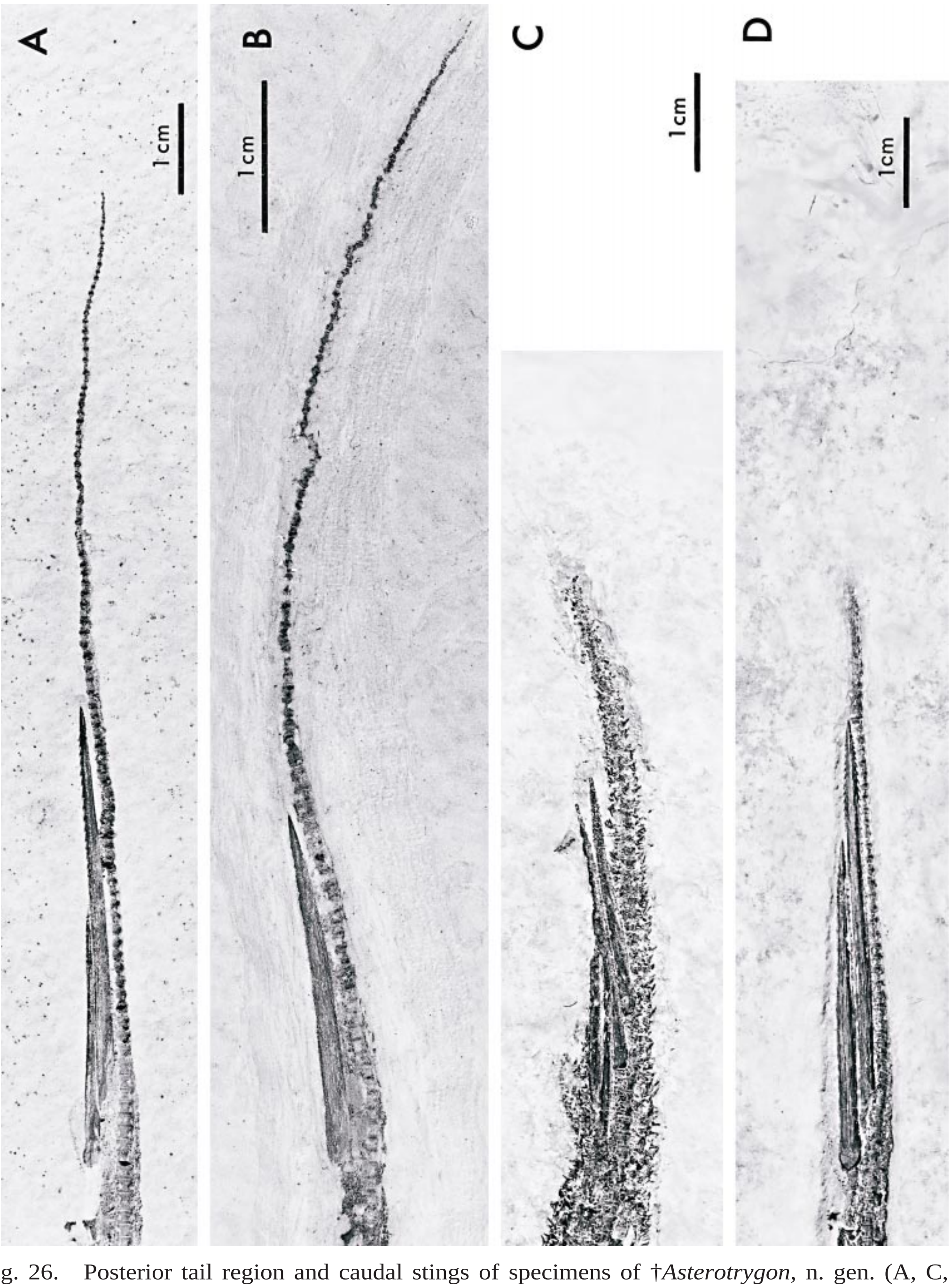


Fig. 26. Posterior tail region and caudal stings of specimens of †*Asterotrygon*, n. gen. (A, C, and D) and †*Heliobatis* (B). Note individual vertebrae continuing posteriorly beyond caudal stings to distal extremity of tail. **A.** FMNH PF 14097 (entire specimen in fig. 9). **B.** AMNH P 19665 (specimen in fig. 28). **C.** FMNH PF 12914 (reversed; specimen in fig. 6). **D.** FMNH PF 14098 (reversed; specimen in fig. 8). Anterior to bottom.

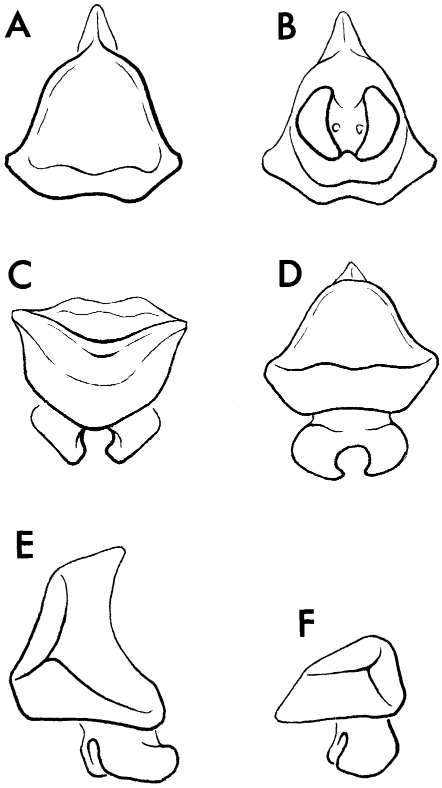


Fig. 27. Teeth of †*Asterotrygon maloneyi*, n.gen., n.sp. Occlusal (dorsal) (**A**), basal (**B**), lingual (**C**), labial (**D**), and lateral (**E, F**) views. Panels A–E from FMNH PF 12989 (paratype; adult male); panel F from FMNH PF 14069 (paratype; female). Teeth are obliquely positioned in order to facilitate comparisons (magnified 60×).

in any specimen. Morphologically, the teeth in †*Asterotrygon* are very similar to †*Heliobatis* and other benthic stingrays (*Dasyatis*, potamotrygonids). Slight sexual dimorphism is evident in the teeth (fig. 27). The root is bilobed, wide, and not very elongated, but not as wide as the root lobes of gymnurids (where root lobes may be wider than the crown in an individual tooth; Cappetta, 1984). There are two nutritive foramina of slightly different sizes present in between both root lobes (one foramen adjacent to each root lobe; fig. 27B). These may correspond to the paracentral foramina of Cappetta (1987). An enlarged central foramen appears to have been absent, as there is no prominent foramen in between both smaller foramina. There are no foramina present directly on the root lobes.

The crown overhangs the root labially and lingually in both sexes. The lingual surface of the crown continues basally to midroot level, while the labial crown surface projects posterodorsally from the top of the root, where a groove separates crown and root (seen in ventral view). It is not possible to establish if heterodonty (monognathic or dignathic) is present due to the scattering of teeth, but smaller teeth appear to be very similar morphologically to larger teeth in the same specimen, the main difference being tooth size and development of the cusp (especially in the male), as smaller teeth have less pronounced cusps than larger teeth.

The tooth crown in the male specimen (fig. 27A–E) is very triangular, lingually oriented, and slightly concave on its lingual side, where the surface is smooth. In females (fig. 27F), the crown is more blunt, less pointed lingually, and may be subtriangular, rounded, or trapezoidal in some specimens (crown shape may also vary within specimens, e.g., FMNH PF 14069). In the male, the crown is more than twice the height of the root in the larger teeth. The teeth are similar between males and females except in differences in the development of the cusps (more pronounced and triangular in males).

ORDER MYLIOBATIFORMES SENSU COMPAGNO, 1973

SUPERFAMILY MYLIOBATOIDEA

†***Heliobatis*** Marsh, 1877

†*Heliobatis* Marsh, 1877 (p. 256; original description, not illustrated; type-species: †*Heliobatis radians* Marsh, 1877, by monotypy; Fossil Butte Member, Green River Formation); Grande, 1980, 1984 (pp. 23–24, figs. II.3–II.5, II.7c; brief description, photographs).

†*Xiphotrygon* Cope, 1879 (p. 333; original description, not illustrated; type-species: †*Xiphotrygon acutidens* Cope, 1879, by monotypy; Fossil Butte Member, Green River Formation); McGrew and Casilliano, 1975 (pp. 21–22; listed, with brief account and illustrated as fig. 14).

Dasyatis: Haseman, 1912 (pp. 98–99; apparently unaware of the availability of †*Heliobatis* Marsh, 1877); Fowler, 1941 (p. 402; listed both †*Heliobatis* and †*Xiphotrygon* as synonyms of *Dasyatis*); Schaeffer and Mangus, 1965 (p. 17); Romer, 1966 (p. 351; †*Heliobatis* Marsh, 1877 listed as a synonym of *Dasyatis* Rafinesque, 1810, along with †*Xiphotrygus* [sic], an unjustified emendation of †*Xiphotrygon* Cope, 1879); Cappetta, 1987 (p. 163; synonymization, without comment, of both †*Heliobatis* Marsh, 1877 and †*Xiphotrygon* Cope, 1879 with *Dasyatis* Rafinesque, 1810).

†*Palaeodasybatis* Fowler, 1947 (p. 14; original description, not illustrated; type-species: †*Palaeodasybatis discus* Fowler, 1947, by original designation and monotypy; Fossil Butte Member, Green River Formation).

DIAGNOSIS (emended): †*Heliobatis* is distinguished from †*Asterotrygon* by lacking intense denticulation composed of minute, closely packed and hooklike denticles over dorsal disc and tail regions; by lacking a dorsal fin anterior to caudal stings; by having a more trapezoidal or subtrapezoidal disc (generally more or less rounded to oval in †*Asterotrygon*); by a more slender tail at base; and tentatively by lacking angular cartilages between the hyomandibula and lower jar (see also diagnosis provided for †*Asterotrygon*, p. 17). †*Heliobatis* is distinguished from all other stingrays that lack a caudal fin, except gymnurids, by presenting individual vertebrae extending beyond caudal stings to the distal tip of tail. From gymnurids, †*Heliobatis* is distinguished by usually having a trapezoidal to subtrapezoidal disc that is longer than wide in most specimens, but never close to twice as wide as long, as is autapomorphic for gymnurids. The lack of a caudal fin distinguishes †*Heliobatis* from urolophids, urotrygonids, *Plesiobatis*, and *Hexatrygon*.

TABLE 4

Measurements and Counts Conducted on Representative Specimens of †*Heliobatis radians*

Values are expressed as mm/percentage of disc width, except for total length (TL) and disc length (DL), which are shown in mm. See Measurements and Terminology for abbreviations of parameters. Specimens are female, except FMNH PF 2020.

	AMNH 19665	FMNH 2020	FMNH 6947
TL	255.2	463.3	336.1[a]
DL	122.0	228.8	192.0[a]
DW	131.2	195.0	194[a]
TAL	155.6/118.6	233.5/119.7	144.0/74.2
TAW	7.0/5.3	8.0/4.1	10.0[a]/5.2
POL	30.0/22.9	56.6/29.0	—
MSC	36.0/27.4	70.8/36.3	—
SCW	33.1/25.2	43.3/22.2	44.4/22.9
PGW	29.3/22.3	41.0/21.0	42.3/21.8
STL	23.9/18.2	42.7/21.9	38.7/19.9
PGT	121.5/92.6	275.9/141.5	185.9/95.8
CL	—	47.0/24.1	—
NCL	31.6/24.1	56.2/28.8	—
NCW	22.1/16.8	34.0/17.4	—
PRO	45	48	32[a]
MES	14	18	15
MET	33	28	31[a]
TPR	93	94	78[a]
PVR	17	17	16
VSP	22[a]	22	25[a]
VPS	80[a]	78	74
VST	115[a]	88	35
TV	217[a]	188	134[a]

[a] Approximate value only due to preservational imperfection, and may represent minimal value for meristic features. In FMNH PF 2020 and FMNH PF 6947, tail width (TAW) actually represents tail height because tail is partially exposed on its side.

DESCRIPTION (emended): Stingrays of moderate size (up to about 500 mm in TL, 240 mm in DL), with generally trapezoidal to subtrapezoidal discs, which are less frequently rounded or oval in outline (slightly rounded in AMNH P 19665, and more oval in FMNH PF 2020). Disc length is greater than disc width in most specimens and is markedly greater in others (FMNH PF 2020; table 4); in some specimens disc length and width are about equal (AMNH P 19665). Disc partially covers pelvic fins, reaching posteriorly to about two-thirds of pelvic fin length in most specimens. Greatest disc width is at about middisc length, at level of scapulocoracoids. Tail length is about equal to disc length but is slightly greater in some specimens (fig. 29); tail is relatively slender at base compared to †*Asterotrygon*, closer to the condition present in some extant benthic genera (e.g., *Urolophus*, *Urotrygon*, *Dasyatis*). Individual vertebrae extend to posterior tip of tail, without a cartilaginous, unsegmented rod posterior to caudal stings, as in extant stingrays that lack a caudal fin (except *Gymnura*). Dorsal surface of disc is mostly naked, without intense shagreen of smaller denticles; smaller denticles over dorsal disc region rarely, if ever, are present (AMNH P 19665 has few very small denticles just anterior to puboischiadic bar; fig. 28); enlarged

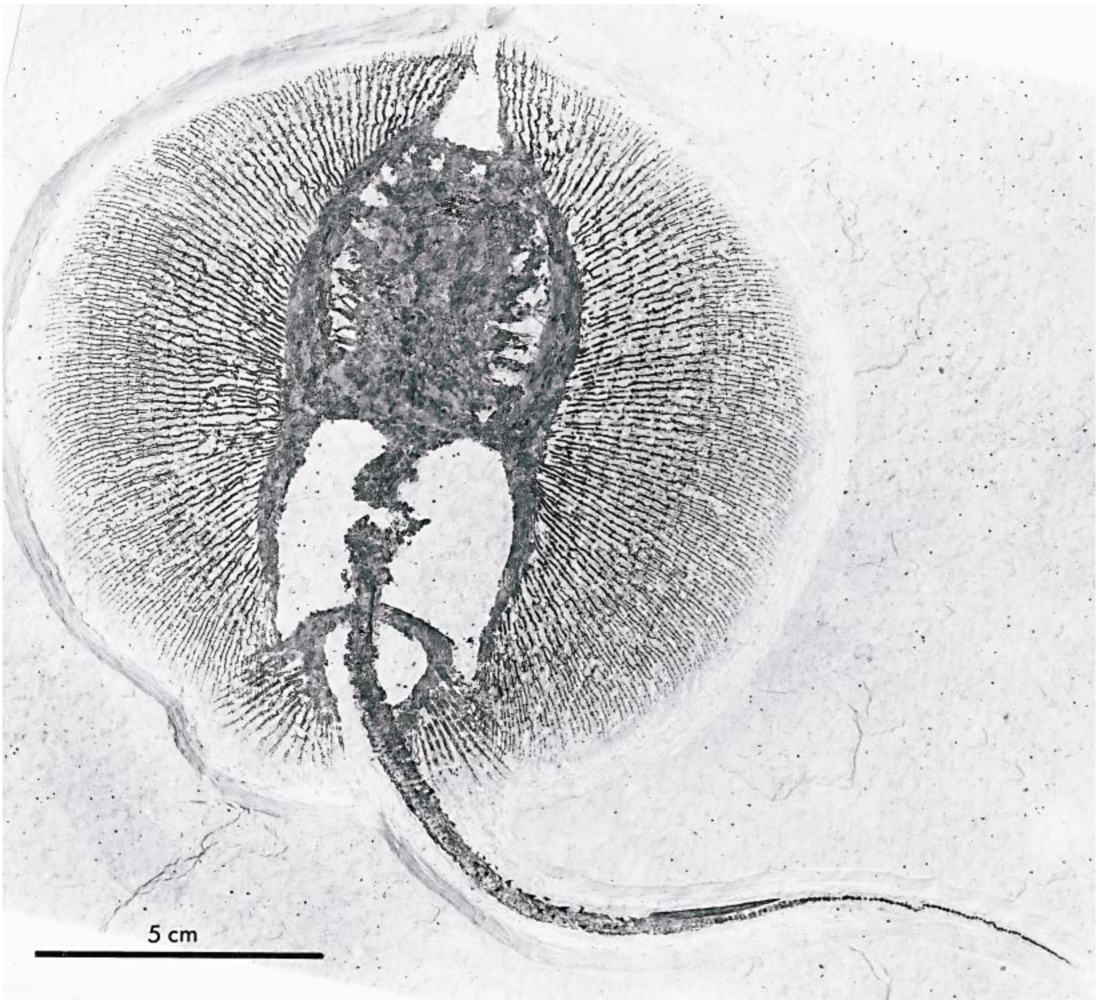


Fig. 28. †*Heliobatis radians*, AMNH P 19665, approximately 255 mm TL subadult (?) female, dorsally exposed (from F-2 locality). Anterior to top.

denticles or spines are present over midline of dorsal disc surface (in some specimens) and dorsally on tail region (in most specimens); spines over midline of disc do not reach scapular area anteriorly, and are confined to region posterior to middisc; smaller and larger denticles on dorsal tail alternate over tail midline in some specimens. Caudal stings are located at midtail region in specimens with intact posterior tail regions (figs. 28, 29), but caudal stings are located farther posteriorly on tail, at about two-thirds of its length, in most specimens. Dorsal and caudal fins are lacking in all specimens.

†*Heliobatis* presents a very similar skeletal anatomy to †*Asterotrygon*, but differs in a few features. Much of the skeleton in †*Heliobatis* is also covered by prismatic calcification. The neurocranium is similar to that of †*Asterotrygon* in general proportions. It also lacks a calcified rostrum or rostral derivatives. There is a median constriction (remnant of the epiphysial bar) at about the anterior one-third of the dorsal fontanelle, as in †*Asterotrygon* and many extant stingrays. The dorsal fontanelle is elongated, becoming slender posteriorly, and occupies a large extent of neurocranial length as in †*Asterotrygon*. In FMNH PF 2020 (fig. 29) the nasal apertures are well preserved and demonstrate

Fig. 29. †*Heliobatis radians*, FMNH PF 2020, approximately 463 mm TL adult male (terminal cartilages of claspers indicated by arrowhead), ventrally exposed (from F-1 locality). Anterior to top.

that the internasal septum was slender, but probably not as much as in specimen FMNH PF 12989 of †*Asterotrygon* (fig. 18). The neurocranium is widest at the level of nasal capsules, and these abut the inside margin of the pectoral propterygium. A median indentation or notch is present anteriorly on the neurocranium between the nasal capsules. A preorbital process is present, but usually is obliterated by the jaws. The antorbital cartilages are slender and triangular, tapered posteriorly and contacting the inner margins of the propterygia. The orbital regions are relatively long, occupying about two-thirds of neurocranial length. Postorbital processes are shelflike, projecting laterally and obliquely, and separated from the supraorbital crest by a notch (very clear in AMNH P 19665 and FMNH PF 2020; figs. 28, 29). Therefore the supraorbital crest bears a small triangular protuberance (the supraorbital process) anterior to postorbital processes. The parietal fossa is not evident in most specimens, and the posterior corners of neurocranium are rectangular in outline. Jugal arches are absent.

The palatoquadrate and Meckel's cartilage have rounded outlines in most specimens, especially at their outer corners, and occupy almost the entire space between pectoral propterygia. The jaw outline varies slightly among specimens, as AMNH P 19665 has more angular lower jaw corners compared to FMNH PF 2020 (this variation is probably preservational). Neither upper nor lower jaws are fused with their antimeres at the midline. Hyomandibulae are well preserved in most specimens, appearing as relatively stout cartilages attached to the neurocranium just posterior to the postorbital processes. Hyomandibulae project ventrally and anteriorly to contact jaws through the hyomandibular-Meckelian ligament (AMNH P 856). There is some evidence in FMNH PF 2020 of prismatic calcification (angular cartilages?) between the hyomandibula and Meckel's cartilage, as observed in some specimens of †*Asterotrygon*, but more specimens are required for confirmation. The hyomandibulae are devoid of hyoid rays. The pseudohyoid and gill arches are not clearly visible in any specimen, but the fifth ceratobranchial (and perhaps the fifth epibranchial) elements contact the scapulocoracoid posteriorly. Anterior epibranchial elements articulate with the lateral surface of the synarcual in FMNH PF 2020. Branchial rays are numerous and extend laterally, almost contacting the propterygia.

The propterygium contacts the pectoral girdle by means of a double articulation, one anterior and one posterior. The propterygium is stout and contains a ridge along most of its length for dorsal constrictor muscles. It appears to become segmented at the midnasal capsule level (FMNH PF 2020). The mesopterygium is small and subtriangular, but its precise morphology is difficult to discern. It does not have a sinuous lateral margin articulating directly with radials as in *Urolophus* and *Trygonoptera*. The metapterygium is almost as long as the propterygium, but is not as stout. The scapulocoracoid is similar to †*Asterotrygon*, with posteromedially directed scapular processes that articulate with the suprascapulae. There is no sign of a dorsal fenestra as in certain extant stingrays (e.g., *Urotrygon*, *Taeniura*). The coracoid bar is transversely elongate and slender, with a concave anterior margin and straight posterior aspect (best preserved in AMNH P 19665). Pectoral radials become bifurcated at the level of their eighth or ninth segment, do not contact each other laterally as in *Gymnura* and some myliobatids (*Myliobatis* and *Aetobatus*), and extend posteriorly to almost cover the pelvic fin radials. The pelvic girdle is slightly arched and has stout corners. No prepelvic process is present, and the girdle is similar to that of most benthic stingrays. It is unclear whether ischial processes are present in †*Heliobatis*. Posteriorly directed iliac processes are present on both sides of the girdle but do not extend as far posteriorly as in †*Asterotrygon* (FMNH PF 12989). The basipterygium is slightly curved posteromedially. Pelvic fin radials become bifid at their third or fourth segment. Claspers of adult males range from about one-third to one-fourth of tail length and are longer than pelvic girdle width. They have a calcified and elongated axial cartilage, and at least three smaller terminal pieces, representing probably the dorsal and ventral terminal cartilages and at least one marginal cartilage (FMNH PF 2020). Beta cartilages cannot be discerned.

The cervicothoracic synarcual is indistinct morphologically to that of †*Asterotrygon*. Neural arches are relatively elongated and flattened laterally, somewhat spatulate (as in extant stingrays and †*Asterotrygon*), with enlarged neural arches posterior to the thoracolumbar synarcual extending caudally to the midlength of the tail. Vertebral centra are morphologically similar to those of †*Asterotrygon*. Ribs are lacking altogether. The thoracolumbar synarcual extends posteriorly about one-third of distance between shoulder and pelvic girdles, and has individual centra throughout its length. In AMNH P 19665, the tail region is laterally exposed, as indicated by the caudal stings situated dorsal to the caudal vertebrae. If †*Heliobatis* had a dorsal fin, it would be clearly evident in this specimen, which lacks any indication that one was originally present.

The enlarged dermal denticles over the midline of the tail and caudal stings are both morphologically similar to those in †*Asterotrygon*. The teeth are closely packed and are as numerous as in many extant stingrays. Morphologically, they are similar to teeth of †*Asterotrygon*, with a single, elevated triangular crown in males and a more blunt, trapezoidal crown in females. In AMNH P 19665, remarkably, the teeth have mostly retained their original configuration, forming partially discrete anteroposterior rows.

REMARKS: Specimens of †*Heliobatis radians* have been collected from both F-1 and F-2 in great numbers, making it the most abundant fossil stingray known from semicomplete skeletons, having been featured in textbooks and popular accounts as representing a ‘‘typical’’ fossil stingray (e.g., Stevens and Last, 1994; Frickhinger, 1995; Long, 1995; note that Stevens and Last [1994: 61] mistakenly credited †*Heliobatis* as being from the Jurassic of Utah). Our smallest adult male specimen is about 330 mm in TL (around 190 mm in DW), but it is probable that the onset of sexual maturity occurred at an earlier stage.

There is some degree of variation in †*Heliobatis radians*, especially in relation to disc shape (cf. figs. 28 and 29). However, the outermost segments of the pectoral fin radials may not leave clear impressions, and the disc is not entirely preserved in many specimens. Therefore, it is difficult to determine whether this ‘‘variation’’ is really intraspecific or merely preservational, or if it is an indication of greater species diversity within †*Heliobatis*.

Examination of photographs and illustrations of the type-specimens of both †*Xipho-*

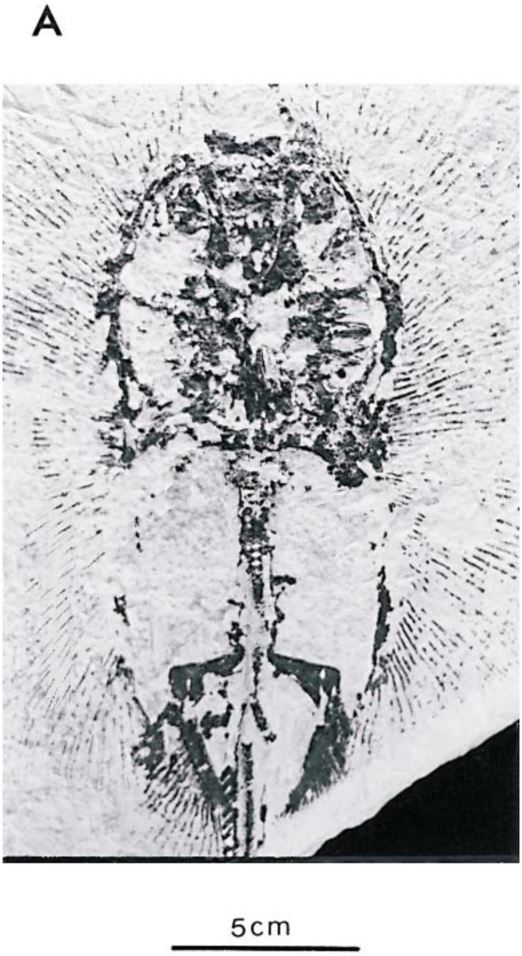


Fig. 30. †*Heliobatis radians*. **A.** Holotype of †*Heliobatis radians* Marsh, 1877 (YPM 528); note that tail region posterior to disc is missing. **B.** Holotype of †*Palaeodasybatis discus* Fowler, 1947 (ANSP 8344), length given as 345 mm TL in original description, but specimen missing distal tip of tail; note that radials of disc and pelvic fins are painted over. This specimen has recently been reported as missing (Spamer et al., 1995: 83). Anterior to top.

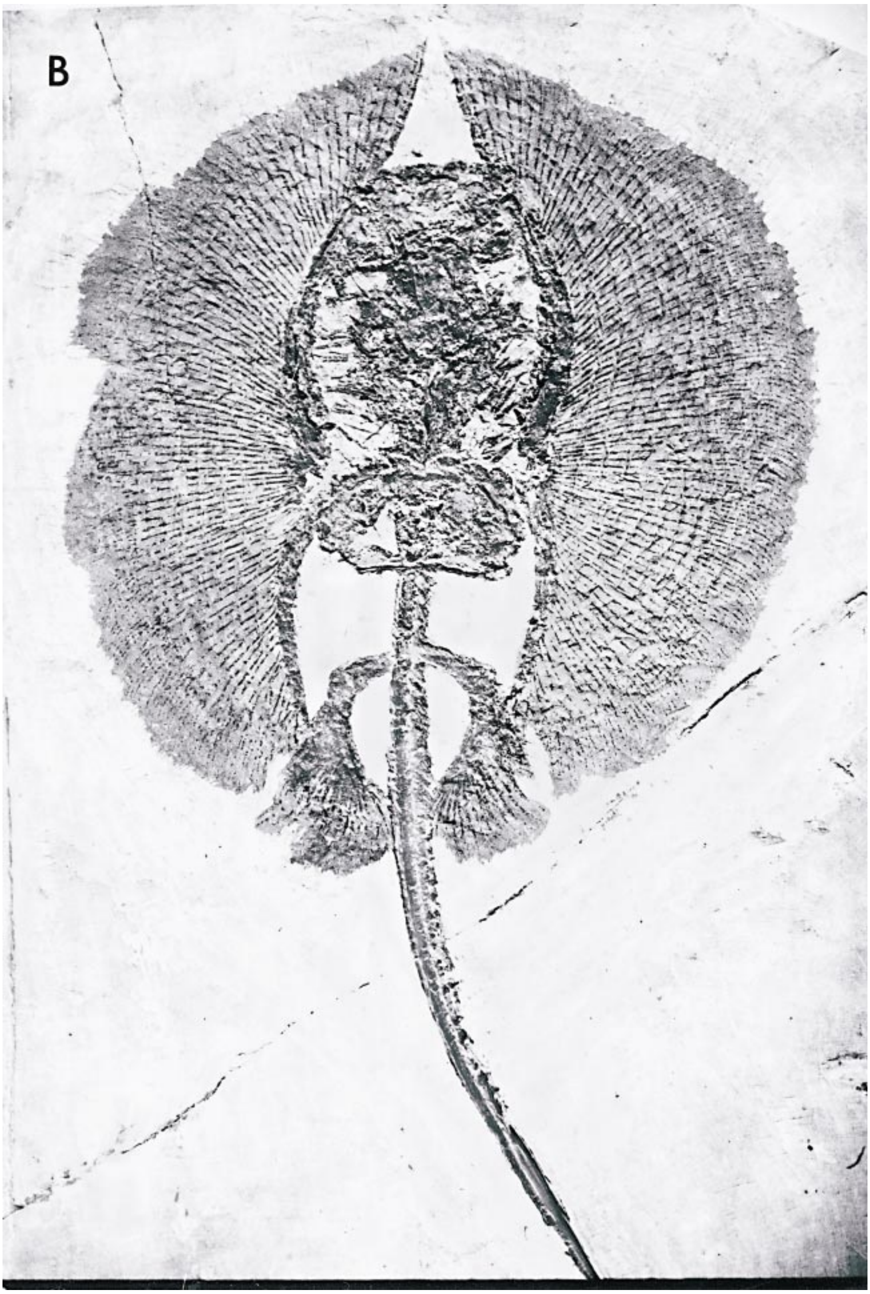


Fig. 30. Continued.

trygon acutidens Cope, 1879 (Cope, 1884) and †*Palaeodasybatis discus* Fowler, 1947 (fig. 30B) support their synonymy with †*Heliobatis radians* Marsh, 1877 (as previously concluded by Grande, 1980, 1984). All three nominal taxa are morphologically similar in disc shape and proportions, and lack the denticulation and dorsal fin of †*Asterotrygon maloneyi*. The tail region is not preserved in the holotype of †*H. radians* (fig. 30A), but because it lacks the minute denticles over disc, snout, and base of tail regions, we can be certain that all three above-mentioned nominal species are synonymous and clearly distinct from †*Asterotrygon maloneyi*. The original types of both Cope's and Fowler's nominal species are reported to be lost (Grande, 1984; Spamer et al., 1995), but the holotype of †*H. radians* is available (YPM 528) (fig. 30A). Bigelow and Schroeder (1953) doubted the synonymy of both †*Heliobatis* Marsh, 1877 and †*Xiphotrygon* Cope, 1879 with *Dasyatis* Rafinesque, 1810, contrary to Fowler (1941).

ETYMOLOGY: The generic name stems from *helios*, the Greek word for sun, and *batis*, which is Greek for ray (the ''sun-ray''). Gender feminine.

INCLUDED SPECIES: Presently monotypic.

†***Heliobatis radians*** Marsh, 1877

Figures 26B, 28–30, table 4

†*Heliobatis radians* Marsh, 1877 (p. 256; original description, not illustrated); Grande, 1980, 1984 (pp. 24–30, figs. II.3–II.5, II.7c; description, photographs); Stevens and Last, 1994 (p. 61; photograph); Frickhinger, 1995 (p. 212; photograph, brief account); Long, 1995 (p. 87; photograph).

†*Xiphotrygon acutidens* Cope, 1879 (p. 333; original description, not illustrated); Cope (1884; further description, illustrated).

Dasyatis sp.: Haseman, 1912 (pp. 98–99).

†*Palaeodasybatis discus* Fowler, 1947 (pp. 14–15; original description, not illustrated); Grande, 1980, 1984 (p. 24, fig, II.5; first published photograph of type specimen, reported lost); Spamer et al., 1995 (p. 83; type-catalog, specimen confirmed as missing).

†*Dasyatis radians*: Cappetta, 1987 (p. 163; transferal without comment of †*H. radians* Marsh, 1877 to *Dasyatis* Rafinesque, 1810).

DESCRIPTION: As for genus.

MATERIALS: *Holotype*: YPM 528, missing tail region (figured in Grande, 1984: 30, fig. II.7c; reproduced here as fig. 30A). *Other specimens examined*: AMNH P 856, male, exposed in ventral view, with tip of tail missing (ca. 370 mm TL, 210 mm DL; Twin Creek); AMNH P 857, female, exposed in ventral view (Newberry coll.); AMNH P 2474, probably female, exposed in ventral view, with tail tip posterior to stings missing (ca. 210 mm DL); AMNH P 2475, appears to be exposed in dorsal view; AMNH P 2985, female, exposed in ventral view, with left side of disc and tail just posterior to base not preserved; AMNH P 4345, adult male, exposed in ventral view (ca. 410 mm TL, 200 mm DL; Twin Creek); AMNH P 7828, adult male (illustrated in Schaeffer and Mangus, 1965), exposed in ventral (?) view; AMNH P 9873, adult male, with distal tip of tail missing, exposed in ventral view (ca. 400 mm TL, 230 mm DL); AMNH P 9874, teeth only; AMNH P 19665, subadult female, exposed in dorsal (?) view, from F-2 (fig. 28); ANSP 8344 (holotype of †*Palaeodasybatis discus* Fowler, 1947, apparently lost, photograph in Grande, 1984: 27, fig. II.5; reproduced here as fig. 30B); DMNH 1530 (no further data); FMNH PF 2020, adult male, exposed in ventral view, from F-1 (fig. 29); FMNH PF 6947, female, exposed in dorsal view, from F-1; FMNH PF 10283 (tentatively identified), adult male, exposed in dorsal view, from Thompson Ranch (F-2); FMNH PF 25009, adult male, exposed in ventral view, from F-2 (specimen on exhibit); SMMP 77.27.1; SMMP 83.2.4; UW 11577; ZMB 1981.0 (adult male, F-2). *Other referred material* (not examined): UW 12309 (figured in McGrew and Casilliano, 1975).

STRATIGRAPHIC HORIZON: Fossil Butte Member of the Green River Formation, Ypresian stage (corresponding to the North American Wasatchian stage) of the late early Eocene epoch (some 52 million years before present).

ETYMOLOGY: The trivial name *radians* is derived from *radius*, Latin for ''spoke'', referring to the radial disposition of the pectoral fin rays. Gender feminine.

STINGRAY CHARACTERS OF †*ASTEROTRYGON*

†*Asterotrygon* and †*Heliobatis* are unquestionably stingrays, sharing with other myliobatiforms the following synapomorphies: (1) caudal sting(s); (2) thoracolumbar (or second) synarcual cartilage; (3) absence of ribs; (4) laterally expanded, shelflike postorbital processes; (5) loss of the jugal arch from the posteroventral corners of the neurocranium; (6) articulation between scapular process of shoulder girdle and cervicothoracic synarcual cartilage of ball-and-socket type; (7) basihyal cartilage transverse, small and a

separate element, located between the first hypobranchials (see phylogenetic analysis below); (8) first pair of hypobranchials relatively straight and obliquely oriented from the ventral pseudohyoid bar to articulate with the basihyal; (9) anterior expansion of the medial (basibranchial) plate (see phylogenetic analysis below). These characters are further discussed in Compagno (1973, 1977), Miyake (1988), Nishida (1990), McEachran et al. (1996), in the morphological description of †*Asterotrygon* above, and in the phylogenetic analysis below. Characters 7, 8, and 9 are considered synapomorphies of stingrays for the first time in this study (see below), but are dependent on the topology considered, as all three features are lacking in pelagic (myliobatid) species; if this monophyletic group is basal to the remaining stingrays (e.g., appendix 2), then these features are derived at a less inclusive node within Myliobatiformes.

Some characters currently accepted as synapomorphies of stingrays cannot be found in our fossil specimens due to incomplete preservation, such as the absence of the abdominal canal of the lateral-line system on the coracoid bar (character 18 of McEachran et al., 1996), and the nasal curtain extending posteriorly to level of the mouth opening (character 10 of McEachran et al., 1996; also present in *Trygonorrhina*, electric rays, and skates, but these are considered by McEachran et al. to have evolved independently).

†*Asterotrygon* possesses other characters traditionally thought to be derived for stingrays, but that have recently been demonstrated to occur in *Zanobatus* as well (*Zanobatus* was previously considered to be a platyrhinid, but hypothesized as being the sister-group of stingrays by McEachran et al., 1996). These are the reduction of the rostral cartilage in adults (even though it is frequently present as the rostral extremity in stingray juveniles, and *Zanobatus* retains a filamentous, hyaline rostral cartilage), and the arched and relatively narrow puboischiadic bar. We have dissected one specimen of *Zanobatus* and examined radiographs of others, and we confirm the presence of the narrow and arched pelvic girdle, along with a stout hyomandibular-Meckelian ligament (the angular cartilages, however, are absent from our dissected material; cf. McEachran et al., 1996). Another feature of †*Asterotrygon* previously thought to be unique to stingrays, but that also has a greater distribution, is the posterior extension of the propterygium beyond the procondyle to contact the scapulocoracoid between the pro- and mesocondyles. McEachran et al. (1996) used this character to further unite *Zanobatus* to stingrays, but it is also present in both species of *Platyrhina* (AMNH 44055, 26413, MNHN 1307, MNHN uncatalogued; Carvalho, in press).

PHYLOGENETIC RELATIONSHIPS OF THE GREEN RIVER STINGRAYS

The objective of this section is to place †*Asterotrygon* and †*Heliobatis* in a larger phylogenetic framework of extant stingrays. Fossil stingrays other than †*Heliobatis* and †*Asterotrygon* are not included in the analysis, but they will be in upcoming studies of the Monte Bolca stingray fauna. The phylogenetic analyses below are not intended to solve all problems regarding the relationships among dasyatid genera, and do not address the larger issue of whether certain benthic stingray genera are monophyletic (e.g., *Taeniura*, *Dasyatis*; *Himantura* is unquestionably not monophyletic and is coded accordingly). The issues of whether the Daystidae and its component genera are monophyletic, as well as the immediate sister-group relationships among ‘‘dasyatid’’ stingrays, are still terra incognita and currently the most persisting problems in stingray systematics.

PHYLOGENETIC PROCEDURES AND CODING

Characters that do not vary within the ingroup (synapomorphies of Myliobatiformes) were excluded from the matrix (characters 1–6 and 8 listed above), as were characters restricted to terminal taxa (autapomorphies). However, autapomorphies were included if a character is present in one terminal and scored as uncertain or unavailable (?) in another, or if the autapomorphy is part of a multistate series. *Dasyatis* and *Urobatis* are each coded as a single terminal, contrary to the coding of Lovejoy (1996), but similar to that of McEachran et al. (1996). Lovejoy coded *Dasyatis* as two separate terminals be-

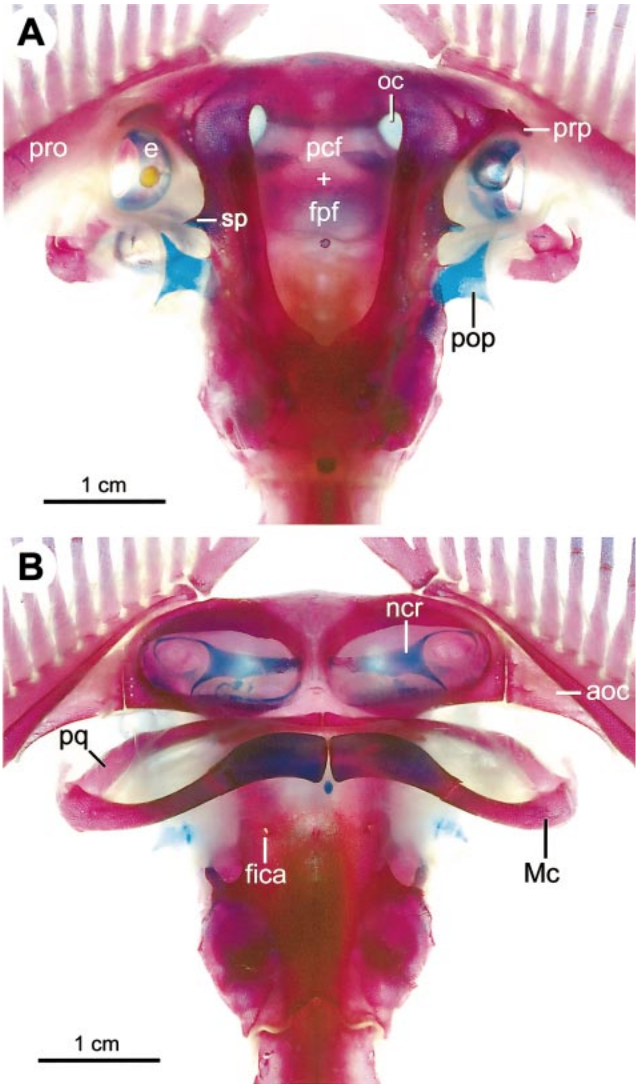


Fig. 31. Neurocranium of cleared-and-stained specimen of *Gymnura micrura* (FMNH 89990) in dorsal (**A**) and ventral (**B**) views (same specimen as in fig. 15). Anterior to top.

cause the species he examined of this genus differed in one character (character 3 below; however, it is not entirely clear what species of *Dasyatis* are included in each of Lovejoy's terminals). We have coded *Dasyatis* as uncertain for this character. *Urobatis* was coded in Lovejoy (1996) as two terminals, one each for Pacific and Atlantic species, which differed in two characters in his matrix (his characters 19 and 21). *Urobatis* is coded here as a single terminal because only one of these characters is included in our analyses (character 25 [= character 19 of Lovejoy, 1996], coded here as polymorphic for *Urobatis*). The other character used by Lovejoy, degree of extension of the lateral stay of the cervicothoracic synarcual cartilage, is not included because the degree of extension of the lateral stay is difficult to properly divide into discrete categories (as also concluded by McEachran et al., 1996). Lovejoy's (1996) matrix coded *Plesiotrygon* and *Potamotrygon* identically, as well as for Indo-west Pacific *Himantura* and ''*Dasyatis* 1''. These

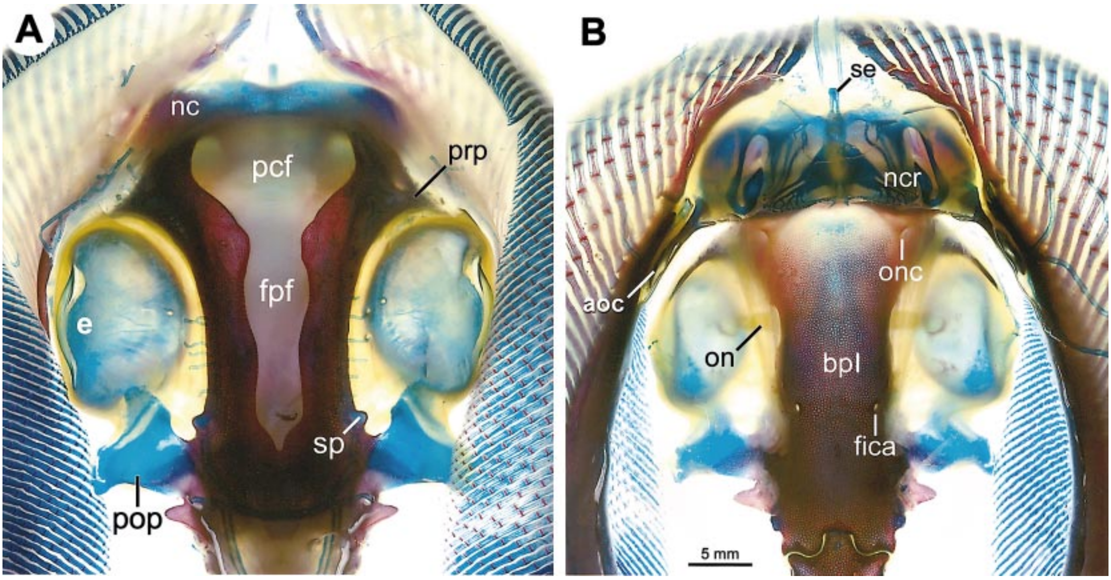


Fig. 32. Neurocranium of cleared-and-stained specimen of *Taeniura lymma* (AMNH 44079) in dorsal (**A**) and ventral (**B**) views. Note that the structure between the nasal capsules (se) is formed by chondrified sensory canals (probably at the junction of the prenasal and subrostral canals), and is not the rudimentary rostral base. Anterior to top.

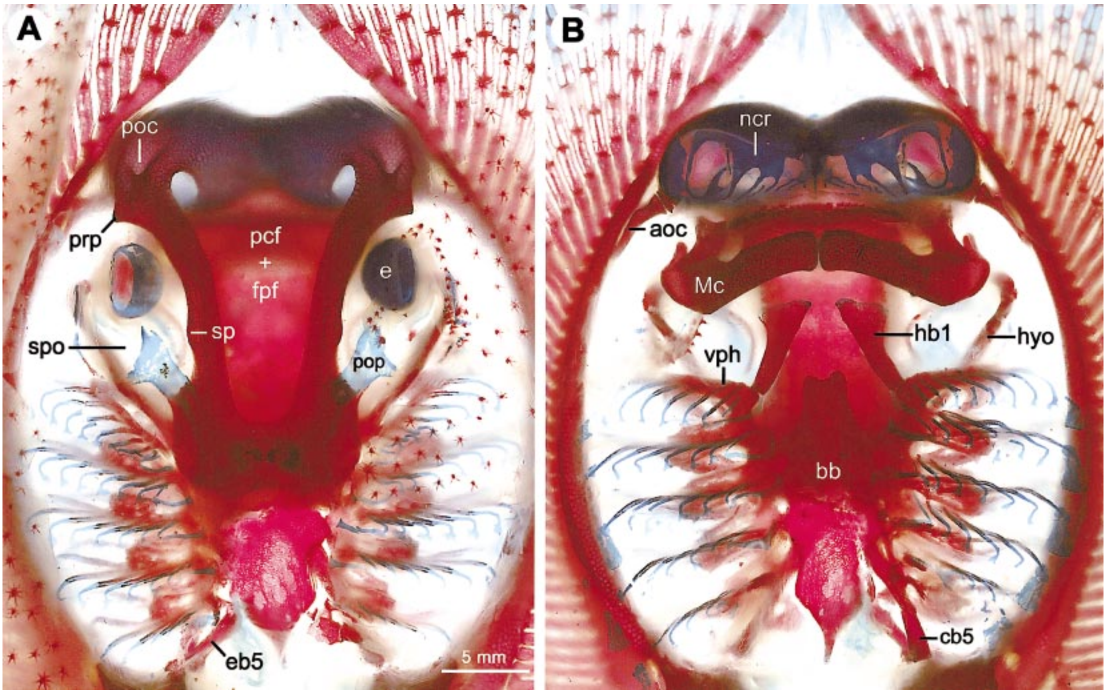


Fig. 33. Neurocranium and visceral arches of cleared-and-stained specimen of *Urotrygon chilensis* (FMNH 93737) in dorsal (**A**) and ventral (**B**) views (same specimen as in fig. 14). Synarcual has been removed, but gill arches remain in original position. Anterior to top.

TABLE 5

Matrix for the Phylogenetic Analysis of Stingrays

Himantura represents Indo-west Pacific species only, whereas "*Himantura*" represents amphi-American species (*H. schmardae* and *H. pacifica*); "P" = polymorphic (0, 1), "-" = inapplicable, and "?" = unknown (see character descriptions for discussion and justifications).

	1	1 1 1 1 1 1 1 1 1 2	2 2 2 2 2 2 2 2 2 3	3 3 3 3 3 3 3 3 3 4	4 4 4 4
	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4
Rhinobatos	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0
Raja	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 0 0 0
†*Heliobatis*	? ? ? ? 0 0 ? ? 0 0	0 ? 1 ? 0 0 0 0 0 ?	? ? ? ? ? 0 0 0 0 0	0 0 1 0 1 ? ? ? ? ?	? ? 0 ?
†*Asterotrygon*	? ? ? ? 0 0 ? ? 0 0	0 ? 1 1 0 0 0 0 0 1	? ? 1 ? ? 0 0 0 0 0	0 0 0 0 1 ? ? ? ? ?	? ? 0 ?
Hexatrygon	0 0 ? ? 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 1	? 0 1 0 0 0 0 0 0 0	0 0 1 0 0 0 ? 0 ? 0	0 0 0 0
Plesiobatis	0 0 0 1 0 0 0 0 1 0	0 1 1 0 0 0 0 0 0 1	1 1 0 0 2 0 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 0 0 1
Urolophus	0 0 0 1 0 0 0 1 1 0	0 1 1 0 1 0 0 0 0 1	1 1 1 0 0 0 0 0 0 2	0 0 P 0 0 0 0 0 0 0	0 0 0 1
Trygonoptera	0 0 0 1 0 0 0 1 0 0	0 1 1 0 0 0 0 0 0 1	1 1 1 0 0 1 0 0 0 2	0 0 0 0 0 0 ? 0 0 0	0 0 0 1
Urobatis	1 0 0 1 0 0 0 0 0 0	0 1 1 0 0 0 0 0 0 2	1 1 1 0 P 1 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 1 0 1
Urotrygon	1 0 0 1 0 0 0 0 0 0	0 1 1 0 0 0 0 0 0 3	1 1 1 0 0 1 0 0 0 0	0 0 1 0 0 0 0 0 0 0	0 1 0 1
Paratrygon	0 0 2 1 0 0 0 0 0 0	0 1 1 0 0 0 0 0 0 2	1 1 1 0 0 0 0 0 0 0	1 0 1 1 2 0 0 0 0 1	1 0 0 1
Plesiotrygon	0 0 1 1 0 0 0 0 0 0	0 1 1 1 0 0 0 0 0 2	1 1 1 0 1 0 1 0 0 0	1 0 1 1 1 0 2 0 0 1	1 0 0 1
Potamotrygon	0 0 1 1 0 0 0 0 0 0	0 1 1 1 0 0 0 0 0 2	1 1 1 0 1 0 1 0 0 0	1 0 1 1 1 0 2 0 0 1	1 0 0 1
"*Himantura*"	0 0 0 1 0 0 0 0 0 0	0 1 1 1 0 0 0 0 0 2	1 1 1 0 0 1 0 0 0 0	0 0 1 1 2 0 2 0 0 0	0 0 0 1
Taeniura	0 0 0 1 0 0 0 0 0 0	0 1 1 0 0 0 0 0 0 2	1 1 1 0 0 1 0 0 0 0	0 0 1 1 1 0 1 0 0 0	0 0 0 1
Himantura	0 1 P 1 0 0 0 0 0 0	0 1 1 0 0 0 0 0 0 2	1 1 1 0 0 1 0 0 0 0	0 0 1 1 2 0 0 0 0 0	0 0 0 1
Dasyatis	0 1 P 1 0 0 0 0 0 0	0 1 1 0 0 0 0 0 0 2	1 1 1 0 0 1 0 P 0 0	0 0 1 1 1 0 0 0 0 0	0 0 0 1
Pteroplatytrygon	0 1 0 1 0 0 0 0 1 0	0 1 1 0 0 0 0 0 0 2	1 1 1 0 0 1 0 0 0 0	0 0 1 1 1 0 0 0 0 0	0 0 0 1
Gymnura	0 1 0 1 0 0 0 0 0 1	0 1 0 0 0 0 0 0 0 1	1 1 1 0 0 0 0 1 1 1	0 1 1 0 2 0 0 0 0 0	0 0 0 1
Myliobatis	0 2 0 1 0 0 1 0 0 1	1 1 1 0 1 ? 1 1 1 3	1 2 0 1 0 1 0 1 1 0	0 0 0 1 2 1 0 1 1 0	0 0 1 1
Aetobatus	0 2 0 1 0 0 1 0 1 1	1 1 1 0 1 1 1 1 1 3	1 2 0 1 - 1 - 2 1 -	0 1 0 1 2 1 0 1 1 0	0 0 2 1
Rhinoptera	0 2 0 1 1 1 1 0 1 1	1 1 1 0 1 1 1 1 1 3	1 2 0 1 - 1 - 2 0 -	0 1 0 1 2 1 0 1 1 0	0 0 3 1
Mobula	0 2 0 1 1 1 1 0 1 1	1 1 0 0 1 1 0 1 0 3	1 2 0 1 - 1 - 2 0 -	0 1 0 1 2 1 0 1 1 0	0 0 3 1

taxa are not identically coded in our matrix, however, due to the inclusion of additional characters and differential coding of others. Genera not available for study, or insufficiently described anatomically in the literature, are not included in our analysis (e.g., *Pastinachus* and *Urogymnus*; the former is monotypic and the latter has two species). Because specimens of *Aetoplatea* were unavailable, only *Gymnura* is coded for the Gymnuridae. *Himantura* is coded as two terminals, following Lovejoy (1996), because the amphi-American species (*H. schmardae* and *H. pacifica*) form a monophyletic group (Carvalho and Lovejoy, in prep.) and are morphologically very distinct from the other species of *Himantura*, all of which are Indo-west Pacific in distribution. The genera of Potamotrygonidae are coded separately because we provide additional observations for some of their characters, some of which may have an effect on relationships within the family. The outgroups included are composed of two more distantly related batoids (a guitarfish and a skate), but our morphological comparisons included all batoid groups. All multistate characters were run as unordered (characters 2, 3, 20, 22, 25, 28, 30, 35, 37, and 43). The final matrix (table 5) is composed of 44 characters, but about a dozen additional characters were considered for inclusion and eventually discarded because they either varied intraspecifically or proved too difficult or arbitrary to divide into discrete states, and were therefore deemed inappropriate for phylogenetic analysis in the present context. Character coding should be as precise and explicit as possible, involving confirmation in more than one specimen of a given terminal when enough material is available, as accurate scoring is a fundamental prerequisite of phylogenetic analysis (Patterson and Johnson, 1997; Grande and Bemis, 1998), especially in groups that have previously manifested high levels of homoplasy.

Phylogenetic analyses were conducted using Hennig86 (Farris, 1988), and implemented with the aid of the software Tree Gardiner (Ramos, 1997) and WinClada (Nixon, 1999). An exact parsimony strategy (*ie) was employed to search for all equally most parsimonious trees. Nodes were diagnosed with the aid of the Dos Equis (xx) function of Hennig86 and with tree diagnostics featured in Tree Gardiner and WinClada. The matrix was also run in Nona (Goloboff, 1999), which produced the same results as Hennig86 (with fewer minimum-length trees, however). Characters used to diagnose nodes are only those that displayed the same optimization on all of the equally most parsimonious trees (i.e., only unambiguous characters were used to diagnose monophyletic groups; the mapping of conflicting characters onto the strict consensus tree artificially increases its length due to its polytomies, and it is therefore less parsimonious than any of the original trees). The strict consensus tree is depicted in figure 43. Characters that are ambiguous due to multiple optimizations that require the same number of steps are resolved by favoring reversals over independent gains. This procedure was also used for characters scored as unknown (?) in the Green River fossils but that could be pushed farther down the tree (which assumes, therefore, that they were present in the fossils), as this procedure saved a step for each character (characters 12, 22, and 44; all ambiguous characters are shown separately in fig. 44). Accelerating the transformations of these characters ascribes a greater generality to their distribution, which is considered to be a more coherent implementation of parsimony (for a review, see discussion in Schuh, 2000). However, ambiguous characters in which a step is *not* saved by accelerating their transformations (characters scored with a ‘‘?’’ in at least one terminal), are placed at the node where they are known to occur only with certainty (see fig. 44; these features were not pushed farther down the tree; in other words, no assumptions were made about their presence in taxa scored as uncertain when no steps could be saved; see legend of fig. 44 for more details).

CHARACTER DESCRIPTIONS

The numbers below correspond to character numbers in the matrix (table 5). Terminals in which the character is present are given in brackets after the respective character-state description (except for state 0). Literature citations containing more morphological information are included for characters when appropriate. Table 6 provides the length (number of steps), consistency index (CI), and retention index (RI) for all characters, as well as the number of minimum-length trees in which each character is present with these indices, including the strict consensus tree (see Farris, 1989, for a discussion of these indexes). For most characters these indices are optimal for all minimum-length trees. If more than one solution is possible for a given character in a subset of the minimum-length trees, than variations in length, CI, and RI are given for each subset in table 6.

LATERAL-LINE CANALS

1. *Tubules of the subpleural components of the hyomandibular lateral-line canals*: not branched at extremities (0); extremities dichotomously branched (1) [*Urobatis*, *Urotrygon*]. This character is described and figured for *Urobatis jamaicensis* and *Urotrygon microphthalmum* in Lovejoy (1996). Garman (1888) and Chu and Wen (1979) provided more detailed descriptions of the lateral-line system in batoids. Both †*Asterotrygon* and †*Heliobatis* are coded as unknown.

2. *Subpleural components of the hyomandibular lateral-line canals*: posterior branch extends caudally more or less parallel to longitudinal body axis (0); posterior branch inflects towards midline to form a ‘‘lateral hook’’ (1) [Indo-west Pacific *Himantura*, *Dasyatis*, *Pteroplatytrygon*, *Gymnura*]; posterior branch inflects to continue anteriorly almost parallel to anterior branch, forming a large indentation (2) [*Myliobatis*, *Aetobatus*, *Rhinoptera* and *Mobula*]. The condition in *Hexatrygon* is unknown. This character is illustrated and described in Lovejoy (1996). Species of *Dasyatis* are slightly variable in relation to the size and shape of the lateral hook; however, they do not present the extreme condition of pelagic stingrays. Both

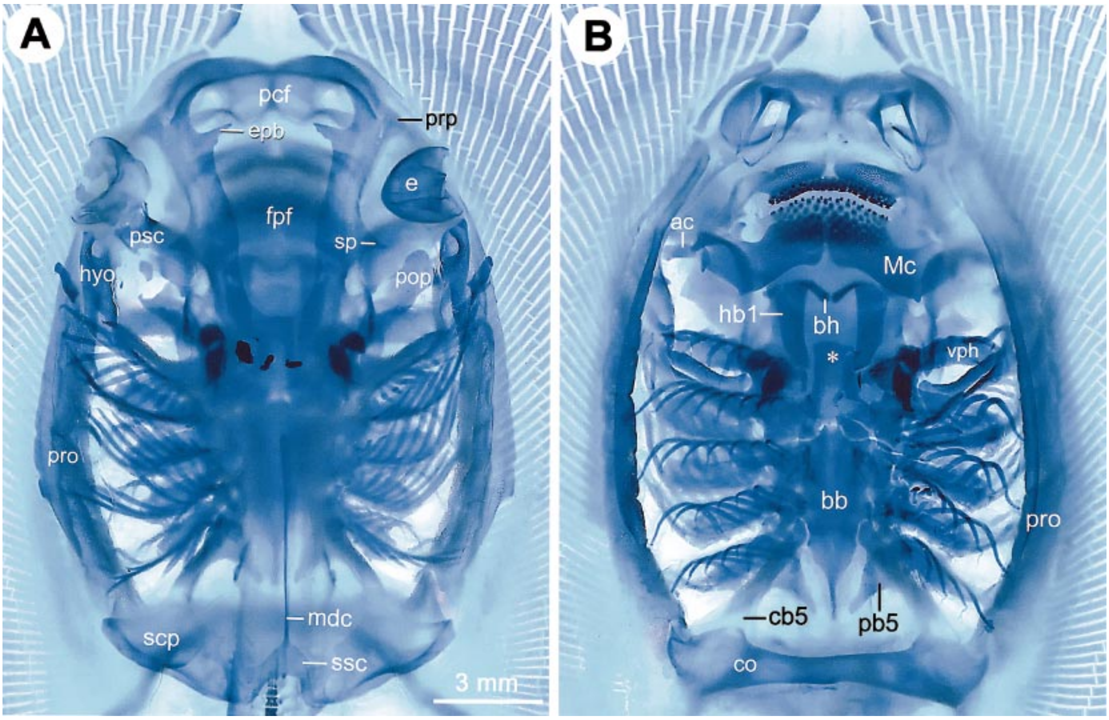


Fig. 34. Neurocranium and visceral arches of *Potamotrygon motoro* (FMNH 94503), stained only with alcian blue, in dorsal (**A**) and ventral (**B**) views (gill arches and synarcual in place). Asterisk denotes anterior extension of basibranchial plate (which is fragmented posteriorly). Anterior to top.

†*Asterotrygon* and †*Heliobatis* are coded as unknown.

3. *Suborbital components of the infraorbital lateral-line canals*: projecting posteriorly lateral to mouth (0); projecting posteriorly lateral to mouth and anteriorly lateral to nasal openings (1) [*Potamotrygon*, *Plesiotrygon*]; forming a complex weblike pattern on lateral aspects of the anteroventral disc region (2) [*Paratrygon*]. According to Lovejoy (1996), certain species of *Dasyatis* and *Himantura* (Indo-west Pacific species) present another state of this character, ''extensive reticulation and looping'' (Lovejoy, 1996: 216). Both taxa were scored here as uncertain, as one species, *Himantura imbricata*, shows yet another condition for this character (Lovejoy, 1996; McEachran et al., 1996). *Hexatrygon*, †*Asterotrygon*, and †*Heliobatis* are coded as unknown.

4. *Scapular loops formed by scapular components of the trunk lateral-line canals*: absence of loops (0); presence of scapular loops (1) [all terminals except *Hexatrygon*, †*Asterotrygon*, †*Heliobatis*, and outgroups]. This character was compiled from McEachran et al. (1996), and first described by Garman (1888). The condition in *Hexatrygon* is coded as unknown, following McEachran et al. (1996). This feature is not available in †*Asterotrygon* and †*Heliobatis*, which are also coded as unknown.

SKELETON

5. *Anterior process of neurocranium*: absent (0); present (1) [*Rhinoptera* and *Mobula*]. In these pelagic genera, the processes (present on each side of the neurocranium, representing forward extensions of the lamina orbitonasalis from the nasal capsules) provide support for the cephalic lobes (fins); the process is absent from both Green River stingrays. This character is also utilized in the analyses of Nishida (1990), Lovejoy (1996), and McEachran et al. (1996). Figured in Nishida (1990: 28, fig. 17). The anterior processes are clearly absent from both †*Asterotrygon* and †*Heliobatis*.

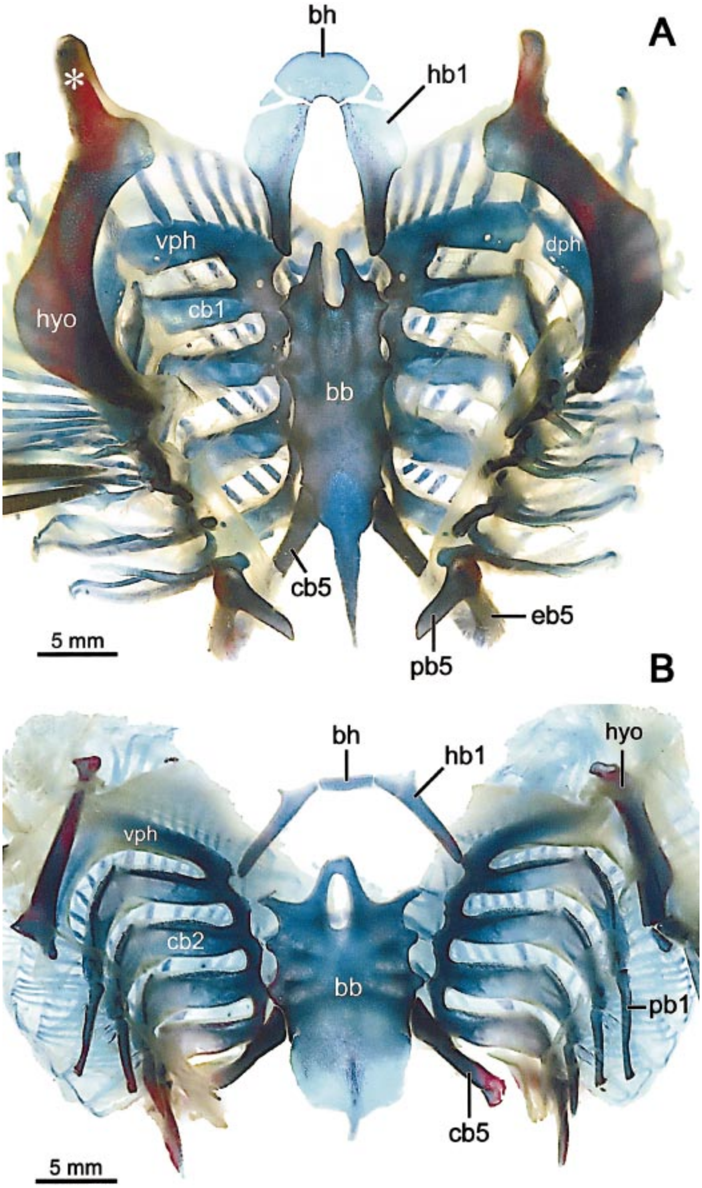


Fig. 35. Dorsal view of gill arches of (**A**) *Taeniura lymma* (AMNH 44079) and (**B**) *Gymnura micrura* (FMNH 89990). Dorsal elements pulled slightly to each side to reveal ventral gill arch structures with more clarity. Asterisk in panel A indicates expanded distal extension of left hyomandibula that articulates with Meckel's cartilage through the hyomandibular-Meckelian ligament. Anterior to top.

6. *Preorbital process*: present (0); absent (1) [*Rhinoptera* and *Mobula*]. The preorbital processes are widespread in batoids, but are also absent in torpediniforms (which lack a supraorbital crest altogether) and in *Rhinoptera* and *Mobula* among stingrays. This character, like the previous one, is formed by the lamina orbitonasalis according to Miyake et al. (1992a), but by a different component of the lamina, justifying its coding as a separate character (also McEachran et al., 1996). The preorbital process is present in both Green River stingrays (e.g., fig. 18).

7. *Preorbital canal for the passage of the*

superficial ophthalmic nerve: dorsally located (0); anteriorly located (1) [*Myliobatis*, *Aetobatus*, *Rhinoptera* and *Mobula*]. This feature was described by Nishida (1990) and utilized by McEachran et al. (1996; as the ‘‘anterior preorbital foramen’’) in their phylogeny. The condition in †*Asterotrygon* and †*Heliobatis* is obscured, and they were therefore coded as unknown for this character, but it is reasonable to infer that the preorbital canal opened dorsally at the junction between the nasal capsules and supraorbital crest, as both fossil taxa have the nasal capsules and anterior cranial roof configured as in other benthic stingrays (changing their coding to state 0 does not affect the resulting phylogeny).

8. *Foramen for the optic (II) nerve*: moderately sized (0); very enlarged (1) [*Urolophus* and *Trygonoptera*]. This condition was first described by Miyake (1988) for ‘‘Australian-western Pacific *Urolophus*’’, and it was included by Lovejoy (1996) in his analysis (as an autapomorphy of *Urolophus*). Even though the different states of this feature may seem at first inspection to be somewhat arbitrary and qualitative, the size of the foramen is very distinct between urolophids and other stingrays according to our observations (see also Miyake, 1988). We confirm its presence in *Trygonoptera* (*Trygonoptera mucosa* [CSIRO H 898–06]; *T. testacea* [CSIRO H 33, CSIRO H 838–05, CSIRO H 837–06]; *T. ovalis* [CSIRO A 2817]). Both †*Asterotrygon* and †*Heliobatis* are coded as unknown.

9. *Postorbital process of neurocranium*: infraorbital lateral-line canal separates postorbital process from small, anterior triangular outgrowth (supraorbital process) of the supraorbital crest (0); postorbital process with small foramen for passage of infraorbital lateral-line canal (1) [*Plesiobatis*, *Urolophus*, *Pteroplatytrygon*, *Aetobatus*, *Rhinoptera*, and *Mobula*]. *Myliobatis* has the infraorbital canal passing ventrally anterior to the postorbital process (Meng, 1984; Nishida, 1990), while most pelagic taxa have the infraorbital canal running through it. There is some doubt as to the condition in *Aetomylaeus*, also a myliobatid. Meng (1984) described and depicted three species of *Aetomylaeus* as having the more general condition (state 0), while Nishida (1990) illustrated *Aetomylaeus nichoftii* as having the more restricted state (specimens of *Aetomylaeus* were not available for dissection). All other pelagic taxa have the more restricted character state (Garman, 1913; Nishida, 1990; McEachran et al., 1996), as observed in *Aetobatus narinari* (AMNH 222833) and *Mobula kuhlii* (AMNH 15319). In *Trygonoptera*, the supraorbital process is clearly present and is somewhat enlarged, with a deep groove for the infraorbital lateral-line canal, according to the material we examined (contra Nishida, 1990: 34). †*Asterotrygon* and †*Heliobatis* both present the supraorbital process (e.g., fig. 18; but see description of †*Asterotrygon* above, p. 42).

10. *Extent of orbital region*: orbital region of neurocranium long (0); shortened orbital region with more anteriorly placed supraorbital and postorbital process (1) [*Gymnura*, *Myliobatis*, *Aetobatus*, *Rhinoptera*, and *Mobula*]. †*Asterotrygon* and †*Heliobatis* have the primitive condition, as do the remainder of stingrays. This feature corresponds to character 28 of McEachran et al. (1996), in which it was coded as part of a multistate character relating to the development of the postorbital process. This feature is less pronounced in *Myliobatis* (Garman, 1913; Meng, 1984; Nishida, 1990).

11. *Postorbital process*: without ventrolateral projection (0); continuing ventrolaterally to form a cylindrical projection (1) [*Myliobatis*, *Aetobatus*, *Rhinoptera*, and *Mobula*]. †*Asterotrygon* and †*Heliobatis* do not show any ventrolateral extensions of their postorbital processes (e.g., figs. 18, 19), but this character would hardly be preserved in fossils (it is not preserved in the myliobatid †*Promyliobatis* from Monte Bolca), as the extensions are very slender, uncalcified filaments. Described in Nishida (1990) and included in the phylogeny of McEachran et al. (1996).

12. *Ventrolateral expansion of nasal capsules*: nasal capsules laterally expanded (0); nasal capsules ventrolaterally expanded (1) [all terminals except *Hexatrygon* and outgroups]. Nishida (1990) described the nasal capsules of *Plesiobatis* as being only laterally expanded, but McEachran et al. (1996) coded *Plesiobatis* as having the more derived

condition, citing Miyake (1988). Miyake (1988) and Lovejoy (1996) both examined the same specimen and agreed that the nasal capsules are ventrolaterally expanded in *Plesiobatis*, and Miyake's figure of its neurocranium (1988: 166, fig 36a) corroborates this. Therefore, ventrolateral expansion of the nasal capsules is coded as derived for *Plesiobatis* and all other myliobatiforms except *Hexatrygon*. Note that electric rays also have (independently) ventrolaterally expanded nasal capsules (Carvalho, 1999).

13. *Articulation between hyomandibula and Meckel's cartilage*: hyomandibulae directly attached to lower jaws (0); hyomandibulae articulating with lower jaws through strong, stout ligament (hyomandibular-Meckelian ligament) at distal tip (1) [all terminals except *Hexatrygon*, *Gymnura*, *Mobula*, and both outgroups]. This ligament, dubbed the ''hyomandibulo-Meckelian tendon'' by McEachran et al. (1996), is very obvious in dissected and cleared-and-stained specimens as a stout and somewhat rigid structure. The thick ligament tightly connects the distal ends of the hyomandibulae to the posterior aspect of Meckel's cartilage on each side. Within the ligament some degree of calcification may occur (see next character). Primitively, the hyomandibulae are positioned closer and more in parallel to the lower jaws, contacting the lower jaws throughout their length by means of smaller ligaments (such as in the electric ray genus *Narke*). This is the general condition in nonmyliobatiform batoids. The hyomandibular-Meckelian ligament is widespread among stingrays (except *Hexatrygon*, mobulids, and gymnurids), but is particularly well developed in *Taeniura lymma*, *Himantura schmardae* and *H. pacifica*, all examined species of *Potamotrygon*, and *Plesiotrygon iwamae*. *Paratrygon aiereba* has a much shorter ligament in comparison to other potamotrygonids. Dissection of *Dasyatis sabina*, *Urobatis jamaicensis*, *U. halleri*, *Urolophus aurantiacus*, *Pteroplatytrygon*, and other taxa revealed a ligament not as robust in comparison. We confirm that *Zanobatus* also has a pronounced hyomandibular-Meckelian ligament (McEachran et al., 1996; these authors regarded *Zanobatus* to be the sister-group of stingrays). Platyrhinids, however, are primitive for this character. Both †*Asterotrygon* and †*Heliobatis* are coded with the derived condition (see anatomical description for details, p. 48).

14. *Angular cartilages*: absence of angular cartilages within hyomandibular-Meckelian ligament (0); presence of angular cartilages within ligament (1) [*Potamotrygon*, *Plesiotrygon*, amphi-American *Himantura*, †*Asterotrygon*]. The presence of angular cartilages has been used previously as an indicator of potamotrygonid monophyly, although *Paratrygon* lacks them altogether according to our radiographed and dissected specimens. There is variation in this character within *Potamotrygon* (fig. 40), as some species have two cartilages lying in parallel in the ligament, while others have only a single cartilage, as in *Plesiotrygon* (fig. 40F). The morphology of the angulars may vary from spool-shaped to very elongated and concave in species of *Potamotrygon* with single angulars. In *Potamotrygon signata* (MCZ 600) the angulars are close to one-half the length of the hyomandibula (fig. 40E). The first angular is usually more robust than the second in species of *Potamotrygon* with paired angulars (*P. leopoldi*, *P. henlei*, *P.* cf. *ocellata*, *P. orbignyi*), but there is variation here as well because in *P. brachyura* the posterior angular element is more stout. The presence of angulars within the ligament has been used as evidence of a monophyletic group composed of amphi-American *Himantura* and potamotrygonids (Lovejoy, 1996; McEachran et al., 1996). The angulars of *Himantura schmardae* and *H. pacifica* are, however, somewhat distinct from the much larger and discretely shaped cartilages of *Potamotrygon* and *Plesiotrygon*, and they are only tentatively coded with state 1 here. *Himatura schmardae* has minute angulars, difficult if not impossible to discern in radiographs, and these may vary intraspecifically. Some specimens of *Himantura schmardae* possess scattered, nonprismatic calcification within the ligament (which strengthens it considerably) in addition to, or in place of, the small angular cartilages. This is very similar to the condition observed in one specimen of *Trygonoptera testacea* (USNM 39993; fig. 40B), but not in other specimens examined of the same species, and all other species of *Trygonoptera* lack discrete angu-

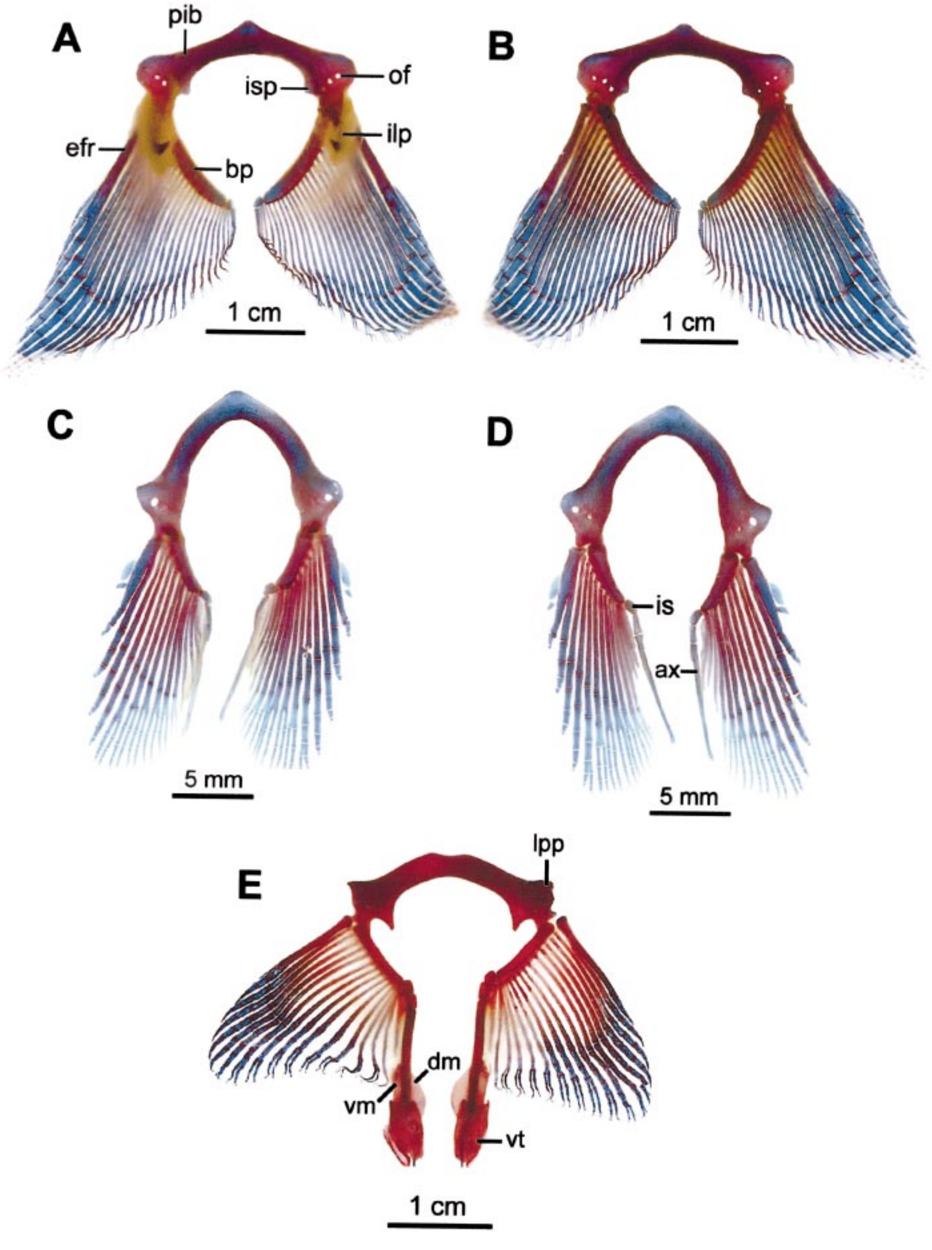


Fig. 36. Pelvic girdles of cleared and stained stingrays. **A.** Dorsal view of *Taeniura lymma* (AMNH 44079). **B.** Ventral view of same. **C.** Dorsal view of *Gymnura micrura* (FMNH 89990). **D.** Ventral view of same. **E.** Ventral view of *Urotrygon chilensis* (FMNH 93737). The pelvic girdle of *Potamotrygon* sp. is shown in figure 16B. Anterior to top.

lars. The occurrence of the small, discrete angulars in more than one specimen of *H. schmardae* indicates that it is probably not simply a result of stress or any other ''external'' factor, as may be the case in *Trygonoptera* and in other putative stingrays with scaterred, nonprismatic calcification. McEachran et al. (1996) illustrated the presence of an angular cartilage in *Zanobatus*, but dissection of a specimen did not reveal it (al-

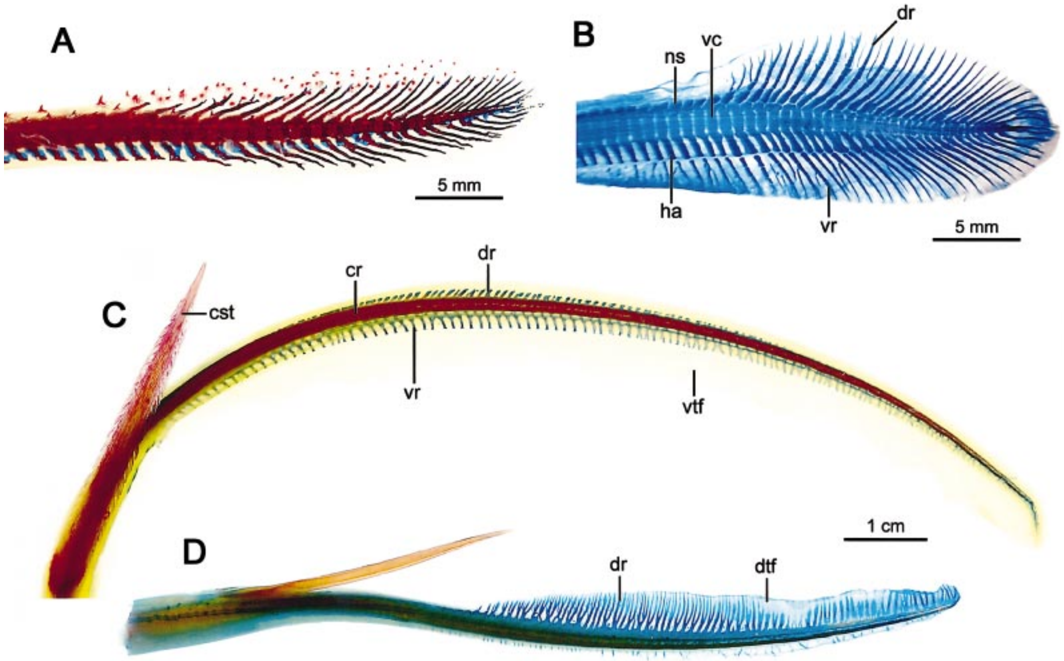


Fig. 37. Caudal fin extremities in representative stingray taxa (cleared and stained). **A.** *Urotrygon chilensis* (FMNH 93737); note dermal denticles on dorsal aspect. **B.** *Urobatis jamaicensis* (stained with alcian blue only; AMNH 30385). **C.** *Taeniura lymma* (AMNH 44079). **D.** *Potamotrygon* cf. *motoro* (AMNH 38138). Scale is same for panels C and D. Anterior to left.

though it has a well-developed hyomandibular-Meckelian ligament). However, a small ‘‘angular’’ does appear in a radiograph of another specimen of *Zanobatus* (ZMH 4617), but this appears more posterior in the ligament and is here interpreted as the secondary hyomandibular cartilage (see next character). Angular cartilages are altogether lacking in platyrhinids. †*Asterotrygon* is coded here as having angulars (see anatomical description above, pp. 48, 49).

15. *Secondary hyomandibular cartilages*: absent (0); present (1) [*Urolophus*, *Myliobatis*, *Aetobatus*, *Rhinoptera*, and *Mobula*]. Lovejoy (1996) and McEachran et al. (1996) described this character, which is figured for pelagic stingrays in Garman (1913). We observed the small cartilage in various species of *Urolophus*. Both †*Asterotrygon* and †*Heliobatis* are coded as not having secondary hyomandibular cartilages, but their absence may be preservational, as the cartilages are generally small and poorly calcified.

16. *Symphysial fusion of upper and lower jaws*: antimeres separate at symphysis (0); both antimeres of jaws symphysially fused (1) [*Aetobatus*, *Rhinoptera*, and *Mobula*]. †*Asterotrygon* and †*Heliobatis* clearly have the antimeres of both the upper and lower jaws separate at symphysis (fig. 21), as do all benthic stingrays and some pelagic taxa (some species of *Myliobatis* and *Aetomylaeus*). *Myliobatis* is coded as polymorphic for this character (as in Lovejoy, 1996; McEachran et al., 1996).

17. *Mandibular width at symphysis*: lower jaws slender at symphysis (0); lower jaws symphysially thickened (1) [*Myliobatis*, *Aetobatus*, and *Rhinoptera*]. †*Asterotrygon* and †*Heliobatis* have the more general condition, as does *Mobula*. This character appears to be functionally correlated with the arrangement of teeth in pelagic taxa (see character 19); those with crushing, flattened teeth also have much stronger lower jaws to accommodate the greater pressures during feeding. These features are considered separate here, but de-

activating one of them does not affect our results.

18. *Lateral projections of lower jaws (''wing-like processes'')*: absent (0); present (1) [*Myliobatis, Aetobatus, Rhinoptera,* and *Mobula*]. These processes, which project laterally from close to the symphysis in pelagic taxa, are absent in both †*Asterotrygon* and †*Heliobatis* (fig. 21). Described and illustrated in Nishida (1990).

19. *Arrangement of teeth in both upper and lower jaws*: teeth with minute cusps and arranged in separate, individual rows (0); teeth flattened, and in a pavementlike arrangement (1) [*Myliobatis, Aetobatus,* and *Rhinoptera*]. †*Asterotrygon* (fig. 27) and †*Heliobatis* again have the more general condition present in all benthic taxa and mobulids, and not the horizontally expanded teeth of most pelagic stingrays (depicted in fig. 50; Garman, 1913; Notarbartolo-di Sciara, 1987).

20. *Basihyal cartilage*: basihyal laterally elongated, fused to first hypobranchials (0); basihyal a single element, but separate from first hypobranchials (1) [†*Asterotrygon, Hexatrygon, Plesiobatis, Urolophus, Trygonoptera, Gymnura*]; basihyal separate from first hypobranchials but fragmented into more than one component (2) [*Urobatis, Paratrygon, Potamotrygon, Plesiotrygon,* amphi-American *Himantura, Taeniura, Himantura, Dasyatis, Pteroplatytrygon*]; basihyal absent (3) [*Urotrygon, Myliobatis, Aetobatus, Rhinoptera,* and *Mobula*]. Pelagic stingrays have also lost the first hypobranchial elements (Miyake and McEachran, 1991). †*Heliobatis* is coded as unknown. The pattern of fragmentation of the basihyal cannot be reliably coded into discrete conditions (cf. Rosenberger, 2001b); the determination by Dingerkus (1995) that a basihyal divided into three separate pieces of equal size unites potamotrygnids with *Taeniura* is entirely without basis. McEachran et al. (1996) credited some stingrays (*Urolophus, Gymnura*; fig. 35B) as having fused basihyals and first hypobranchials, but this is not the same as in more generalized batoids, where these elements cannot be distinguished from each other and form a continuous structure.

21. *Fusion of ventral pseudohyoid and first ceratobranchial*: absent (0); present (1) [all taxa except outgroups]. *Hexatrygon,* †*Heliobatis,* and †*Asterotrygon* are coded as unknown. The condition is simply not preserved in both fossil taxa, and conflicting accounts regarding it in *Hexatrygon* have been published. Nishida (1990) illustrated *Hexatrygon* as having both elements fused, but Miyake and McEachran (1991) depicted them as unfused, following Heemstra and Smith (1980). As we have not been able to examine the gill arches of *Hexatrygon,* we code it as unknown. Another related character, fusion of anterior ceratobranchial elements to each other, used by previous authors (Rosa, 1985; Dingerkus, 1995) to unite different benthic stingray genera, must be used with caution, as in many cases the elements are not fused but juxtaposed, superficially appearing to be fused. This is the case in *Taeniura lymma* (fig. 35A; Carvalho, 1996b). Also, anterior ceratobranchial fusion is variable within certain genera (*Potamotrygon*), and therefore can only be properly incorporated in a species-level analysis.

22. *Arrangement of posterior ceratobranchials*: separate from each other (0); ankylosis between fourth and fifth ceratobranchials (1) [all taxa except outgroups, *Hexatrygon,* and pelagic taxa]; fourth and fifth ceratobranchials fused to each other (2) [*Myliobatis, Aetobatus, Rhinoptera,* and *Mobula*]. This character is described and illustrated by Miyake and McEachran (1991). State 1 refers to the contact and partial overlapping between the last two ceratobranchials, forming part of the insertion for the coracobranchialis muscle (Miyake, 1988). In pelagic taxa, the ceratobranchials are fused medially, even though the limits of each ceratobranchial element may be clearly demarcated, as in *Aetobatus*). This character is unknown in both †*Asterotrygon* and †*Heliobatis*.

23. *Median projection of the basibranchial medial plate*: absent (0); present (1) [all taxa except outgroups, *Plesiobatis, Myliobatis, Aetobatus, Rhinoptera,* and *Mobula*]. The basibranchial copula, or medial plate, projects anteriorly in most nonmyliobatid stingrays from the level of the first ceratobranchial (or ventral pseudohyoid) to occupy a small space between both anterior hypobranchials. The medial plate is the result of fusion

of hypobranchial and basibranchial elements (Miyake, 1988). †*Heliobatis* is coded as unknown.

24. *Articulation between fifth epi- and ceratobranchial elements to scapulocoracoid*: close together (0); widely separated (1) [*Myliobatis*, *Aetobatus*, *Rhinoptera*, and *Mobula*]. Both Green River stingrays are coded as unknown. This character is described and figured in Nishida (1990: 51, fig. 33).

25. *Lateral stay of synarcual*: originates ventral to spinal nerve foramina (0); originates dorsal to spinal nerve foramina (1) [*Potamotrygon*, *Plesiotrygon*]; contacting synarcual both dorsally and ventrally to foramina (2) [*Plesiobatis*]. This character is compiled from Lovejoy (1996), but we added an additional character state for *Plesiobatis* because of the unique configuration of its lateral stay (figured in Nishida, 1990: 60, fig. 38a). We have confirmed the distribution of this feature in additional benthic stingrays (in species of *Urotrygon*, *Urobatis*, and *Taeniura*). †*Asterotrygon* and †*Heliobatis* are coded as unknown. *Aetobatus*, *Rhinoptera*, and *Mobula* are coded as inapplicable because their lateral stay is extremely reduced or lacking altogether.

26. *Fossa on dorsal scapular region*: absent (0); present (1) [*Trygonoptera*, *Urobatis*, *Urotrygon*, amphi-American *Himantura*, *Taeniura*, *Himantura*, *Pteroplatytrygon*, *Dasyatis*, *Myliobatis*, *Aetobatus*, *Rhinoptera*, and *Mobula*]. Miyake (1988), Nishida (1990), Lovejoy (1996), and McEachran et al. (1996) described this character, which is incorporated into their phylogenetic studies. Both †*Asterotrygon* and †*Heliobatis* appear to lack the fossa on the scapular process (and are coded as such), but this may be due to poor preservation.

27. *Contact between pro- and mesopterygium in the pectoral fin*: absent (0); present (1) [*Potamotrygon* and *Plesiotrygon*]. Lovejoy (1996) used this character as further evidence for monophyly of *Potamotrygon* plus *Plesiotrygon*, and we tentatively confirm it here, although some stingray taxa appear to be somewhat intermediate (*Paratrygon*). Both †*Asterotrygon* and †*Heliobatis* have the more general condition, but the interface between the mesopterygium and propterygium is poorly preserved in the fossils. *Aetobatus*, *Rhinoptera*, and *Mobula* lack a discrete mesopterygium (see next feature), and therefore this character is coded as inapplicable, contrary to Lovejoy (1996), who coded them with the more general state.

28. *Distinct components of the mesopterygium*: mesopterygium single element (0); fragmented (1) [*Gymnura*, *Myliobatis*]; missing altogether (2) [*Aetobatus*, *Rhinoptera*, and *Mobula*]. *Dasyatis* is coded with a polymorphism because both conditions occur in component species (*D. zugei* has fragmented mesopterygia, as does *D. matsubarai* according to Nishida, 1990); coding *Dasyatis* as having the more general condition (present in all other *Dasyatis* species examined), however, does not alter tree topology. *Myliobatis* has fragmented mesopterygia, but other pelagic genera (including *Aetomylaeus*) are lacking them altogether, with radials articulating directly to the scapulocoracoid.

29. *Lateral expansion of radials in pectoral region*: absent (0); present (1) [*Gymnura*, *Myliobatis*, and *Aetobatus*]. Compiled from Nishida (1990). The expanded pectoral radial segments are more pronounced anteriorly but are present throughout most of the disc (the segments appear enlarged in *Gymnura*; fig. 15). Both †*Asterotrygon* and †*Heliobatis* have the more general condition present in most benthic stingrays (fig. 39C–F). This character (shown in fig. 39A, B) is further modified (lost) in more derived myliobatids (*Rhinoptera*, *Mobula*, and *Manta*; Nishida, 1990).

30. *External margin of mesopterygium*: more or less straight, not fused to radials (0); undulated, not fused to radials (1) [*Gymnura*; fig. 38C]; highly sinuous, appearing to be fused with articulating radial elements (2) [*Urolophus*, *Trygonoptera*]. The ‘‘fused’’ condition of radials with the mesopterygium is unique to *Urolophus* and *Trygonoptera*, which differ from each other in their nasal flap arrangement (*Trygonoptera* has fleshy external lobes, absent from *Urolophus*; Last and Stevens, 1994) and in other features (such as the passage of the infraorbital lateral-line canal through postorbital process in *Urolophus*). The mesopterygia of these genera have markedly sinuous external margins (fig. 42), a condition not observed in any other stingray. The pelagic stingrays *Aetobatus*,

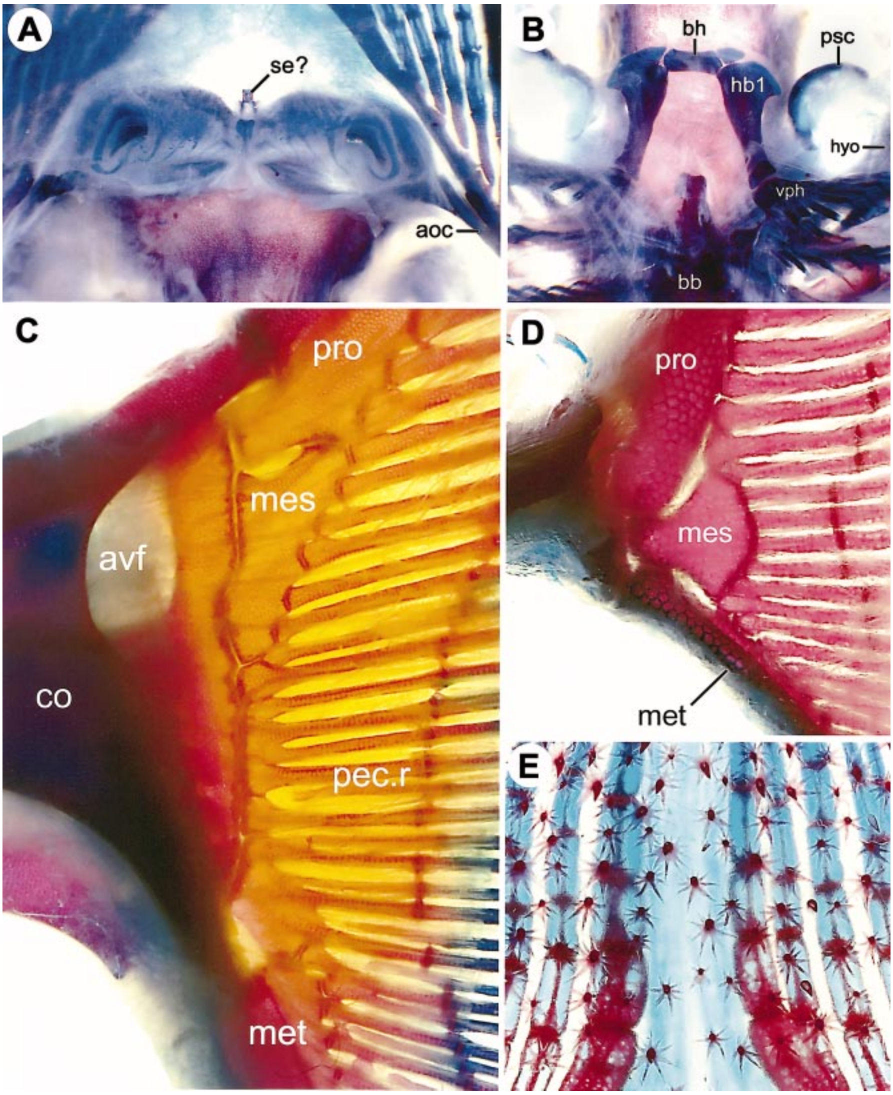


Fig. 38. Selected anatomical features of representative cleared-and-stained stingrays. **A.** Ventral aspect of anterior neurocranium of *Urobatis halleri* (FMNH 42601). **B.** Anterior portion of ventral gill arches (ventral view) of *Urobatis halleri* (FMNH 42601). **C.** Ventral aspect of pectoral fin basal elements of *Gymnura micrura* (FMNH 89990), left side. **D.** Pectoral fin basals of *Urotrygon chilensis* (FMNH 93737) in ventral view (left side). **E.** Denticles of *Urotrygon chilensis* (FMNH 93737) from anterior disc region between pectoral radials in dorsal view. Note that our identification of chondrified sensory canals (se) in panel A is tentative (structure may represent the rostral base). Not to scale. Anterior to top.

Rhinoptera, and *Mobula* are coded as inapplicable for this feature (see character 28 above).

31. *Median prepelvic process*: absent or weakly developed (0); very elongated (1) [*Potamotrygon*, *Paratrygon*, and *Plesiotrygon*]. This character has traditionally been used as evidence of potamotrygonid monophyly (Garman, 1877, 1913; Rosa, 1985; Rosa et al., 1987). *Aetobatus*, *Rhinoptera* and *Mobula*, and, to a lesser extent, *Myliobatis* have a moderately developed median prepel-

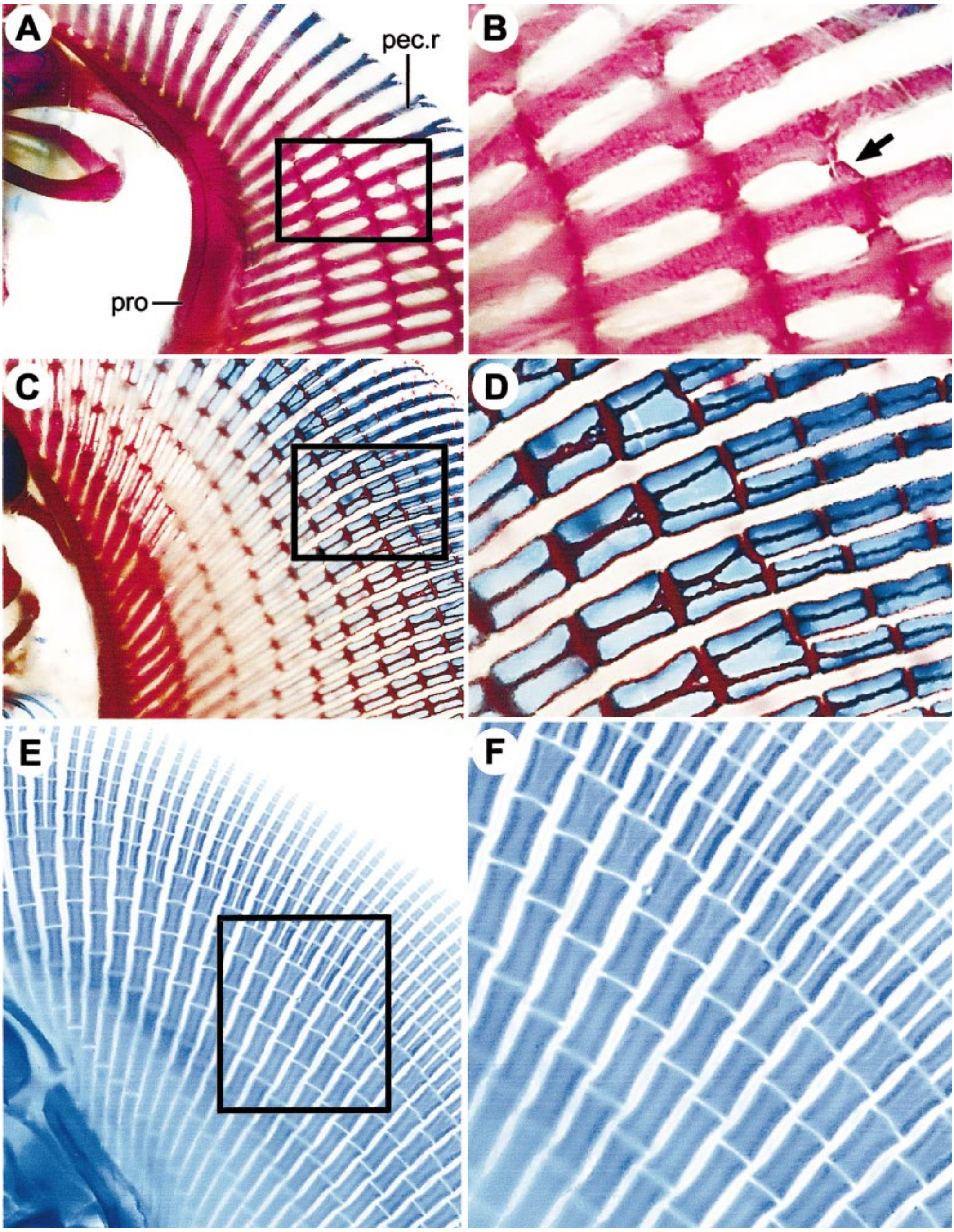


Fig. 39. Pectoral skeleton of representative stingray taxa (in left column), magnified (in right column, from box at left) to show relationship between adjacent radial elements (character 29 of phylogenetic analysis). **A, B.** *Gymnura micrura* (FMNH 89990), left side, ventral view (arrow indicates derived state of character 29). **C, D.** *Urotrygon chilensis* (FMNH 93737), left side, ventral view. **E, F.** *Potamotrygon motoro* (FMNH 94503), left side, ventral view. Not to scale. Anterior to top.

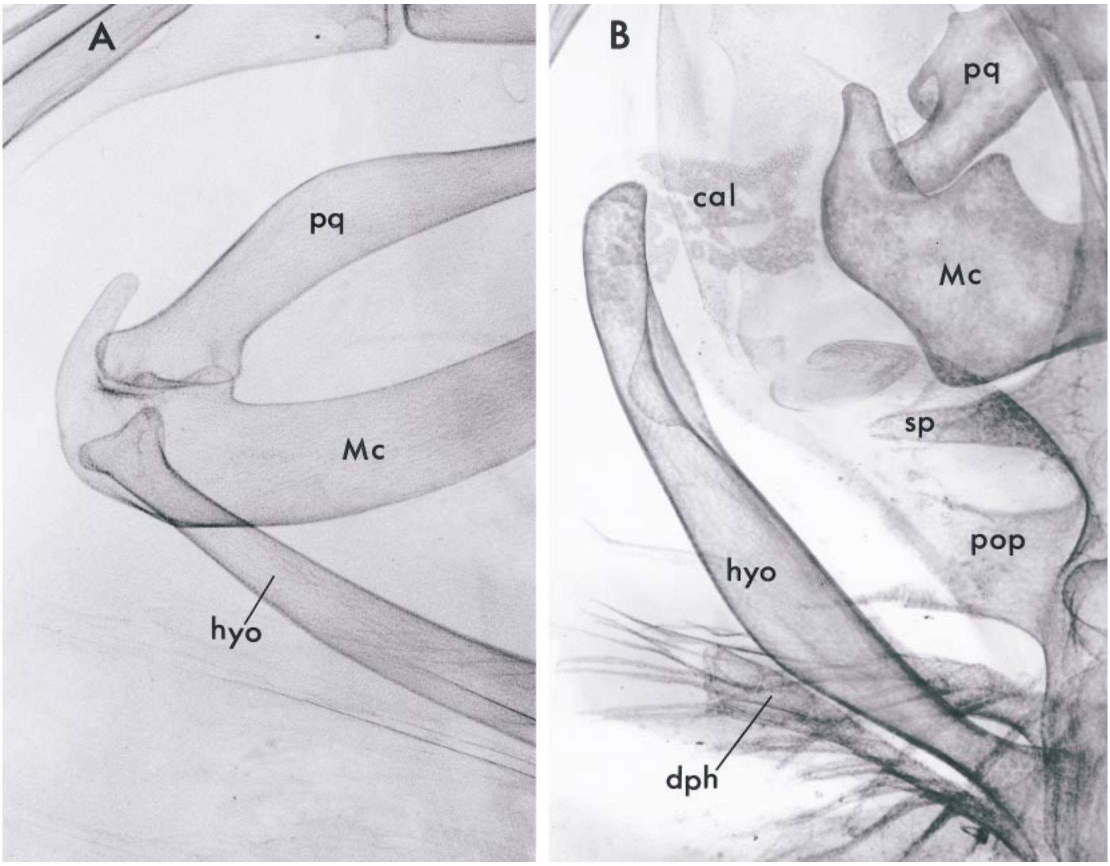


Fig. 40. Enlarged dorsoventral view (positive prints from x-ray radiographs) of the articulation between the hyomandibula and jaw joint or lower jaw of some extant stingrays showing different states of characters 8 (presence of hyomandibular-Meckelian ligament) and 9 (referring to the arrangement of the angular cartilages) of phylogenetic analysis. **A.** *Gymnura japonica* (AMNH 26691), with hyomandibula articulating directly to jaws, that is, without developed hyomandibular-Meckelian ligament (angular cartilages absent; see also fig. 15, ventral view). **B.** *Trygonoptera testacea* (USNM 39993), with scattered calcification present within well-developed hyomandibular-Meckelian ligament connecting hyomandibula to lower jaw and with lack of discrete angular elements. **C.** *Potamotrygon leopoldi* (UERJ 719), with two angular cartilages present within stout ligament (lower angular cartilage is roughly two-thirds the width of the upper angular element). **D.** *Potamotrygon*, sp. nov. (MZUSP 25580), with two angulars of more or less equal dimensions. **E.** *Potamotrygon signata* (MCZ 600) showing elongated and slender angular cartilage (roughly one-half length of hyomandibula) associated with much smaller angular closely contacting hyomandibula. **F.** *Plesiotrygon iwamae* (MZUSP 42848), depicting single angular cartilage (presumably anterior angular cartilage), positioned at a slightly oblique angle to hyomandibula (and not so much at a right angle to it, as seen in panels C–E). Figures are not to scale. Anterior to top.

vic process, but it is not nearly as elongated as that of potamotrygonids. Some benthic stingrays also have weakly developed median prepelvic processes (some species of *Dasyatis*, *Taeniura*, gymnurids; fig. 36), but these are much smaller than the condition in potamotrygonids. This feature could alternatively be treated as a multistate character with the smaller condition of pelagic genera and some benthic species coded as an intermediate step. We chose to include only the highly modified potamotrygonid prepelvic process, although not ideal, because accurately coding the many different weakly de-

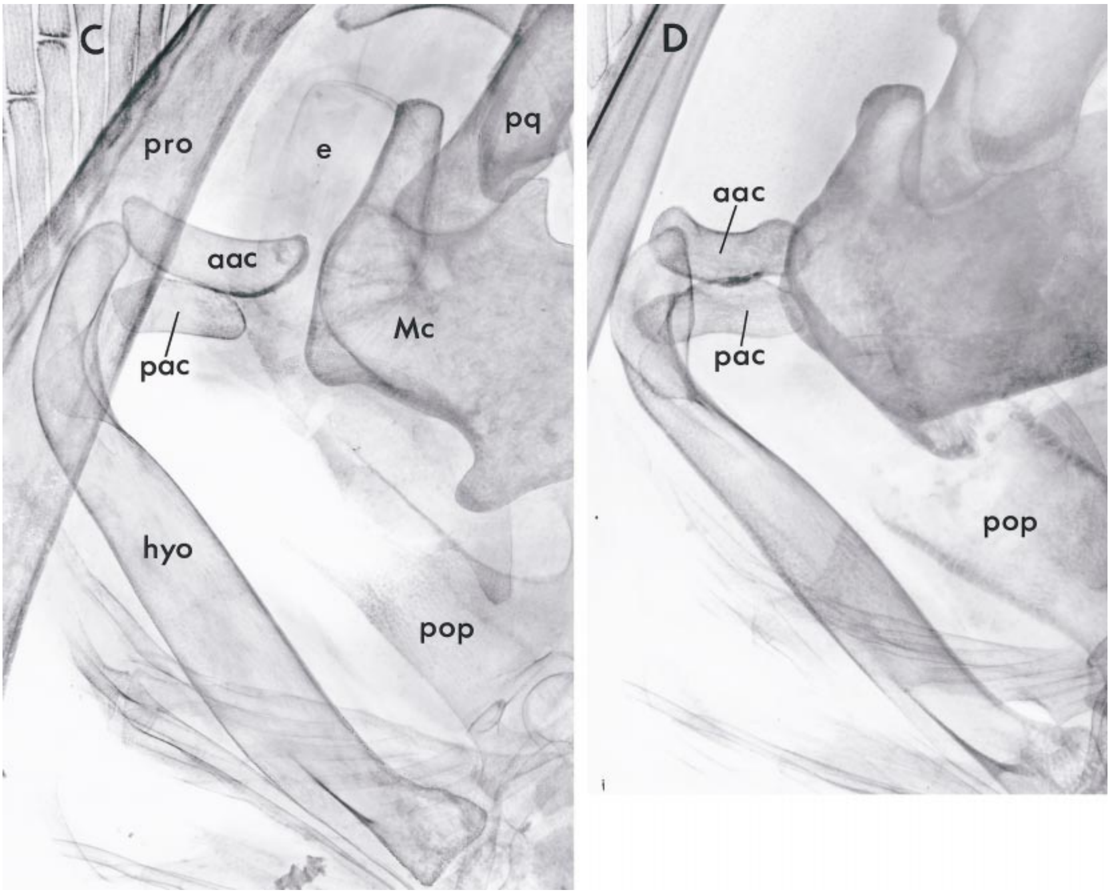


Fig. 40. Continued.

veloped prepelvic processes would require a more inclusive species-level matrix.

32. *Pelvic girdle shape*: not arched or only moderately so (0); greatly arched (1) [*Gymnura*, *Aetobatus*, *Rhinoptera*, and *Mobula*]. Both fossil Green River taxa have the more general condition. Coding the relative degree of arching among benthic stingrays proved difficult and arbitrary (cf. Rosenberger, 2001b), so only the extreme condition of *Gymnura* (fig. 36C, D) and pelagic genera, in which the pelvic girdle is shaped like a wishbone, was included (as in Lovejoy, 1996).

33. *Dorsal fin*: present (0); absent (1) [all terminals except †*Asterotrygon*, *Trygonoptera*, *Myliobatis*, *Aetobatus*, *Rhinoptera*, *Mobula*, and outgroups]. Dorsal fins are primitively present in batoids. *Urolophus* is scored as uncertain, as some species have a small, indistinct dorsal fin anterior to the caudal stings, but it is absent from most species. The vast majority of butterfly rays lack a dorsal fin (all species of *Gymnura*); coding this feature as uncertain (taking into account that it is present in both species of *Aetoplatea*) would just add an extra step without any change in topology. Lovejoy coded the presence of the dorsal fin as derived, because the outgoups he employed (*Hexatrygon* and *Plesiobatis*) lack this character. It is coded differently here because we did not assume that these genera are basal to other stingrays, and more basal batoids were used as outgroups. The dorsal fin of stingrays, when present, is always single as opposed to the presence of two dorsals in almost all other batoids. Coding this feature to reflect the anatomical arrangement of the radials and basals proved very complex. Outgroups generally display

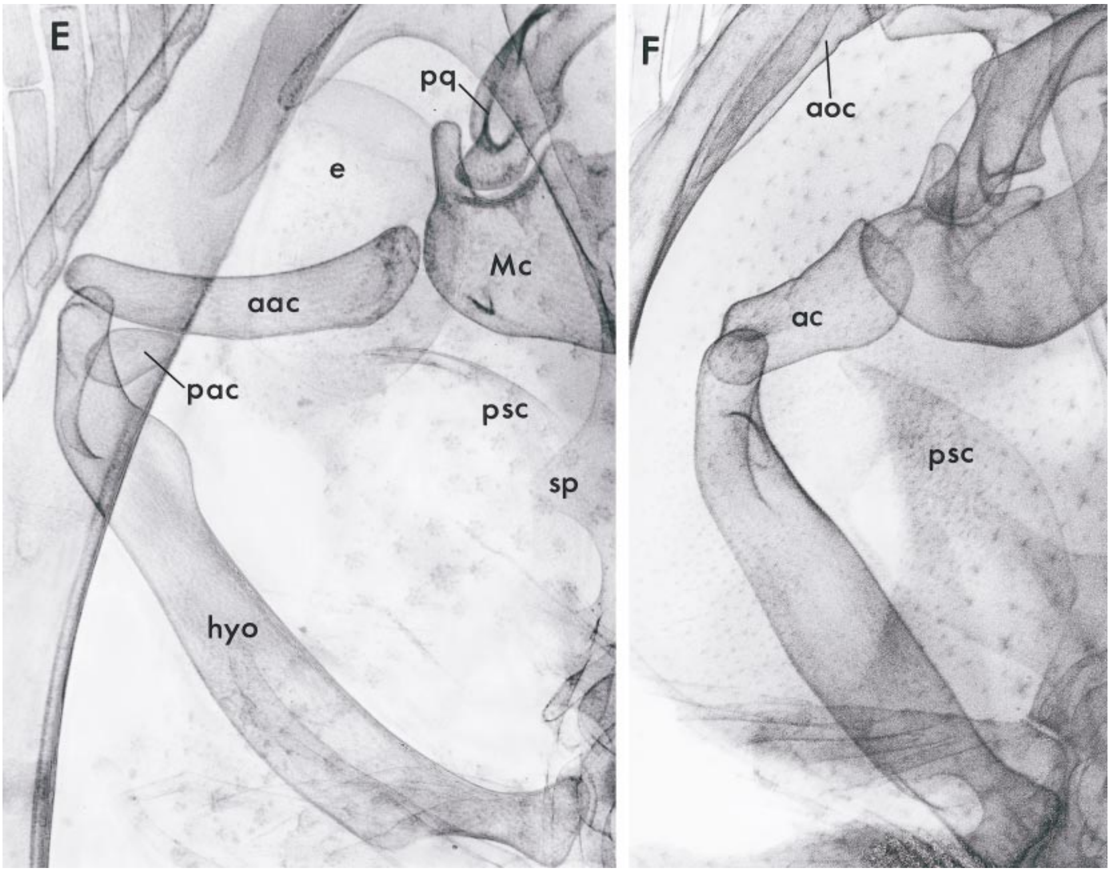


Fig. 40. Continued.

aplesodic dorsal fins internally supported by radials and ceratotrichia (guitarfishes), but skates are somewhat intermediate with radials extending to almost the fin margins. The internal structure of the dorsal fin of *Trygonoptera* needs to be investigated to ascertain if it is similar to that of †*Asterotrygon*, that is, plesodic without enlarged basals (as opposed to pelagic genera, which have enlarged basal elements in the dorsal fin; fig. 41). Coding †*Asterotrygon* and *Trygonoptera* identically to reflect a putative similarity in dorsal fin internal structure may support the placement of †*Asterotrygon* as a basal urolophid (a relationship present in 21 of the 35 equally most parsimonious trees; see below), but more information is needed to properly code the dorsal fin skeleton in benthic stingrays.

34. *Cartilaginous rod in tail*: absent (0); present (1) [*Paratrygon*, *Potamotrygon*, *Plesiotrygon*, *Dasyatis*, amphi-American *Himantura*, *Taeniura*, *Himantura*, *Pteroplatytrygon*, *Myliobatis*, *Aetobatus*, *Rhinoptera*, and *Mobula*]. The Green River stingrays have the more general batoid condition (fig. 26), as do all taxa with a caudal fin (urolophids, urotrygonids, *Plesiobatis*, *Hexatrygon*). All four species of *Gymnura* examined also have discrete vertebrae extending to the distal tip of the tail (state 0). This contrasts with the coding given to *Gymnura* by both Lovejoy (1996) and McEachran et al. (1996).

35. *Caudal fin*: present (0) [outgroups, *Plesiobatis*, *Hexatrygon*, *Urolophus*, *Trygonoptera*, *Urotrygon*, and *Urobatis*]; reduced to tail-folds (1) [†*Heliobatis*, †*Asterotrygon*, *Dasyatis*, *Potamotrygon*, *Plesiotrygon*, *Taeniura*, *Pteroplatytrygon*]; absent (2) [*Paratrygon*, amphi-American *Himantura*, *Himantu-*

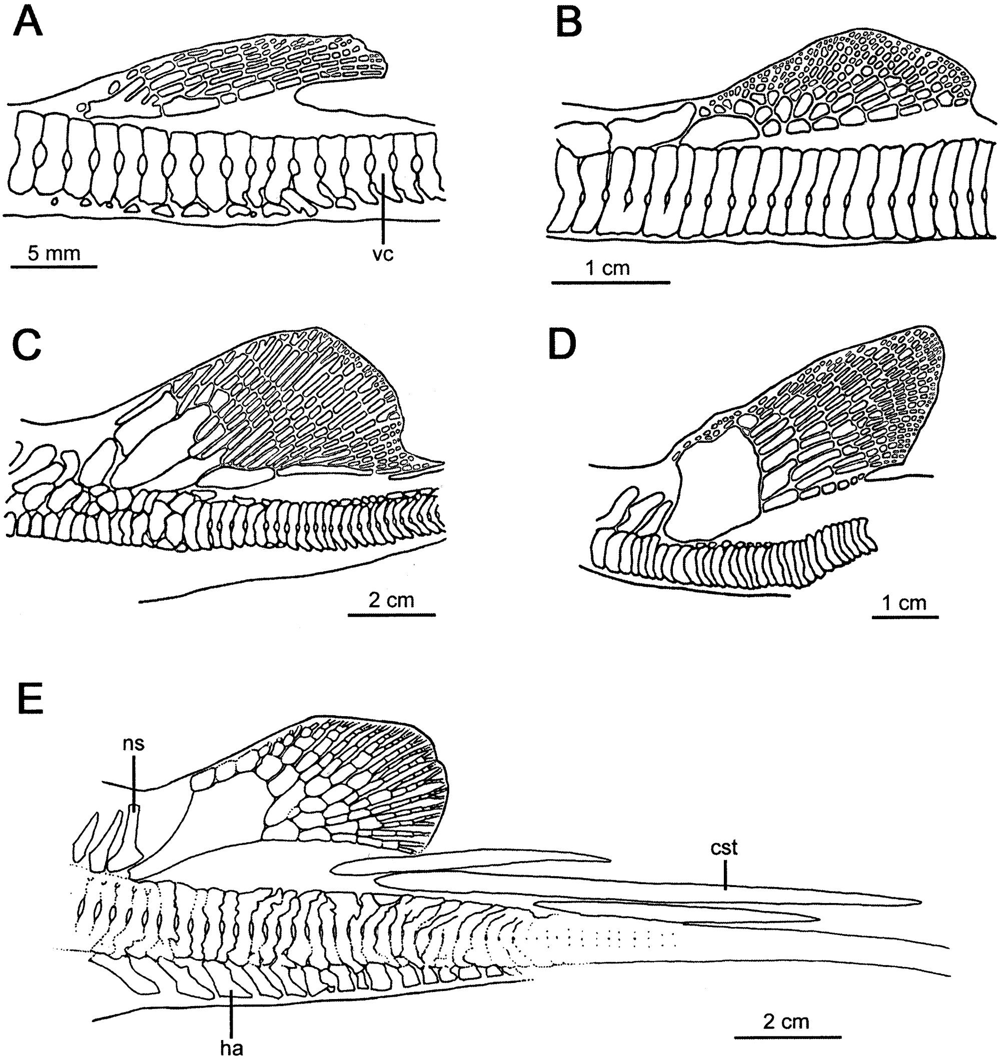


Fig. 41. Dorsal fin skeleton of extant stingrays. **A.** *Aetoplatea zonura*. **B.** *Myliobatis tobijei*. **C.** *Rhinoptera javanica*. **D.** *Mobula japanica*. **E.** *Aetobatus narinari* (from AMNH 44142 XR). Panels A–D modified from Nishida (1990: fig. 40); panel E is original. Note that caudal stings and vertebral elements are schematic. Anterior to left.

ra, *Gymnura*, *Myliobatis*, *Aetobatus*, *Rhinoptera*, and *Mobula*]. Because the caudal fin of stingrays (when present) is different from that of outgroups in being plesodic as opposed to aplesodic, we experimentally coded this character differently to reflect this, adding an extra character state. This produced no change in topology, and therefore the caudal fin was coded more simplistically. This character is independent from character 34 above, because †*Asterotrygon* and †*Heliobatis* have vertebrae extending posteriorly well beyond caudal stings as far as can be observed *and* caudal fins reduced to tail-folds (figs. 24, 26). The tail-folds of numerous taxa (such as in species of *Dasyatis* and *Potamotrygon*) exhibit what has been termed ‘‘rudimentary radial elements’’ (Nishida, 1990), justifying the coding of tail-folds as part of a multistate character encompassing the caudal fin of stingrays in general. We have observed these rudimentary radials in

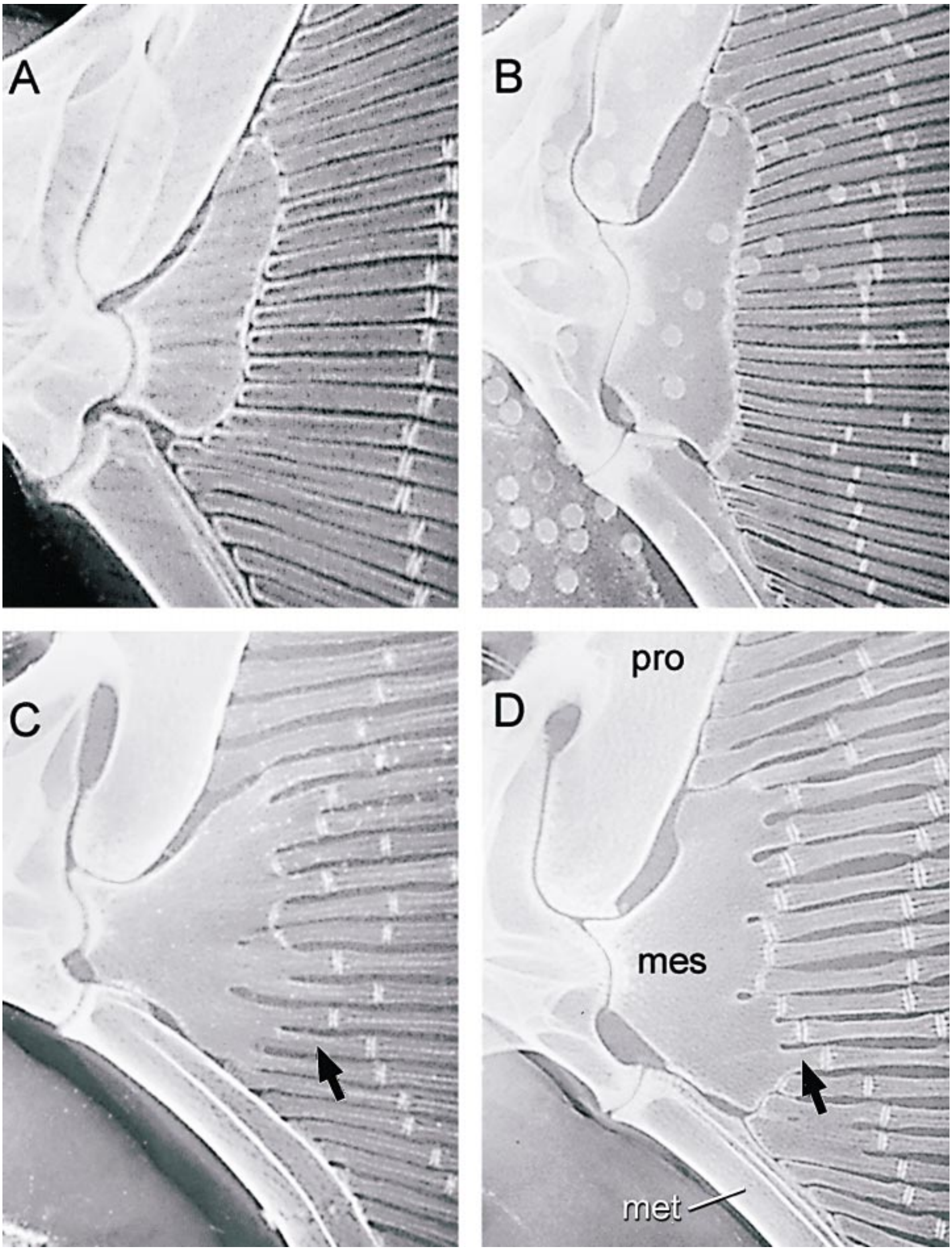


Fig. 42. Articulation between mesopterygium and pectoral radials (character 20 in phylogenetic analysis) of representative extant stingray taxa in dorsoventral view. **A.** *Potamotrygon leopoldi* (UERJ 719), right side (inverted), ventral view. **B.** *Dasyatis margarita* (AMNH 41512), left side (inverted), dorsal view. **C.** *Urolophus lobatus* (CSIRO P8197), right side (inverted), ventral view. **D.** *Trygonoptera testacea* (USNM 39993), right side (inverted), ventral view. Arrows depicts sinuous margin of mesopterygium where it articulates to radials in panels C and D. Figures are not to scale. Anterior to top.

countless specimens of *Potamotrygon*, *Dasyatis*, and *Taeniura* (fig. 37).

MANDIBULAR MUSCLE PLATE

36. *Adductor mandibulae complex*: without posteromedial extension (0); posteromedial extension present (1) [*Myliobatis*, *Aetobatus*, *Rhinoptera*, and *Mobula*]. This character is unknown in both †*Asterotrygon* and †*Heliobatis* and is described in Miyake (1988) and Nishida (1990; as the ‘‘depressor mandibulae’’). Our coding follows McEachran et al. (1996).

37. *Spiracularis muscle*: projecting ventrally to insert on either palatoquadrate, Meckel’s cartilage, and/or hyomandibula (0); projecting ventrally and posteriorly beyond hyomandibulae and both sets of jaws to insert dorsal to coracomandibularis (1) [*Taeniura*]; projecting ventrally and posteriorly beyond jaws and hyomandibulae to insert ventral to coracomandibularis (2) [*Potamotrygon*, *Plesiotrygon*, amphi-American *Himantura*]. This muscle originates on the otic region of the neurocranium and projects ventrally to form part of the spiracular wall. Miyake (1988) and Miyake et al. (1992a) provided descriptions of the different conditions of the spiracularis in batoids. This is a complex muscle with many variations in batoids (more character states are described and utilized by McEachran et al., 1996). Lovejoy (1996) described this muscle for various stingrays, and our use of this character follows his analysis to a large degree.

We have confirmed the different insertion patterns of the spiracularis in many stingrays. In *Potamotrygon falkneri*, *P. motoro*, *P. orbignyi*, *P.* cf. *schroederi*, and ‘‘*Himantura*’’ *schmardae*, the spiracularis is thick, well developed and very closely associated with the depressor hyomandibularis posterior to the lower jaw, inserting with its antimere ventral to the coracomandibularis (state 2). In these taxa the spiracularis and the depressor hyomandibularis are difficult to separate from one another, but the spiracularis is generally dorsal to the depressor hyomandibularis. In *Paratrygon*, the spiracularis is very slender and is not continuous posteriorly with the depressor hyomandibularis (state 0). In *Plesiotrygon*, this muscle is more slender than in *Potamotrygon* (but more robust than in *Paratrygon*) and is more difficult to delimit due to an abundance of connective tissue. It is more strongly anastomosed with the depressor hyomandibularis (and also partly with the coracohyoideus and coracohyomandibularis) and is similar to the condition depicted for ‘‘*Himantura*’’ *pacifica* by Lovejoy (1996) (state 2). *Taeniura* also has a very developed spiracularis that inserts medially, but dorsal to the coracomandibularis (state 1). The spiracularis is absent in *Urolophus aurantiacus* and is very slender and generally does not continue posteriorly beyond the lower jaw (inserting for the most part on lower jaw itself) in *Urobatis* (*U. jamaicensis* and *U. halleri*), *Urotrygon microphthalmum*, and *Himantura imbricata*. In *Dasyatis sabina* and *Pteroplatytrygon*, the spiracularis is also slender but projects posterior to the lower jaws to some degree, however, but not as much as in *Taeniura*, *Potamotrygon*, *Plesiotrygon*, and amphi-American *Himantura*. More comparative data for *Dasyatis* and *Himantura* are needed, especially as Kesteven (1942) described the posterior extension of the spiracularis in *Dasyatis brevicaudata*. Myliobatids are coded as in Lovejoy (1996) and McEachran et al. (1996). In *Zanobatus*, the spiracularis does not project posteroventrally to the same extent as in stingrays. Because the muscle is very complex (Kesteven, 1942; Miyake, 1988), more descriptions are needed to corroborate our use of it here. This character is unavailable in both †*Asterotrygon* and †*Heliobatis*.

38. *Depressor mandibularis muscle*: present (0); absent (1) [*Myliobatis*, *Aetobatus*, *Rhinoptera*, and *Mobula*]. This character is unavailable in both †*Asterotrygon* and †*Heliobatis*. We code this character following McEachran et al. (1996), and it is described for stingrays in Miyake (1988) and Nishida (1990; as the ‘‘intermandibularis posterior’’).

HYPOBRANCHIAL MUSCLE PLATE

39. *Coracohyoideus muscle*: not connected at midline (0); connected at midline (1) [*Myliobatis*, *Aetobatus*, *Rhinoptera*, and *Mobula*]. This character is unknown in both †*Asterotrygon* and †*Heliobatis*. Coded as in McEachran et al. (1996), and described in

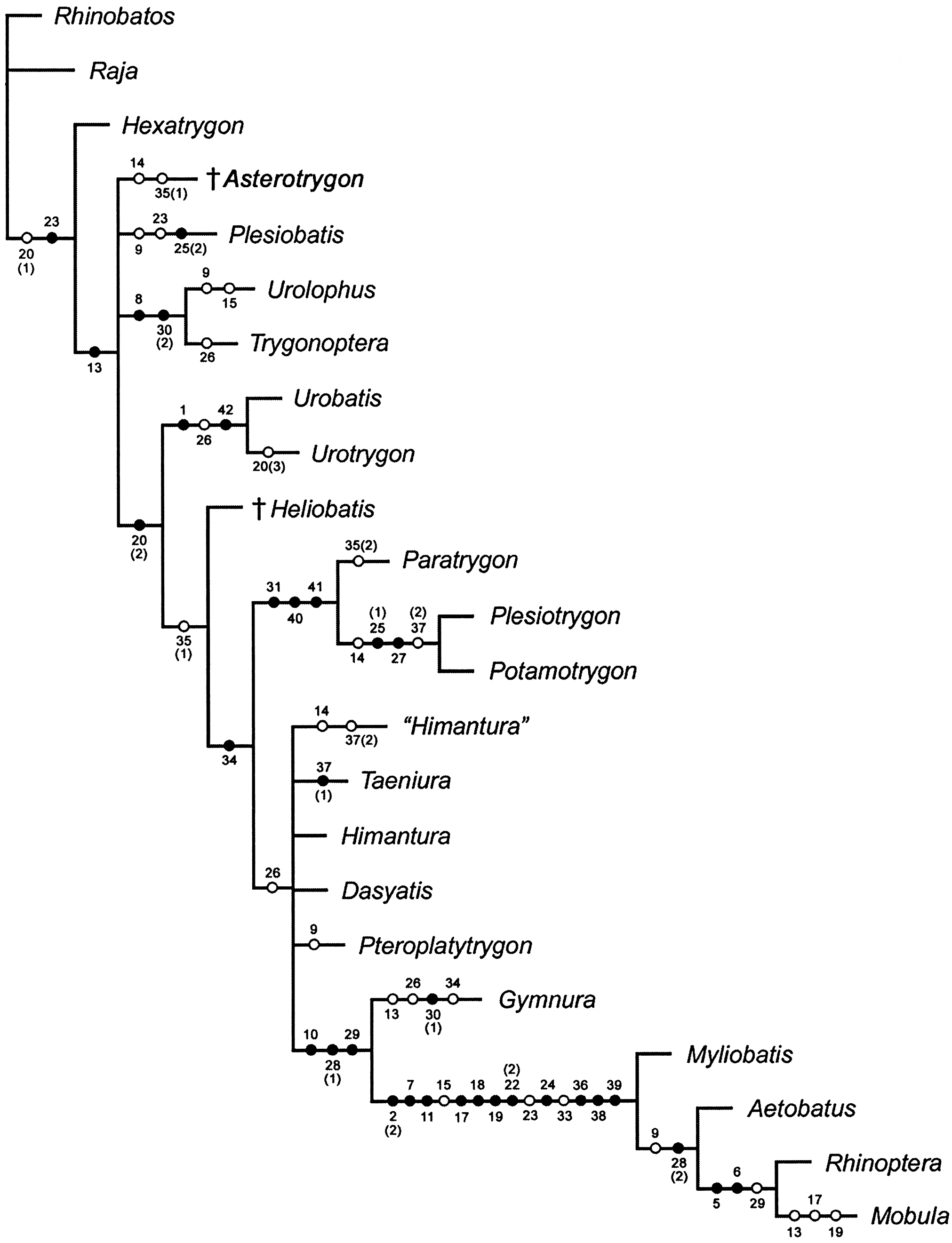


Fig. 43. Strict consensus tree (length = 86 steps, CI = 0.65, RI = 0.79) obtained from 35 equally most parsimonious trees (length = 82 steps, CI = 0.68, RI = 0.82), derived from the matrix in table 5. Characters are numbered as in the text and in table 5 (see text for character descriptions). Only unambiguous characters are shown; unique derivations depicted as closed circles, characters with homoplasy as open circles; character states in parentheses (figure is modified from output generated directly from WinClada).

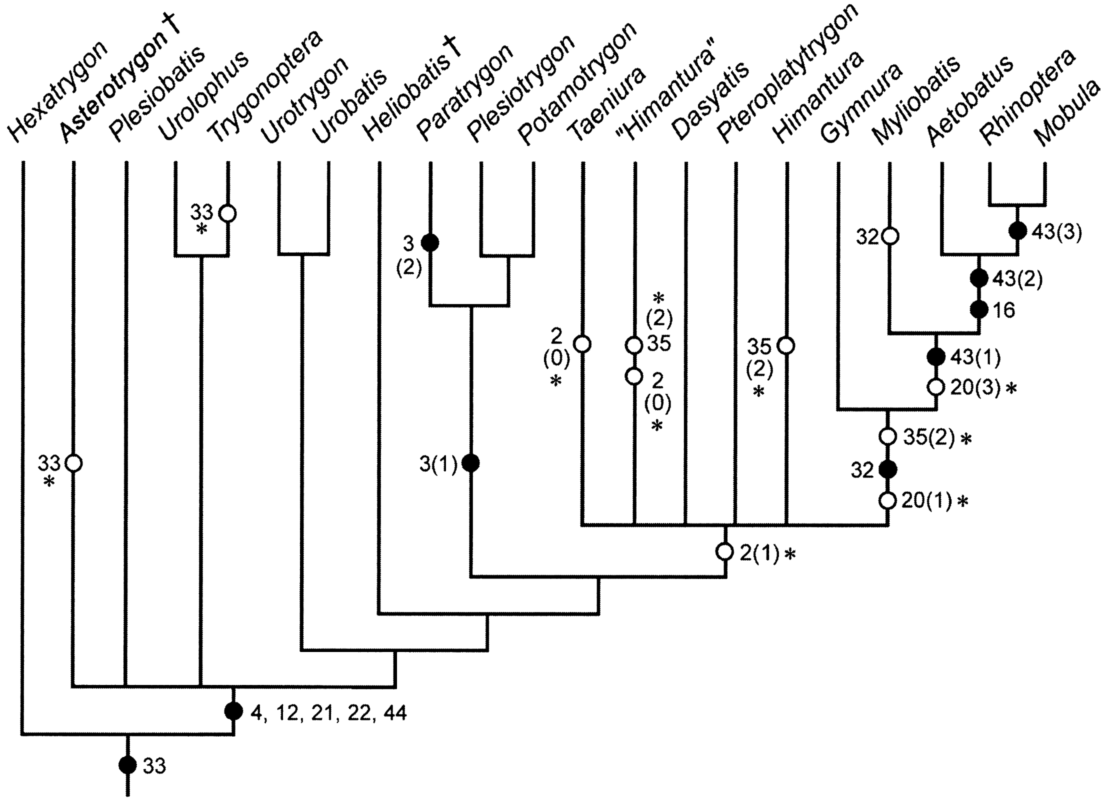


Fig. 44. Tree topology taken from figure 43 (strict consensus tree) with ambiguous characters mapped (numbered as in text and matrix in table 5, unambiguous characters in fig. 43). Some of the characters are ambiguous because they are scored as uncertain in *Hexatrygon* (characters 4 and 21) and in *Myliobatis* (character 16); these are displayed conservatively on the tree (i.e., it is not simply assumed that they will be found in these taxa). Other characters have more than one equally parsimonious optimization (characters 3, 20, 32, 43), whereas others are scored as uncertain in the Green River stingrays (characters 12, 22, and 44). The optimization chosen in both of these cases is accelerated transformation, favoring reversals over independent gains. Characters denoted with an asterisk (*) are part of multistate transformation series that have unambiguous character states in figure 43.

Miyake (1988; as the ‘‘y’’ muscle) and Nishida (1990). The state in *Hexatrygon* is unknown.

MISCELLANEOUS

40. *Urea retention*: urea retained in blood (0); urea excreted in urine (1) [*Potamotrygon, Paratrygon, Plesiotrygon*]. This character is unavailable in †*Asterotrygon* and †*Heliobatis*, and both are coded as unknown. Potamotrygonids produce copious, diluted urine (Thorson, 1970; Thorson et al., 1967, 1983a). As the Green River stingrays were freshwater inhabitants (see ‘‘Geological Setting’’ above), it is likely that they employed some physiological mechanism to eliminate excess water from their metabolism.

41. *Rectal gland*: present (0); reduced (1) [*Paratrygon, Potamotrygon, Plesiotrygon*]. Coded as unavailable in †*Asterotrygon* and †*Heliobatis*. Inhabiting freshwater does not necessarily imply that the rectal gland is absent, as it is present in species of *Dasyatis* that are strictly confined to freshwater (e.g., *Dasyatis garouaensis*; Thorson and Watson, 1975), and the rectal gland of *Potamotrygon* is atrophied, not completely lacking (Thorson et al., 1978). Potamotrygonids are not capable of retaining urea or secreting salt via the rectal gland if placed in saline waters (references in Brooks et al., 1981).

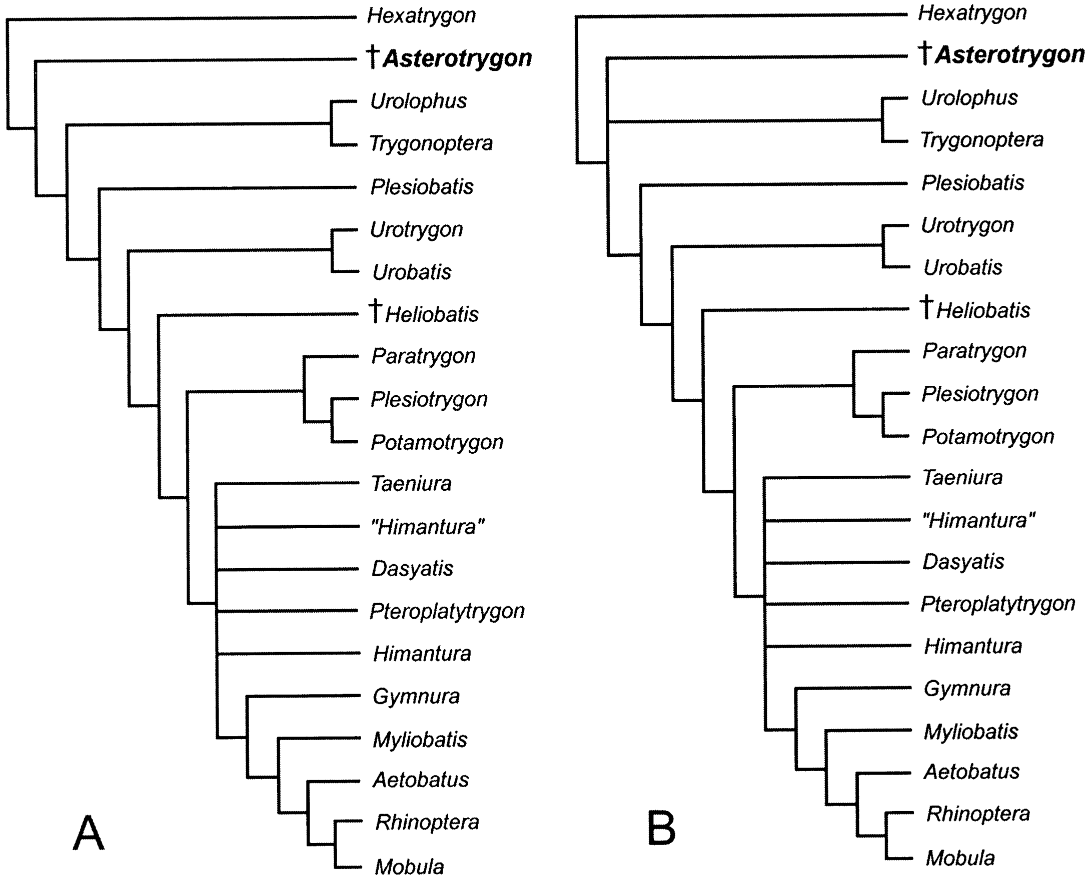


Fig. 45. Five subgroups of trees showing the different phylogenetic positions of †*Asterotrygon* that result once uncertainty concerning the relationships among dasyatid genera is eliminated from the minimum-length trees obtained in this study (based on matrix in table 5; strict consensus in fig. 43). †*Asterotrygon* pairs with urolophids in the subgroups depicted in C–E, representing 21 of the 35 equally most parsimonious trees (see text for details).

42. *Spiracular tentacle*: absent (0); present (1) [*Urobatis*, *Urotrygon*]. The structure of the spiracular tentacle or lobe was first described in detail by LaMarca (1963) for *Urobatis jamaicensis*, but it is also present in *Urotrygon* (Bigelow and Schroeder, 1953; Miyake, 1988). The tentacle is present in embryonic specimens and is resorbed shortly before birth. It has been used previously in the phylogenetic analyses of Lovejoy (1996) and McEachran et al. (1996). This character is unknown in both †*Asterotrygon* and †*Heliobatis*.

43. *Cephalic lobes*: absent (0); single and continuous (1) [*Myliobatis*]; single with an indentation (2) [*Aetobatus*]; paired (3) [*Rhinoptera* and *Mobula*]. †*Asterotrygon* and †*Heliobatis* display the more general condition in benthic stingrays, that is, the disc continues anterior to the neurocranium without forming a separate (cephalic) lobe. Our use of this character strictly follows McEachran et al. (1996). The cephalic lobes are internally supported by radial elements of the propterygia, which are interrupted at more or less the level of the eyes and resume anterior to the neurocranium. The lobe is continuous anteriorly in *Myliobatis*, but a median indentation divides the lobe into two smaller ones in *Aetobatus*. *Rhinoptera* and *Mobula* have two prehensile lobes, one on each side, that are completely separated (further supported

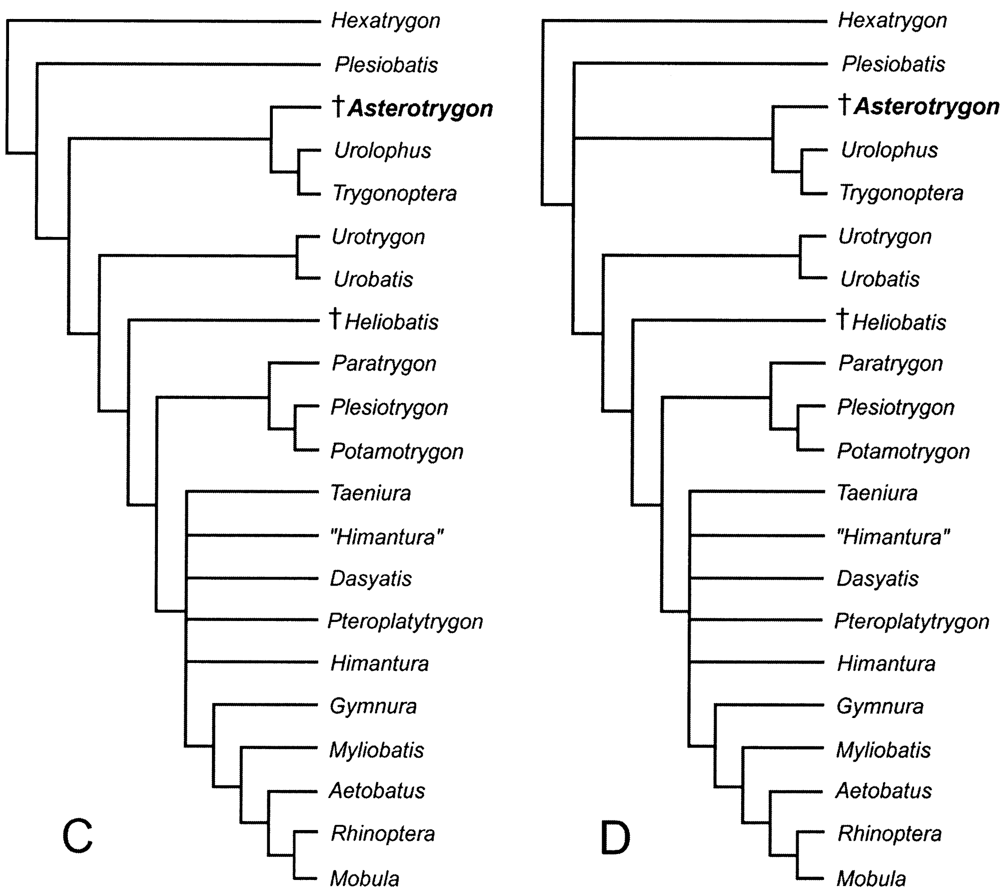


Fig. 45. Continued.

internally by the anterior process of the neurocranium).

44. *Nasal curtain*: not reaching mouth region (0); extending posteriorly as far as mouth opening (1) [all taxa except outgroups and *Hexatrygon*]. This character is also unknown in †*Asterotrygon* and †*Heliobatis*. The condition in the monotypic *Hexatrygon* is described by McEachran et al. (1996), and we follow their interpretation here, which is supported by the depictions of *H. bickelli* in Heemstra and Smith (1980), Shen and Liu (1984), Shen (1986), and Last and Stevens (1994), as well as by the specimens we examined. Even though the failure of the nasal curtain to reach the mouth opening may be influenced by postmortem distortion due to poor preservation, the condition in *Hexatrygon* is extreme compared to other stingrays. The nasal curtain in *Plesiobatis* may be more variable. We coded this genus as having the nasal curtain reaching the mouth opening (cf. McEachran et al., 1996), as observed on a large specimen from New Caledonia and a smaller one from Fiji (both deposited in the MNHN).

RESULTS OF PHYLOGENETIC ANALYSIS

Phylogenetic analysis of the matrix presented in table 5, summarizing the anatomical information described above, resulted in 35 equally most parsimonious trees (length = 82 steps, CI = 0.68, RI = 0.82), the strict consensus of which is shown in figure 43 (ambiguous characters are shown separately in fig. 44). The strict consensus tree (length = 86 steps, CI = 0.65, RI = 0.79) is not entirely dichotomous, but contains various monophyletic components and only two un-

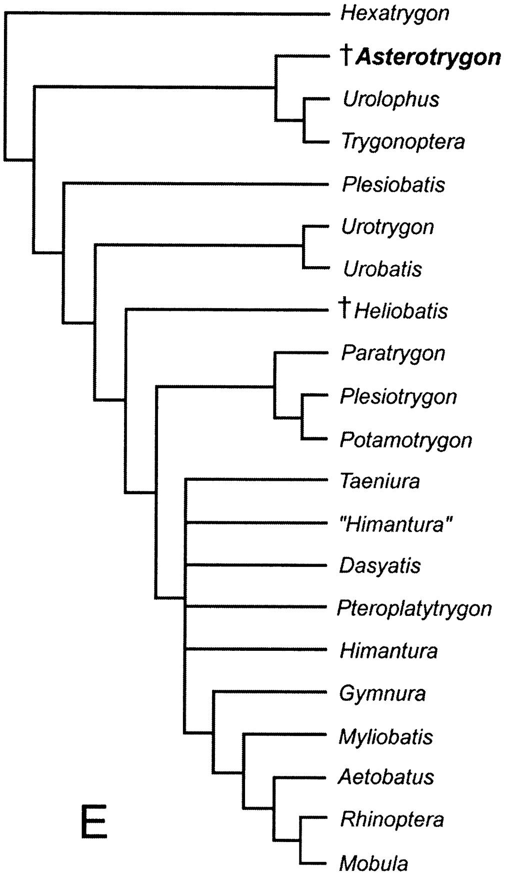


Fig. 45. Continued.

resolved nodes (the monophyletic groups discovered, some of which are novel, are described below). The unresolved relationships mostly concern the various dasyatid genera, which are placed in a large polytomy with the node Gymnuridae + Myliobatidae in the strict consensus, and the affinities of †*Asterotrygon* and *Plesiobatis*. The 35 minimum-length trees can be reduced to five subgroups of trees once the uncertainty regarding the relationships of dasyatid genera are removed; the five subgroups of trees vary only in the positions of †*Asterotrygon* and *Plesiobatis* (summarized in fig. 45). The nonmonophyly of the whiptailed stingrays (Dasyatidae) in the strict consensus is not surprising, given that there are no unequivocal characters known to support it (a monophyletic Dasyatidae does not occur in any of the equally most parsimonious trees either). The presence of tail-folds has traditionally been used to diagnose the family (Bigelow and Schroeder, 1953; Compagno and Roberts, 1982, 1984; Nishida, 1990), but these are absent in amphi-American *Himantura* and *Himantura* sensu stricto, and are also present in potamotrygonids and †*Heliobatis* and are therefore plesiomorphic at this level.

In relation to the Green River stingrays, our analysis indicates that both genera do not form a monophyletic unit. But this is not surprising given that no putative homologies were discovered and included in the matrix. The phylogenetic placement of †*Asterotrygon* varied in the minimum-length trees; it was resolved as either the next most basal stingray genus after *Hexatrygon* (in 7 of the 35 minimum-length trees), as the next most basal stingray genus after *Hexatrygon* but in a polytomy with urolophids (also in 7 of 35

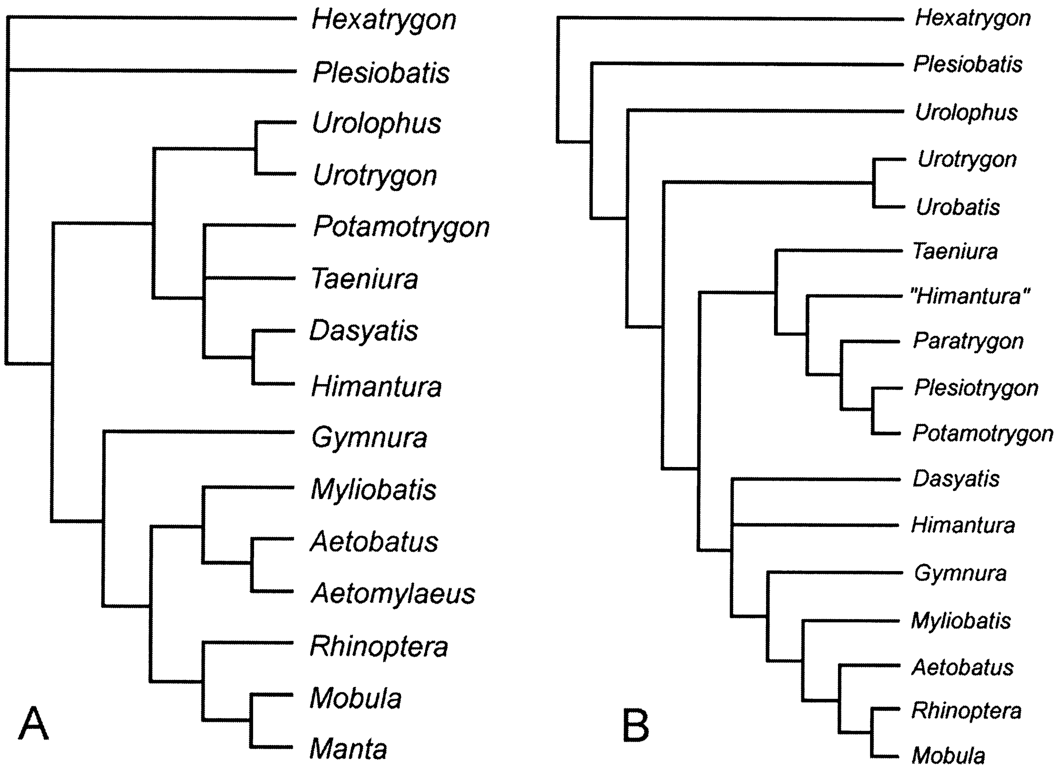


Fig. 46. Previous morphological phylogenies of stingrays (Myliobatiformes). **A.** Nishida (1990). **B.** Lovejoy (1996) and McEachran et al. (1996). Nishida's analysis contained many species, and what is shown is only a summary of his scheme (e.g., *Trygonoptera* was shown nested within *Urolophus*). The trees of Lovejoy and McEachran et al. originally differed in relation to the taxa included (see text) but are summarized here identically for simplicity without altering the pattern of relationships that they obtained.

trees), or as the sister-group to the Urolophidae (in 21 of the 35 trees; fig. 45C–E). †*Heliobatis* is resolved as the most basal genus of the Myliobatoidea, sister-group to the clade Potamotrygonidae + ("Dasyatidae" + (Gymnuridae + Myliobatidae)) in all equally most parsimonious trees. Therefore, †*Asterotrygon* and †*Heliobatis* (or their direct ancestors) probably independently invaded the freshwater system of Fossil Lake and were phylogenetically divergent well before this invasion occurred (further discussed below under "Biogeographical Implications").

The relationships of *Plesiobatis* varied considerably in our minimum-length trees (fig. 45); it was either sister-group to the remaining stingrays except *Hexatrygon* (in 7 out of 35 trees), sister-group to the remaining stingrays except *Hexatrygon* but in a polytomy with †*Asterotrygon* + Urolophidae (again in 7 of 35 trees), or (in 21 of 35 trees) sister-group of the large node Urotrygonidae + Myliobatoidea (where Myliobatoidea = †*Heliobatis* + (Potamotrygonidae + ("Dasyatidae" + (Gymnuridae + Myliobatidae)))). The latter relationship is a departure from previous studies, in which *Plesiobatis* has figured as either the most basal stingrays genus or the next most basal genus after *Hexatrygon* (Nishida, 1990; Lovejoy, 1996; McEachran et al., 1996).

Our phylogenetic analysis uncovered two additional stingray synapomorphies that are present in all minimum-length trees: characters 20 (state 1) and 23. The latter feature, anterior expansion of the medial (basibranchial) plate, requires homoplasy as it is reversed in myliobatids, while *Plesiobatis* has

TABLE 6

Length (number of steps), Consistency (CI) and Retention (RI) Indices for Each Character, and the Number (*N*) of Trees in Which Each Optimization Occurs

Based on the phylogenetic analysis of matrix in table 5 (strict consensus in fig. 43); MPTs = equally most-parsimonious trees.

	Steps	CI	RI	*N*
Character 1	1	1.0	1.0	all
Character 2	2	1.0	1.0	19
	3	0.66	0.83	16
	4	0.50	0.66	consensus
Character 3	2	1.0	1.0	all
Character 4	1	1.0	1.0	all
Character 5	1	1.0	1.0	all
Character 6	1	1.0	1.0	all
Character 7	1	1.0	1.0	all
Character 8	1	1.0	1.0	all
Character 9	4	0.25	0.40	all
Character 10	1	1.0	1.0	all
Character 11	1	1.0	1.0	all
Character 12	1	1.0	1.0	all
Character 13	3	0.33	0.50	all
Character 14	3	0.33	0.33	all
Character 15	2	0.50	0.75	all
Character 16	1	1.0	1.0	all
Character 17	2	0.50	0.50	all
Character 18	1	1.0	1.0	all
Character 19	2	0.50	0.50	all
Character 20	5	0.60	0.80	all
Character 21	1	1.0	1.0	all
Character 22	2	1.0	1.0	all
Character 23	3	0.33	0.66	all
Character 24	1	1.0	1.0	all
Character 25	2	1.0	1.0	all
Character 26	4	0.25	0.70	all
Character 27	1	1.0	1.0	all
Character 28	2	1.0	1.0	all
Character 29	2	0.50	0.50	all
Character 30	2	1.0	1.0	all
Character 31	1	1.0	1.0	all
Character 32	2	0.50	0.66	all
Character 33	3	0.33	0.71	all MPTs
	4	0.25	0.57	consensus
Character 34	2	0.50	0.90	all
Character 35	4	0.50	0.84	15
	5	0.40	0.76	20
	6	0.33	0.69	consensus
Character 36	1	1.0	1.0	all
Character 37	3	0.66	0.50	all
Character 38	1	1.0	1.0	all
Character 39	1	1.0	1.0	all
Character 40	1	1.0	1.0	all
Character 41	1	1.0	1.0	all
Character 42	1	1.0	1.0	all
Character 43	3	1.0	1.0	all
Character 44	1	1.0	1.0	all

independently lost the basibranchial anterior expansion (a further autapomorphy for this genus). Character 20, regarding the basihyal cartilage, is highly modified in stingray evolution: it is lost in *Urotrygon*, becomes fragmented for the the large node Urotrygonidae + (†*Heliobatis* + (Potamotrygonidae + (“Dasyatidae” + (Gymnuridae + Myliobatidae)))), but is further lost for myliobatids (note that there is more than one possible optimization of this latter transformation as shown in fig. 44). The loss of the dorsal fin (character 33) is a putative stingray synapomorphy but is not optimized in this way in all resulting trees (it is in some, however; see fig. 44). Myliobatids, *Trygonoptera*, *Aetoplatea*, and †*Asterotrygon* have all regained the dorsal fin independently. In trees that support a monophyletic †*Asterotrygon* + Urolophidae, it is possible that the dorsal fin evolved only once and was subsequently lost in *Urolophus*, which would render the mere presence of the dorsal fin plesiomorphic for †*Asterotrygon*; our use of this character to diagnose this fossil taxon is not compromised in this scenario, however, as the fin is uniquely covered in denticles and has a well-defined plesodic internal structure (whereas the internal structure of the dorsal fin of *Trygonoptera*, if present, is unknown; it may not be arranged as in †*Asterotrygon*).

The node comprising all stingrays with the exception of *Hexatrygon* is unequivocally supported by a single character: presence of the hyomandibular-Meckelian ligament (character 13). Additional features that are placed at this node in the tree in figure 44 are the ventrolaterally projecting nasal capsules (character 12), ankylosis of fourth and fifth ceratobranchial cartilages (character 22; further modified for Myliobatidae), and the nasal curtain reaching posteriorly to level of mouth opening (character 44). These three characters are unknown in the Green River stingrays, precluding their inclusion in the strict consensus of figure 43. There are two additional characters featured at this node, but both are scored as unknown for *Hexatrygon*: the scapular loop of the trunk lateral-line canal (character 4) and the fusion of the ventral pseudohyoid with the first ceratobranchial (character 21). The former character is unknown in *Hexatrygon* (and we were unable to examine prepared material), and the latter has been conflictingly described in the literature (see character description above). If both characters prove upon further examination to be absent from *Hexatrygon* they will represent additional synapomorphies for this node (as in fig. 44), but if present they will be synapomorphic for stingrays.

The node uniting Urotrygonidae and the large group composed of †*Heliobatis* + Potamotrygonidae + ''Dasyatidae'' + Gymnuridae + Myliobatidae is supported by the fragmented basihyal cartilage (character 20, state 2), which further reverts to an unfragmented (complete) state in *Gymnura*, and is independently lost in *Urotrygon* and pelagic stingrays (figs. 43, 44). This character requires five steps in all equally most parsimonious trees (as well as in the consensus). The component †*Heliobatis* + Potamotrygonidae + ''Dasyatidae'' + Myliobatidae is monophyletic, as evidenced by the reduction of the caudal fin to tail-folds (character 35; but homoplasy is required for this character as *Paratrygon*, amphi-American *Himantura*, *Himantura*, and the node *Gymnura* + Myliobatidae have all lost the tail-folds independently [state 2], and †*Asterotrygon* has acquired them independently). The clade Potamotrygonidae + ''Dasyatidae'' + Myliobatidae is supported by the cartilaginous unsegmented rod in the tail (character 34, devoid of homolasy).

The most innovative result of our phylogenetic study is the relationship between dasyatid genera (not as a monophyletic unit, however) and the group Gymnuridae + Myliobatidae. This relationship, not present in the phylogenies of Nishida (1990), Lovejoy (1996), and McEachran et al. (1996), is supported by the dorsal fossa on the scapular process (character 26), which occurs independently in Urotrygonidae and *Trygonoptera*, and is secondarily lost in *Gymnura* (note that this character was also included in the analyses of both Lovejoy and McEachran et al.). Even though there is much homoplasy in this character, it supports a more recent relationship between dasyatid genera (not as a clade however) with gymnurids and myliobatids in all minimum-length trees. The subpleural components of the hyomandibular lateral-line canal (character 2) are highly modified in dasyatid genera and in the node Gymnuridae + Myliobatidae, and were scored with different conditions of a multistate character; however, because dasyatid genera do not form a monophyletic unit, placing state 1 of this feature as a synapomorphy of ''Dasyatidae'' + (Gymnuridae + Myliobatidae) is equivocal (see fig. 44). There are important biogeographic implications derived from this relationship, and these are further discussed below.

Gymnuridae forms a monophyletic group with pelagic stingrays (Myliobatidae), sharing a shortened orbital region (character 10), fragmented mesopterygium (character 28; further lost in higher myliobatids), and lateral extension of radial segments in the pectoral fin (character 29). Loss of the tail-folds (character 35, state 2) is ambiguous at this node (fig. 44). Other characters putatively synapomorphic at this level are the presence of the lateral hook of the subpleural component of lateral-line canal (state 1 of character 2), and the highly arched pelvic girdle (character 32) (see fig. 44). Character 2 has multiple optimizations (either states 1 or 2 can be equally interpreted as a defining feature for this node), while character 32 is absent in *Myliobatis*, allowing for its independent acquisition in *Gymnura* and the node *Aetobatus* + (*Rhinoptera* + *Mobula*). The transverse, unfragmented state of the basihyal (character 20, state 1) can also be placed at this node (fig. 44; further modified for myliobatids).

The Australian stingarees, *Trygonoptera* and *Urolophus*, are united as a monophyletic Urolophidae based on the enlarged optic nerve foramen (character 8) and the greatly sinuous external margin of the mesopterygium (apparently fused to radials, character 30). Urotrygonidae, containing amphi-American stingrays with a caudal fin (*Urobatis* and *Urotrygon*), is monophyletic based on the branched extremities of the subpleural canal (character 1), dorsal fossa on scapular process (character 26, independently acquired elsewhere), and spiracular tentacle (character 42). South American freshwater stingrays (Potamotrygonidae) share the following unambiguous evolutionary novelties: a greatly extended median prepelvic process (character 31), loss of urea retention (40), and reduction of the rectal gland (41) (note that modifications of the suborbital components of the infraorbital lateral-line canal [character 3] may be optimized at this node as well; fig. 44).

DISCUSSION AND COMPARISON TO PREVIOUS STINGRAY PHYLOGENIES

Some of our monophyletic components are present in previous phylogenies of stingrays, including Gymnuridae + Myliobatidae (and two additional clades within Myliobatidae: *Aetobatus* + (*Rhinoptera* + *Mobula*)), South American freshwater stingrays (Potamotrygonidae), *Potamotrygon* + *Plesiotrygon*, Urotrygonidae (*Urotrygon* + *Urobatis*), and a large clade that includes all stingrays except *Hexatrygon*. The relationships within the large monophyletic group comprising potamotrygonids, ''dasyatids,'' gymnurids, and myliobatids, which contains most extant species of stingrays, differ substantially from the relationships within this clade advocated by Nishida (1990), Lovejoy (1996), and McEachran et al. (1996) (their phylogenetic schemes are shown in fig. 46). The clade †*Heliobatis* + (Potamotrygonidae + (''Dasyatidae'' + (Gymnuridae + Myliobatidae))) and the group comprising dasyatid genera + (Gymnuridae + Myliobatidae) are novel to our analysis, not being present in previous stingray phylogenies. The node *Urolophus* + *Trygonoptera* (Urolophidae) is also unique, as *Trygonoptera* was not included as a separate terminal by Lovejoy (1996) or McEachran et al. (1996), and Nishida (1990) included only *Trygonoptera testacea*, the type-species of *Trygonoptera*, in his study (as *Urolophus testacea*). Our phylogenetic analysis is also the first to include both fossil and extant stingrays, and includes more informative characters (44 with potential for grouping within stingrays; Lovejoy's matrix contains 33 characters that vary within stingrays, whereas McEachran et al.'s phylogeny includes 35 with potential to unite stingray genera; note that McEachran et al.'s analysis was broader in scope, designed to clarify relationships among extant batoids). Molecular approaches to the phylogeny of stingrays are still in their infancy, and some recent results appear highly controversial (such as *Gymnura* forming a monophyletic group with *Potamotrygon*; Dunn et al., 2003).

Our strict consensus tree has more components in common with the stingray relationships presented by Lovejoy (1996) and McEachran et al. (1996) than with the phylogeny of Nishida (1990) (cf. figs. 43 and 46). Comparison with Nishida's phylogeny is difficult because his tree was not generated by computerized phylogenetic procedures, and when implemented by Hennig86 the results are entirely at odds with the phylogeny he advocates (Carvalho, 1996a; McEachran et al, 1996). Nonetheless, the tree he favors shares just one node in common with our phylogeny, Gymnuridae + Myliobatidae, which is supported by similar features (see above). None of these authors supports a monophyletic Dasyatidae (neither do we, but see appendix 2). However, our resulting phylogeny also differs in many respects from the cladograms of Lovejoy (1996) and McEachran et al. (1996), which are very similar to each other. Although we included characters discussed by these workers, some of these are coded differently (e.g., characters 13, 34, 35 and 44) and contribute to differences in tree topology. Other characters included in the analyses of Lovejoy (1996) were excluded from consideration. These include the degree of lateral projection of the lateral stays of the first synarcual (Lovejoy's character 21) and the level of first segmentation of the propterygium (his character 25). We found it difficult to quantify both characters, which varied intragenerically to a large degree according to our observations (especially in *Dasyatis* and *Urolophus*). Other excluded characters are autapomorphic for individual genera (5 of Lovejoy's 39 characters). We also excluded from consideration the direct insertion of the depressor rostri muscle on the pectoral propterygium (i.e., inserting without an aponeurosis; Nishida, 1990), as it only occurs in gymnurids and *Manta*, and the latter genus was not included in our matrix.

Relationships among myliobatid genera in our phylogeny are in accordance with the results of Lovejoy (1996) and McEachran et al. (1996), but contrary to the topology advocated by Nishida (1990), who favored a restricted Myliobatidae including only *Myliobatis* + (*Aetobatus* + *Aetomylaeus*), which in turn is sister-group to *Rhinoptera* + Mobulidae. Most of the characters used by Nishida for this arrangement are optimized differently on our trees (we did not include the ‘‘hyomandibular accessory cartilage 1’’ because it is highly variable within genera), supporting the group *Myliobatis* + (*Aetobatus* + (*Rhinoptera* + *Mobula*)). Furthermore, the characters that support *Aetobatus* + *Aetomylaeus* in Nishida's phylogeny also occur for *Rhinoptera* + Mobulidae, so that on Nishida's tree more than one optimization exists for these features (they could also be interpreted as synapomorphies for all pelagic stingrays, lost in *Myliobatis*).

The major difference between our phylogeny and the trees of Lovejoy (1996) and McEachran et al. (1996) is the recognition of a large component uniting all dasyatid genera and Gymnuridae + Myliobatidae. The position of the clade Gymnuridae + Myliobatidae as a monophyletic group nested within successive higher level taxa of benthic stingrays is common to all stingray phylogenies generated to date (cf. appendix 2). Differences between these phylogenies and ours are the result of the inclusion of different taxa and characters, as well as alternative interpretations for certain features. Lovejoy (1996) and McEachran et al. (1996) placed *Dasyatis* (including Indo-west Pacific *Himantura* in Lovejoy, 1996) as sister-group to Gymnuridae + Myliobatidae, a grouping not at odds with our phylogeny. These authors, however, also support a group comprising *Taeniura*, amphi-American *Himantura*, and the Potamotrygonidae, a relationship contradicted by our results. The characters advanced by these authors supporting this relationship were also included in our analyses (relating to the angular cartilages and patterns of insertion of the spiracularis muscle). The results of Lovejoy (1996) concerning potamotrygonid relationships are not verified here not only because of differential coding of certain features, but also because we implemented our analyses without ordering multistate characters, a prerequisite to achieve the topology advocated by Lovejoy. When his analysis is run without ordering multistate characters, the results obtained are somewhat more varied, and amphi-American *Himantura* is no longer unequivocally supported as the sister-group to potamotrygonids. We have included the characters supporting Lovejoy's clade *Taeniura* + (amphi-American *Himantura* + Potamotrygonidae) in our matrix (see characters 14 and 37 above), but these were not sufficient to support their monophyly in any of our equally most parsimonius trees. This holds true even when character 37 (describing the different insertion patterns of the spiracularis muscle) is run as an ordered multistate feature.

Relationships within Potamotrygonidae, however, are resolved identically as in the analysis of Lovejoy (1996), with *Potamotrygon* and *Plesiotrygon* as sister-groups, contrary to the hypothesis of Rosa (1985) and Rosa et al. (1987). We concur with Lovejoy's reasoning for excluding two of the characters used by Rosa to unite *Potamotrygon* and *Paratrygon* (modal numbers of pectoral fin radials and pelvic fins covered by pectoral disc). These characters are difficult to code, and more comparative data are needed before numbers of pectoral fin radials can be confidently used. The proximal fusion of the first and second ceratobranchials also used by Rosa (1985) and Rosa et al. (1987) to unite *Potamotrygon* to *Paratrygon* occurs in other taxa, such as gymnurids and many myliobatids, and in at least one species of *Urotrygon* and *Urolophus* (Miyake and McEachran, 1991). However, this character is a putative synapomorphy of both genera (requiring homoplasy), but it must be included in a more comprehensive species-level phylogeny of stingrays.

Our phylogenetic analysis reinforces that tree topology can be dramatically altered with only small modifications in character coding, or with the addition of characters or terminals, when taxa exhibit such high levels of homoplasy. For instance, scoring character 44 (nasal curtain) identically to the coding given in McEachran et al. (1996; with *Plesiobatis* displaying the primitive condition of having a shortened nasal curtain) resolves *Plesiobatis* as sister-group to *Urolophus* + *Trygonoptera* and alters resolution elsewhere on our phylogeny (†*Asterotrygon* is then placed in a polytomy at the node with †*Heliobatis*, potamotrygonids, dasyatids, gymnurids, and myliobatids). We have coded *Plesiobatis* differently but accurately in our assessment (with a nasal curtain reaching very close to the mouth; also J.D. McEachran, personal commun.). Another example of this sensitivity emerges if pelagic stingrays are scored as a single terminal (as Myliobatidae), as opposed to the inclusion of various myliobatid genera in the matrix (as in our final matrix of table 5; this experimental analysis is presented in appendix 2). This form of ‘‘groundplan’’ (as opposed to ‘‘exemplar’’) coding seriously alters the relationships among benthic genera that are more distantly related to pelagic stingrays (i.e., that are not their direct sister-groups), perhaps unexpectedly (for theoretical considerations, see Bininda-Emonds et al., 1998; Wiens, 1998, 2000; Kornet and Turner, 1999; Prendini, 2001; Simmons and Geisler, 2002). Elasmobranchs are notorious for elevated levels of character conflict (see, for example, the phylogenies of Naylor, 1992; Shirai, 1992; McEachran et al., 1996; McEachran and Dunn, 1998; cf. Carvalho, 1996a), and stingrays are no exception. Coding must be done cautiously if taxa are to be combined into a single family-level entry (which should be avoided if possible), either because of inadequate sampling or for the sake of simplifying tree construction, as this single entry will, undoubtedly, contain a high degree of character variation (taxonomic polymorphism in the sense of Nixon and Davis, 1991). This is precisely the case of pelagic stingrays in the analysis of appendix 2 regarding the hyomandibular-Meckelian ligament. When the single terminal Myliobatidae was coded as having the ligament in that analysis (appendix 2), on the basis of this being the inferred ancestral state (‘‘IAS coding’’ of Rice et al., 1997), resolution was substantially decreased in the strict consensus, and the number of equally most parsimonious trees increased considerably. Similarly, adding to our matrix (table 5) only two characters with potential to unite dasyatid genera would be enough to support a monophyletic Dasyatidae in all minimum-length trees obtained. A monophyletic Dasyatidae, in turn, dramatically affects the relationships of other stingray genera in the analysis, and the outcome would be more similar to the topology presented in appendix 2. To date, however, there have been no unambiguous characters discovered and correctly included in a phylogenetic analysis to support dasyatid monophyly (but see appendix 2).

Removing the Green River fossils from our matrix reduces resolution considerably. Parsimony analysis of the matrix in table 5 without †*Asterotrygon* and †*Heliobatis* resulted in 273 trees (length = 80 steps, CI = 0.70, RI = 0.82), and the strict consensus (length = 86 steps, CI = 0.65, RI = 0.78) does not support a monophyletic Urolophidae or the large clade Potamotrygonidae + (‘‘Dasyatidae’’ + (Gymnuridae and Myliobatidae)), the major contribution to stingray phylogeny presented in this study; dasyatid genera are placed in a polytomy with potamotrygonids. The other components of our phylogeny in figure 43 remain unaltered. Successive approximations weighting of this modified matrix resulted in 123 trees (length = 474 steps, CI = 0. 88, RI = 0.93), and the strict consensus of these (length = 478 steps, other tree indices remain unchanged) adds two clades: (1) Urolophidae + *Pteroplatytrygon*; (2) *Dasyatis*, *Himantura* sensu stricto + (Gymnuridae + Myliobatidae). The former clade (1) is highly counterintuitive; amphi-American *Himantura*, *Taeniura* and potamotrygonids remain in a polytomy. The impact of †*Heliobatis* on the relationships among extant stingrays is greater than that of †*Asterotrygon*; when only †*Asterotrygon* was removed, relationships were identical to those presented in figure 43 (derived from the matrix in table 5, with both fossil taxa included). Implementing the analysis solely without †*Heliobatis* produced the highly modified and more ambiguous results described above. The influence on extant stingray phylogeny of the Green River stingrays is therefore substantial, but differs for both fossil genera. The more dramatic changes caused by the inclusion of †*Heliobatis* stems from its additional missing entries in the matrix (†*Heliobatis* has three more unknown entries than †*Asterotrygon*); both taxa differ otherwise in only one additional feature (dorsal fin, character 33). The different influence of †*Asterotrygon* and †*Heliobatis* on stingray phylogeny is therefore determined by this particular combination. This is further evidence that the impact a fossil taxon may have on a phylogeny of living forms depends more on its specific combination of features than on any other factor (Gauthier et al., 1998; Donoghue et al., 1989; Huelsenbeck, 1991; Novacek, 1992; Graybeal, 1998; O'Leary and Geisler, 1999 [cf. Naylor and Adams, 2001]; Kearney, 2002; contra Patterson, 1981; Rosen et al., 1981).

SYSTEMATIC ISSUES WITHIN MYLIOBATIFORMES

The hyomandibular-Meckelian ligament requires further comparisons within the Myliobatidae. The ligament is present in three of the seven genera of pelagic stingrays (*Myliobatis*, *Aetobatus*, and *Rhinoptera*), but its presence in *Myliobatis* is based on conflicting evidence (Garman, 1913; Nishida, 1990). The condition in *Pteromylaeus* is unknown. Lovejoy (1996) excluded this character from his analysis, but he was influenced by the ambiguous account given by Nishida (1990) concerning the condition in *Plesiobatis*. The hyomandibular-Meckelian ligament was included in the matrix of McEachran et al. (1996), who correctly coded *Plesiobatis* as having the ligament, the condition present in benthic stingrays except *Hexatrygon* and gymnurids.

Dissection of various stingrays revealed that the spiracularis muscle is more complex than was indicated in previous interpretations (Lovejoy, 1996; McEachran et al., 1996), including our own observations summarized in the matrix (table 5), which largely follows Lovejoy. We included the character somewhat tentatively to see how it would affect the relationships of *Taeniura*, amphi-American *Himantura*, and potamotrygonids, hypothesized by Lovejoy as forming a monophyletic group (it does not support this node in our analysis, even when run as ordered; see above). The spiracularis of these taxa (except *Paratrygon*) is indeed robust and projects posteroventrally, more so than in most other stingrays examined. However, *Pteroplatytrygon* and some species of *Dasyatis* may have the spiracularis inserting posterior to the lower jaws and somewhat continuous with the depressor hyomandibularis muscle as well (also Kesteven, 1942; Miyake, 1988; see character description above). Dissection of additional taxa is still needed. Deactivating this character in our matrix does not alter the strict consensus, but it reduces the number of equally most parsimonious trees to 28 (length = 79 steps, CI = 0.68, RI = 0.82; strict consensus tree: length = 79 steps, CI = 0.65, RI = 0.79).

Previous authors have advocated that *Dasyatis* and *Himantura* may not be monophyletic genera, a proposition that we have only partially tested in our analysis (Compagno and Roberts, 1982; Last and Stevens, 1994; Lovejoy, 1996; Rosenberger, 2001b). *Himantura*, on morphological grounds alone, should be divided into separate genera, one for amphi-American species (*H. schmardae* and *H. pacifica*) and one for *Himantura* sensu stricto for Indo-west Pacific species (Lovejoy, 1996). Both amphi-American species share unique specializations of the dermal skeleton, disc proportions, and shape, and perhaps even of the caudal sting (Carvalho and Lovejoy, in prep.). They were consequently coded as two separate terminals in our matrix (following Lovejoy, 1996), and they do not form a monophyletic *Himantura* on any of the minimum-length trees obtained. There are characters that may potentially unite species of *Himantura* sensu stricto (Indo-west Pacific species) as a monophyletic unit, such as arrangement of their nasal capsules (which are anteroposteriorly abbreviated), anterior projection of the scapular process (e.g., Nishida, 1990: fig. 30f), and a narrow, anteriorly rounded pelvic girdle. We have observed these features in various species of *Himantura*, but they vary among species to a certain degree, and in order to verify this claim they must be included in a more comprehensive species-level matrix.

The situation concerning *Dasyatis* is more complex. This genus presently includes from 35 to 40 species (Compagno, 1999), many of which are poorly known morphologically. Rosenberger (2001b) attempted the first cladistic test of its monophyly. Her phylogenetic analysis included 13 *Dasyatis* species (15 if both *Pastinachus sephen* and *Pteroplatytrygon violacea* are considered in *Dasyatis*, as she did), in addition to five species belonging to the genera *Gymnura*, *Taeniura*, amphi-American *Himantura, Himantura* sensu stricto, and *Urobatis*. Her resulting phylogeny nests *H. gerrardi*, *Gymnura micrura*, *Pteroplatytrygon*, and *Pastinachus* within *Dasyatis*. *Gymnura micrura* clearly does not belong in *Dasyatis*, as would have been concluded had more species of *Gymnura* been coded and their many generic synapomorphies included in the matrix. We included *Pteroplatytrygon* as a separate entry in our analysis because it differed in relation to the postorbital process of the neurocranium (character 9), a feature that did not vary among species of *Dasyatis* examined (*Pteroplatytrygon* is also considered valid in recent compilations, e.g., Compagno, 1999; McEachran and Carvalho, 2002). Rosenberger's analysis was partially based on features that are difficult, if not impossible, to divide into discrete states because their variation is either too subtle or continuous (cf. Rae, 1998) (such as her character 1, snout length less than 25% of disc length [state 0], greater than 25% [1]; character 14, midregion of frontoparietal fontanelle greatly constricted and narrow [0], moderately constricted [1], wide [2]; character 15, anterior margin of frontoparietal fontanelle rounded [0], slightly rounded [1], straight [2]; character 24, mesopterygium wide [0], narrow [1]). The frontoparietal fontanelle (her character 14), for example, may be greatly constricted *and* wide (e.g., in *Potamotrygon*; fig. 34A), and the difference between a wide and narrow mesopterygium in many species of *Dasyatis* may be trivial or somewhat arbitrary (the mesopterygium can even vary slightly in length and width on both sides of the same specimen, e.g., *Dasyatis pastinaca* AMNH 32796). Other characters vary among specimens within certain species according to our data (her character 27, number of metapterygial segments; e.g., in *Dasyatis margarita*, *D. zugei*, *Urobatis jamaicensis*; of course, this does not necessarily imply that they vary among Rosenberger's terminals) or they are simply not very clear (her character 31, ''posterior portion of pelvic gridle arch''). Rosenberger's conclusions regarding the validity of *Pteroplatytrygon* and *Pastinachus* may eventually prove to be correct, but the former genus did not pair with *Dasyatis* in any of our minimum-length trees, and there is even a hint of evidence that it may be more closely related to the clade Gymnuridae + Myliobatidae (see comments on swimming patterns below). Rosenberger's analysis is a step in the right direction, but in addition to complementing her matrix with more species, morphological characters that are more reliable at the species level must be included, and these have been highly elusive so far (i.e., characters that are constant within species but that vary among them).

Subdividing the larger benthic genera into geographical components, if these are demonstrated to be monophyletic (as is the case with amphi-American *Himantura*), may alleviate difficulties in coding generic-level matrices, as an all-inclusive species-level matrix is still too prohibitive at present. This is precisely what has transpired in the systematics of skates, in which very large, traditional taxonomic units (e.g., *Raja*) have been subdivided into putative monophyletic groups that were previously given subgeneric ranking. These ''subgenera'' are now recognized as separate genera that are geographically more restricted (McEachran and Miyake, 1990; McEachran and Dunn, 1998). Geographically restricted monophyletic subunits may exist within *Dasyatis*, but this hypothesis, contradicted by Rosenberger (2001b), remains to be fully explored.

Our observations indicate that *Taeniura* is probably monophyletic (note that our matrix did not test *Taeniura* monophyly), as all three species have the first (or anterior) pair of hypobranchials conspicuously cleaver- or club-shaped. Species of other stingray genera may have hypobranchials in which the anterior portion is wider than the posterior half, but in *Taeniura* the anterior portion is conspicuously broad, with the broad segment extending posteriorly to at least one-half of hypobranchial length (therefore extending posteriorly farther in comparison to other genera in which the first hypobranchial has a broad anterior segment). The anterior hypobranchials also have slightly concave internal (medial) margins in *Taeniura*. These elements are particularly similar in *Taeniura lymma* (AMNH 44077) and *T. grabata* (MNHN 1989–1793). The anterior hypobranchials of *T. meyeni* are also markedly broad (Nishida, 1990) and resemble the hypobranchials of the other species of *Taeniura* more than those of other stingrays. More specimens of *T. meyeni* are needed for further comparisons. Other features that may be indicative of *Taeniura* monophyly are the shape of the basihyal (uniquely anteroposteriorly extended, about two-thirds as long as wide), the anterior projection of the hyomandibulae (this process is set at an angle to the main ramus of the hyomandibula, accommodating the hyomandibular-Meckelian ligament; marked with an asterisk in fig. 35A), and the arrangement of the ceratobranchials (in which the forward extensions that contact the anterior ceratobranchial element are particularly slender and elongated). These features require confirmation on additional specimens; they may be autapomorphies of *Taeniura lymma*, synapomorphies of *Taeniura*, or prove unreliable due to intraspecific variation.

Trygonoptera Müller and Henle, 1841 has been considered a junior synonym of *Urolophus* Müller and Henle, 1831 by some previous authors (e.g., Whitley, 1940; McEachran, 1982; Nishida, 1990), but others have recognized it as a valid genus (Bigelow and Schroeder, 1953; Last and Gomon, 1987; Last and Stevens, 1994; Compagno, 1999; Last and Compagno, 2000). Although they can be distinguished on the basis of external morphology (primarily by the fleshy nasal lobe in *Trygonoptera*), skeletal features further separate both genera, particularly those from the neurocranium. *Trygonoptera* has the infraorbital lateral-line canal passing between the postorbital process and the more anterior lateral projection (supraorbital process), while *Urolophus* has the canal passing through a large foramen in the postorbital process per se as in most myliobatids (character 9 in our analysis). The dorsal internasal septum is also somewhat distinct in both genera, being relatively wider in *Trygonoptera* (similar to *Plesiobatis*; however, the phylogenetic significance of the dorsal internasal septum has yet to be fully explored). Both genera also differ in character 26 (fossa on dorsal scapular region, present in *Trygonoptera* but absent in *Urolophus*). Furthermore, in *Trygonoptera* the supraorbital process is particularly elongated compared to other genera in which it is present (genera with state 0 for this character, listed above). We have observed this feature in all species of *Trygonoptera* examined (in five of the six species recognized by Last and Stevens, 1994) and accept it as evidence of its monophyly along with the fleshy lateral nasal lobes. Yearsley (1988) arrived at similar conclusions and presented more (and different) skeletal evidence distinguishing both genera.

The degree of development of the tail-folds may still be of some value in delimiting groups within dasyatids, but a comprehensive species-level phylogeny is necessary to evaluate this character more thoroughly, and more information is needed for many stingray species before this can be attempted. Our analysis demonstrates that lack of tail-folds occurs independently for at least four stingray groups (Gymnuridae + Myliobatidae, *Paratrygon*, amphi-American *Himantura*, and *Himantura*), and that possession of only ventral tail-folds appears, when mapped on our trees, independently at least twice (for *Taeniura* and *Plesiotrygon*) but probably more times because certain species of *Dasyatis* also lack dorsal tail-folds (presenting only a dorsal keel in its place; Garman, 1913; Bigelow and Schroder, 1953; Nishida and Nakaya, 1990). As there is much variation in the pattern of tail-folds within *Dasyatis* (some authors have used *Amphotistius* Garman, 1913 for species with both dorsal and ventral tail-folds; e.g., Paxton et al., 1989), this character cannot be fully evaluated until a species-level phylogeny is available. In fact, because many characters appear, disappear, and reappear in stingray evolution, amounting to high levels of character variation within genera, a species-level phylogeny is necessary to fully evaluate their potential for grouping (e.g., arrangement of orbital foramina, degree of development of lateral stays of first synarcual, extent of internasal septum, patterns of subdivision of the propterygium).

The phylogenetic analysis presented here allows for some consideration of swimming in stingrays, which is accomplished by the following patterns (or modes, Rosenberger, 2001a): undulatory (wavelike, with anterior to posterior motions of the disc), oscillatory (birdlike, with flapping of the disc), or a combination of these (the ‘‘intermediate’’ condition of Rosenberger, 2001a). Even though the extreme manifestations of ‘‘wavelike'' and ''birdlike'' swimming are quite distinct (such as between a skate and a manta ray, respectively), there is a large gray zone of in-between conditions (the undulation/oscillation continuum of Rosenberger, 2001a), rendering the divisions into discrete states somewhat arbitrary. Nonetheless, adding this character to our matrix (i.e., coding swimming patterns) resulted in 107 equally most parsimonious trees (length = 85 steps, CI = 0.68, RI = 0.82) and a strict consensus (length = 89 steps, CI = 0.65, RI = 0.79) identical to the tree obtained without this character (fig. 43, from the matrix in table 5). However, after successive approximations weighting was applied to this dataset (with swimming as a character, resulting in 33 trees: length = 489 steps, CI = 0.89, RI = 0.93), the resulting consensus tree (length = 491 steps, CI = 0.88, RI = 0.93) supported the placement of *Pteroplatytrygon* as sister-group to the clade containing Gymnuridae and Myliobatidae. We obtained this result with weighting when coding *Pteroplatytrygon* identical to *Gymnura* (i.e., with state 1, intermediate) or to myliobatids (state 2, oscillatory). Even though optimization-dependent, this indicates that the oscillatory swimming mode indicative of a pelagic lifestyle may have arisen only once within stingrays (with gymnurids subsequently settling back into a benthic niche), and not twice as advocated by Rosenberger (2001a). Rosenberger's (2001a) study of swimming patterns within stingrays revealed that there may be additional characters for *Pteroplatytrygon* and myliobatids (and gymnurids), but these were not included in our modified matrix because they either appear to be correlated to the oscillatory swimming mode (and therefore not independent) or we could not yet confirm them in dissections (e.g., greater proportion of red muscle fibers in the disc as opposed to white [red fibers are more important for slow, steady swimming in pelagic forms], angle of articulation between scapular processes and suprascapulae).

CLASSIFICATION OF MYLIOBATIFORM GENERA

Successive approximations weighting (Farris, 1969; Carpenter, 1988, 1994; Fitzhugh, 1989) further resolves one of the polytomies of the strict consensus, resulting in 20 equally most parsimonious trees (strict consensus in fig. 47). The relationships of †*Asterotrygon* are not altered, but three (*Pteroplatytrygon*, *Dasyatis*, *Himantura*) of the five dasyatid genera form an additional node with the Gymnuridae + Myliobatidae clade, which conforms to the results of Lovejoy (1996) and McEachran et al. (1996). Implementing the weighting scheme of Goloboff (1993; using implied weights, with his program Piwe) produces results identical to those obtained from successive approximations weighting. The following sequenced classification of stingrays is derived from our study of stingray phylogeny:

- Order Myliobatiformes
  - Suborder Hexatrygonoidei
    - Family Hexatrygonidae (*Hexatrygon* Heemstra and Smith)
  - Suborder Myliobatoidei
  - Suborder Myliobatoidei incertae sedis (†*Asterotrygon*, n.gen.)
    - Superfamily Urolophoidea, new combination
      - Family Urolophidae (*Urolophus* Müller and Henle, *Trygonoptera* Müller and Henle)
    - Superfamily Plesiobatoidea
      - Family Plesiobatidae (*Plesiobatis* Nishida)
    - Superfamily Urotrygonoidea, new combination
      - Family Urotrygonidae (*Urotrygon* Gill, *Urobatis* Garman)
    - Superfamily Myliobatoidea, new combination
      - Family Heliobatidae (†*Heliobatis* Marsh)
      - Family Potamotrygonidae (*Potamotrygon* Garman, *Paratrygon* Duméril, *Plesiotrygon* Rosa, Castello, and Thorson)
      - Genera incertae sedis (*Dasyatis* Rafinesque [including *Urolophoides* Lindberg], *Himantura* Müller and Henle [Indo-west Pacific species], *Pastinachus* Rüppell, *Pteroplatytrygon* Fowler, *Urogymnus* Müller and Henle, *Taeniura* Müller and Henle, ''amphi-American *Himantura*'')
      - Family Gymnuridae (*Gymnura* Kuhl, *Aetoplatea* Valenciennes)
      - Family Myliobatidae (*Myliobatis* Cuvier, *Aetomylaeus* Garman, *Pteromylaeus* Garman, *Aetobatus* Blainville, *Rhinoptera* Kuhl, *Mobula* Rafinesque, *Manta* Bancroft)

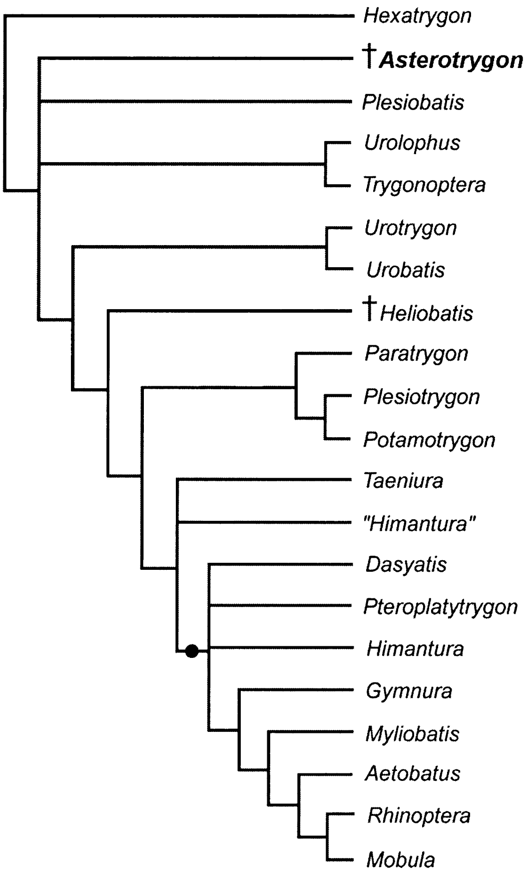


Fig. 47. Strict consensus tree (length = 477 steps, CI = 0.87, RI = 0.92) of the 20 equally most parsimonious trees (length = 472 steps, CI = 0.88, RI = 0.93) that resulted after successive approximations weighting. The marked node indicates the extent of further resolution obtained with weighting (compare with phylogeny in fig. 43). An identical tree was produced with implied weights (see text for discussion).

BIOGEOGRAPHICAL IMPLICATIONS

The myliobatiform phylogeny presented in this study (fig. 43) allows for some consideration of stingray distribution through time, particularly in relation to the origin of the freshwater stingrays of the Green River Formation and the origin of South American potamotrygonids, events that are completely independent. A more comprehensive historical biogeographic analysis of Myliobatiformes would have to take into account the myriad widespread fossil stingray taxa that have been described (see Introduction). As the overwhelming majority of these are too fragmentary to be reliably included in a phylogenetic analysis, a more complete historical appreciation of their distribution may be beyond our comprehension.

Origin of the Green River Stingrays

None of the equally most parsimonious trees recovered in our phylogenetic study allows for a single invasion of Fossil Lake by an ancestral stingray form which subsequently underwent speciation to result in the two known stingray genera (see area cladogram in fig. 48). In other words, †*Asterotrygon* and †*Heliobatis* do not from a monophyletic unit in any of the resulting trees (figs. 43, 45), nor do they form successive sister-groups to the node Potamotrygonidae + (''Dasyatidae'' + (Gymnuridae + Myliobatidae)), a topology that would still allow for a single invasion of Fossil Lake by an ancestral stingray taxon. Quite the contrary, the Green River stingrays are phylogenetically placed far apart from each other in all of the minimum-length trees recovered. It may seem counterintuitive that more than one stingray lineage entered and successfully adapted to the freshwater environment of Fossil Lake, especially given that the lake is hypothesized to have existed for ''only'' some 5 million years (which is not insignificant if compared to the much more species-diverse and younger Lake Victoria in eastern Africa, however; cf. Verheyen et al., 2003), and that Fossil Lake is considered to have been of modest size throughout its history by most estimates compared to the other extinct Green River lakes (even though its size fluctuated through time, Fossil Lake was never much greater than perhaps 70 km north–south by 35 km west–east; Grande and Buchheim, 1994). But the extensive actinopterygian fauna of Fossil Lake is by no means monophyletic either, nor is it expected to be. †*Asterotrygon* and †*Heliobatis* are presently unknown from the other extinct lakes of the Green River lake complex (Lake Uinta and Lake Gosiute), so their presence in Fossil Lake cannot be considered a remnant of a previously more widespread continental distribution. The presence of stingrays in the Green River Formation is therefore more similar to the separate fresh-

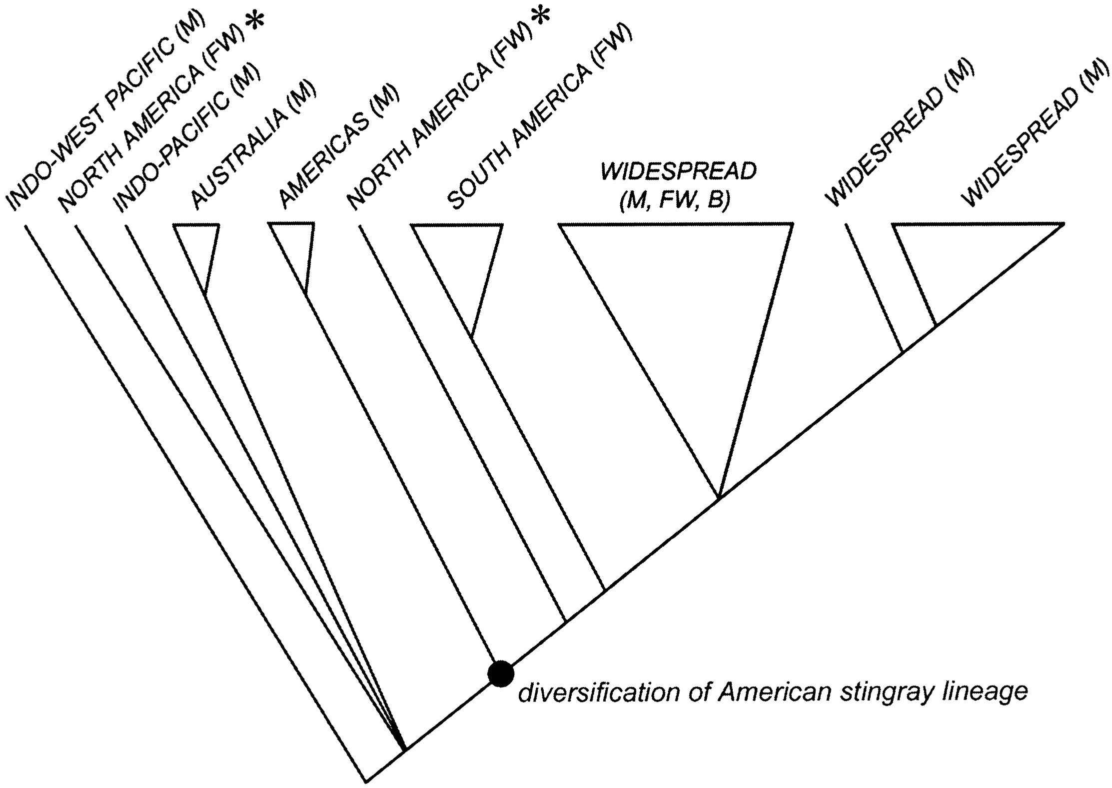


Fig. 48. Area cladogram derived from phylogeny (fig. 43) of stingrays (Myliobatiformes) presented in this paper (see Biogeographical Implications for discussion). The sequence of branches (mostly family-level terminal taxa) from left to right is as follows: Hexatrygonidae, †*Asterotrygon*, Plesiobatidae, Urolophidae, Urotrygonidae, †*Heliobatis*, Potamotrygonidae, Dasyatidae, Gymnuridae, Myliobatidae. Asterisks (*) indicate phylogenetic position and distribution of Green River stingrays. M = marine; FW = freshwater; B = brackish water.

water colonizations by endemic living species of *Dasyatis* and *Himantura* in Africa, Australia, and southeast Asia, and it is not analogous to the single (monophyletic) potamotrygonid radiation in South American freshwaters.

A phylogenetic analysis of our matrix (table 5) with †*Asterotrygon* and †*Heliobatis* constrained as a monophyletic unit resulted in 58 minimum-length trees that are only a single step longer than our original trees summarized in figures 43–45, 47 (this analysis was run in Nona; length = 83 steps; CI = 0.67, RI = 0.81). However, resolution in the strict consensus is dramatically decreased in this constrained analysis, with only a few nodes present: all stingrays except *Hexatrygon*, Urotrygonidae, Green River stingrays, Potamotrygonidae, and a node uniting Gymnuridae + Myliobatidae; all other stingray genera form a large polytomy together with all of these clades. The only character that is optimized as uniting †*Asterotrygon* and †*Heliobatis* in the strict consensus of this constrained analysis is the absence of the dorsal fossa of the scapular process, which is hypothesized to have been lost in their common ancestor (i.e., its presence united all stingrays except *Hexatrygon* in the constrained analysis). Evidence for the monophyly of the Green River stingrays is consequently meager (individual vertebrae extending to the distant tip of the tail is another putative synapomophy, but is not optimized in this fashion in all minimum-length trees obtained in this analysis). We are therefore confident, given our present understanding of their morphology, that the genera of Green River stingrays are not sister-groups, which unequivocally discards the possibility that they evolved within Fossil Lake from a common ancestor. Note that their phylogenetic positions (figs. 43, 48) still allow for a single invasion of Fossil Lake (such as through a common biogeographical event), but both stingray genera (or their direct ancestors) were phylogenetically separated when the colonization of Fossil Lake occurred.

The phylogenetic placement of †*Asterotrygon* close to the base of our strict consensus tree (fig. 43), or its placement as the sister-group to urolophids (*Urolophus* + *Trygonoptera*) in 21 of the original 35 minimum-length trees (fig. 45C–E), is an indication of a strong Indo-west Pacific association. Both *Hexatrygon* and *Plesiobatis* are widely (but sporadically) distributed in the Indian and Pacific Oceans (Last and Stevens, 1994). Urolophids (*Urolophus, Trygonoptera*) are somewhat more restricted, occurring off southern Japan and Korea (East China Sea) and in the South China Sea, but they are more diverse and common around Australia (Last and Stevens, 1994). Because the most basal living stingrays are all Indo-west Pacific (with more or less restricted distributions), and †*Asterotrygon* is nested among them in our phylogeny (figs. 43, 45; area cladogram in fig. 48), it is reasonable to infer that an Indo-west Pacific relationship is implied by †*Asterotrygon*. This historical relationship is even more geographically restricted in the trees in which †*Asterotrygon* forms a clade with urolophids (the majority of our equally most parsimonius trees). This hypothesis would not be contradicted if stingrays even more basal to *Hexatrygon* are discovered.

A transoceanic Indo-Pacific historical association has also been recognized for other Green River Formation fishes (Grande, 1985, 1989, 1994; Li et al., 1997), as well as for its fossil plants (MacGinitie, 1969). In fact, most Green River fishes that have been included in phylogenetic studies indicate a trans-Pacific relationship (Grande, 1985, 1994), as corroborated by independent studies of the Polyodontidae (†*Crossopholis*; Grande and Bemis, 1991) and the teleosts Hiodontidae, Osteoglossidae (†*Phareodus*; Li et al., 1997), Pellonulinae, †Ellimmichthyidae (= †Paraclupeidae; Chang and Grande, 1997), Catostomidae, and, to a lesser extent, the Percopsidae (†*Amphiplaga*; Patterson and Rosen, 1989; cf. Murray and Wilson, 1999). This trans-Pacific component has been demonstrated, therefore, for groups that are strictly freshwater (e.g., paddlefishes, Polyodontidae, known only from freshwater or freshwater deposits in China and North America; Grande and Bemis, 1991) as well as from those that are primarily marine (such as stingrays). The area relationships imposed by the putative †*Asterotrygon* + Urolophidae clade recovered in most of our minimum-length trees is congruent with area relationships among some species of †*Phareodus*, in which the Australian †*P. queenslandicus* is considered to be the sister-group to the Green River †*P. encaustus* (Li, 1994; Li et al., 1997).

The phylogenetic position of †*Heliobatis*, on the other hand, is indicative of a more recent historical affinity with the Americas (fig. 48), possibly (but not necessarily, see above) indicating an independent stingray invasion of Fossil Lake. The clade basal to †*Heliobatis* in our stingray phylogeny (fig. 43) is *Urobatis* + *Urotrygon*, and both genera are distributed in North and Central America with a few species reaching as far south as northern South America (Meek and Hildebrand, 1923; Bigelow and Schroeder, 1953; Miyake and McEachran, 1986; McEachran, 1995). The node above †*Heliobatis* in our tree is divided into two clades, one containing species distributed in South American freshwaters (Potamotrygonidae), and another, the most species-diverse of all stingray lineages (‘‘Dasyatidae’’ + (Gymnuridae + Myliobatidae)), with species presently occurring in most temperate and tropical marine regions, as well as some eight exclusively freshwater species (in the genera *Dasyatis* and *Himantura* in Africa, southeast Asia, and Australia). Our phylogeny therefore is congruent with the hypothesis that the largest radiation of species of stingrays (the clade ‘‘Dasyatidae’’ + (Gymnuridae + Myliobatidae)) originated only after an American stingray lineage was established (fig. 48).

This early American stingray component may have shared an ancestry with the species of stingrays described from Cretaceous and

Paleocene formations from central and eastern North America. Many of these stingrays inhabited the Late Cretaceous Seaway, a large inland sea that occupied an immense trough in western North America that at one point extended from present-day Gulf of Mexico to Alaska, with a maximum width of some 2000 km (Smith et al., 1994; cf. Funnell, 1990; see fig. 52). These stingray species are known from isolated teeth, including forms from the early Late Cretaceous (Cenomanian) of Texas (Meyer, 1974) and Late Cretaceous of Wyoming (Estes, 1964) and Texas (Welton and Farrish, 1993). The stingrays described from the Late Cretaceous of New Jersey (Monmouth group; Cappetta and Case, 1975) occurred at the opposite (eastern) margin of the North American continent during the Maastrichtian (fig. 52), but represent a very similar if not identical stingray fauna, as this coastline was probably contiguous with the Late Cretaceous Seaway over central North America. The Paleocene stingrays from the Cannonball Formation, which inhabited the last marine incursion (the Cannonball Sea) into central North America (Cvancara and Hoganson, 1993), may also be related to this early American stingray lineage. These stingrays (known only from isolated teeth) include two species of *Dasyatis* (note that one tooth referred by Cvancara and Hoganson [1993: fig. 3, v–x] to their new species †*D. concavifoveus* probably represents a gymnurid), †*Hypolophodon sylvestris*, and a myliobatid (see also Best, 1987). Unfortunately, it is not possible to compare any of the above taxa in a meaningful way to the Green River stingrays (and more precisely to †*Heliobatis*) to determine if they share a more recent common ancestry. However, it is certainly conceivable that such a relationship existed, which would indicate that an ancestral stingray taxon originally present in the Late Cretaceous Seaway, or in some other marine incursion into North America, is historically correlated with †*Heliobatis* of Fossil Lake.

ORIGIN OF THE SOUTH AMERICAN FRESHWATER STINGRAYS

The origin of the South American freshwater stingrays (Potamotrygonidae) has been the subject of much debate and has consequently become a benchmark problem in historical biogeography (Brooks et al., 1981; Rosa, 1985; Brooks and McLennan, 1993; Brooks, 1995; Lovejoy, 1996, 1997; Hoberg et al., 1998; Marques, 2000). The discussions concern primarily the sister-group of the Potamotrygonidae and the nature of the data used to infer potamotrygonid origin or affinity (for a more detailed summary of the different points of view, see Lovejoy, 1996, 1997). The theory advanced by Lovejoy (1996, 1997) and Lovejoy et al. (1998), that potamotrygonids originated from a common ancestor with amphi-American *Himantura* from the Caribbean Sea by way of an early Miocene epicontinental seaway (the ‘‘proto-Caribbean/*Himantura*’’ hypothesis), was recently given support by a molecular phylogenetic analysis of parasites and their potamotrygonid hosts by Marques (2000). This contrasts with the earlier theory of Pacific origin of the family by means of a phylogenetic relationship with ‘‘urolophids’’ (= Urotrygonidae), with the potamotrygonid common ancestor having been confined to freshwater as a result of the orogeny of the Andean Cordilleras, an ongoing process that started in the Late Cretaceous some 90 million years ago (Brooks et al., 1981; Rosa, 1985; Brooks and McLennan, 1993; Brooks, 1995). The parasite data from which much of the latter theory is founded are beyond our concern but have been extensively criticized by Straney (1982), Caira (1990), and more recently by Lovejoy (1997; cf. Hoberg et al., 1998), who provided an arrant discussion of problems pertaining to Brooks et al.'s (1981) data, host/parasite coevolution in general, and the implicit assumptions of their ‘‘Pacific/urolophid’’ hypothesis. This hypothesis is completely contradicted by our phylogenetic results (and previously by those of Lovejoy, 1996) and will not be further explored here (cf. Rosa, 1985). All of the above authors, however, are in agreement that the Potamotrygonidae is monophyletic (even though their different parasite lineages may not be), a crucial point that we fully corroborate and which is congruent with the theory of a single freshwater invasion into South America by the potamotrygonid ancestor. Our focus on the problem here stems solely from inferring potamotrygonid biogeography on the basis of their phylogenetic relationships, which in our view takes precedence over data concerning the affinities of their parasites (also Straney, 1982; Lovejoy, 1997). Our stingray phylogeny (fig. 43) has prompted us to reevaluate the origin of the potamotrygonids, coupled with a radically different assessment of their minimum age.

The phylogenetic relationships of potamotrygonids advocated by Lovejoy (1996) have been reviewed above and compared to our results (cf. figs. 43 and 46B). His novel clade *Taeniura* + (amphi-American *Himantura* + Potamotrygonidae), the basis of his biogeographic hypothesis for potamotrygonids, was not present in any of our equally most parsimonius trees (even when the multistate character pertaining to the insertion of the spiracularis muscle was run as ordered, a constraint necessary to obtain this clade in his analysis). Instead, we found support for a clade comprising Potamotrygonidae + (*Taeniura*, amphi-American *Himantura*, *Pteroplatytrygon*, *Dasyatis*, *Himantura* + (Gymnuridae + Myliobatidae)), with some evidence (implementing the weighting schemes of Farris, 1969 and Goloboff, 1993) for an additional node uniting *Pteroplatytrygon*, *Dasyatis*, *Himantura* + (Gymnuridae + Myliobatidae)).

The amphi-American *Himantura* + Potamotrygonidae clade permitted Lovejoy (1996) to postulate that potamotrygonids were derived from a freshwater-invading ancestor that was distributed along the northern coast of South America (similar to the present-day ranges of *H. pacifica* and *H. schmardae*). The timing of this derivation was established by reference to the earliest putative potamotrygonid fossils known (from the late Miocene of Peru; e.g., Frailey, 1986). This, in turn, led to the inference that an epicontinental (probably Miocene) seaway was the route of the South American invasion by the potamotrygonid ancestor, which subsequently underwent extensive speciation (some 20 species are presently recognized in the family, with as many as six known undescribed forms; Carvalho et al., 2003). Lovejoy's theory also allowed for a vicariant explanation for the origin of the two species of amphi-American *Himantura*, which occurred as a result of the formation of the Panamanian Isthmus in the Pliocene, after the initial divergence between amphi-American *Himantura* and the Potamotrygonidae. Lovejoy et al. (1998) further supported this specific marine-incursion hypothesis and gave it a more precise Miocene timeline, by analyzing rates of divergence of the gene-encoding mitochondrial cytochrome *b*, DNA sequences from which were used to corroborate the amphi-American *Himantura* + Potamotrygonidae clade. The divergence rate inferred for the cytochrome *b* gene was calibrated based on the orogeny of both the eastern cordillera of the Andes and the Merida Andes (which took place some 8 million years ago [mya]; Lovejoy et al., 1998). The resulting molecular clock estimate placed the origin of the Potamotrygonidae at between 15 and 23 mya, in early Miocene to late Oligocene times (Lovejoy et al., 1998). These results were further supported by the molecular phylogenetic analysis of Marques (2000), based mostly on mitochondrial rDNA sequences (12S, 16S, CO I, and again cyt-*b*). Marques' molecular clock estimates placed the origin of this clade at approximately 19 mya, well within the mostly early Miocene range of Lovejoy et al., but his consideration of molecular clock confidence limits allowed for the potamotrygonid original divergence to have occurred from between 6 and 38 mya, as early as the late Eocene (Marques, 2000).

The application of molecular clock estimates as a method to establish dates of evolutionary events is highly controversial, and many researchers consider molecular clocks to be mostly unreliable (review in Hillis et al., 1996). Molecular clocks must be calibrated by benchmark dates from geology, paleontology, or biogeography (Smith, 1992; Lundberg, 1998), and the rate of genetic divergence in a given gene may vary significantly even within a single taxonomic lineage (Knowleton et al., 1993; Hillis et al., 1996). Furthermore, there is much discrepancy among methods used to infer actual amounts of genetic divergence (see references in Lundberg, 1998), and the confidence limits allowed by rate calibrations may, in many cases, be as great as the age of the actual events being dated (Hillis et al., 1996; precisely the situation concerning potamotrygonids described above). Hillis et al. (1996) and Lundberg (1998) provided cogent remarks on the use and accuracy of molecular clocks, which need not be repeated here. It is our view that the fossil record, even though frequently imprecise, will provide better estimates of divergence times even if these are underestimates (minimum divergence dates), as also argued by Lundberg (1998). There are two prerequisites to employ fossils as benchmarks for dating: they must unequivocally possess derived features that permit them to be placed with confidence in a phylogeny, and their geological dating must be relatively accurate.

Fossil stingrays that are pertinent for establishing a minimum age of the potamotrygonid lineage (or for the invasion of the potamotrygonid common ancestor into South American freshwaters) were added to our strict consensus tree, allowing for a more precise consideration of the relative ages of certain stingray lineages. These taxa stem from the Monte Bolca deposits of northeastern Italy and are represented by well-preserved skeletons (figs. 49, 50) that retain characters indicative of their placement in our stingray phylogeny (fig. 51). These stingray taxa have not been incorporated into our phylogenetic analysis because the Monte Bolca batoid fauna is still under investigation, but their phylogenetic positions in figure 51 are well supported by uniquely derived features.

One of the most remarkable stingrays from Monte Bolca is †*Promyliobatis gazolae* (figs. 49A, 50). This stingray is unquestionably a myliobatid, as evidenced by its teeth that are coalesced into a horizontally expanded, grinding pavement, as in pelagic stingrays except mobulids (which have reversed to having small, individual teeth). The dentition of †*Promyliobatis* is more similar to the dentition of *Myliobatis* or *Aetomylaeus*, with a much wider central tooth articulating laterally with smaller, hexagonal pavementlike teeth (De Zigno, 1885; fig. 50 here). This contrasts with the dentition of *Rhinoptera*, where the central tooth is only slightly wider than the lateral ones, which are also hexagonal (or with *Aetobatus*, in which a single, greatly expanded tooth is present in each horizontal row). †*Promyliobatis* presents the cartilaginous rod in the tail posterior to the caudal stings in place of individual vertebrae (contrary to the Green River stingrays). The caudal stings in †*Promyliobatis* are located farther posteriorly than in any other stingray, fossil or extant, and because its tail was very long (which is mostly preserved), this stingray had enormous reach with its caudal stings. On our tree, †*Promyliobatis* may be more closely related to *Myliobatis* or simply to an unresolved myliobatid (the most conservative hypothesis of relationship); in any case, the placement of †*Promyliobatis* at the node with pelagic stingrays is very well supported (fig. 51).

†‘‘*Dasyatis*’’ *muricata* (fig. 49B) is also unquestionably a stingray, but its position on the tree in figure 51 is not as well resolved. Because it presents the cartilaginous rod in the tail, it is phylogenetically positioned at least at the node uniting potamotrygonids, ‘‘dasyatids,’’ gymnurids, and myliobatids. The dorsal fossa on the scapular process is difficult to discern in this fossil, but it appears to be present according to our observations, and consequently †‘‘*Dasyatis*’’ *muricata* belongs at the next more derived node (uniting ‘‘dasyatids,’’ gymnurids, and myliobatids; fig. 51). This species clearly does not present any of the derived characters that unite other monophyletic components positioned at lower nodes in our phylogeny (urolophids, urobatids, potamotrygonids); its phylogenetic position is therefore strongly corroborated.

The Monte Bolca Formation of northeastern Italy represents an extinct coral reef embayment of the tropical Tethys Sea that was frequently exposed to the vagaries of fluvial systems and open lagoons (Sorbini, 1983; Landini and Sorbini, 1996). The deposits of the two main fossil-bearing sites, Pesciara and Monte Postale (the third site, Purga di Bolca has not yielded fossil fishes), are firmly dated as early Eocene (Lutetian, NP 14, *Discoaster sublodoensis* nanoplankton zone; Barbieri and Medizza, 1969; Patterson, 1993; Landini and Sorbini, 1996), even though previous authors have given a slightly older age to these beds (as topmost Ypresian; Blot, 1969, 1980). These discrepancies in dating are minor, however, and the 50 million-year-old early Eocene age of the Monte Bolca deposits is presently not disputed (note that some authors have interpreted the lowermost Lutetian as middle Eocene; Tyler and Santini, 2002).

Our phylogeny (fig. 51) indicates that potamotrygonids must be at least as old as †*Promyliobatis gazolae* and †''*Dasyatis*'' *muricata*, taking into account their relative phylogenetic positions (and using a stepwise correlation between nodes, moving ''down'' the tree as outlined by Lundberg, 1993, 1998). The Monte Bolca stingrays provide benchmarks by which the origin of the Potamotrygonidae can be dated, imposing a minimum age of at least 50 mya to this lineage (early Eocene). This is much older than their Miocene origin proposed by Lovejoy (1996, 1997) and Lovejoy et al. (1998). This specific age correlation with the Monte Bolca stingrays is not possible in Lovejoy's phylogeny (or in the tree of McEachran et al., 1996), due to existence of the node uniting *Taeniura*, amphi-American *Himantura*, and Potamotrygonidae, which could have originated well after the divergence of their common ancestor from the main stem of stingray evolution (fig. 46B); moreover, the clade amphi-American *Himantura* + Potamotrygonidae could only have come into existence at an even later time. Conversely, this inference is not possible in our phylogeny, as potamotrygonids branch out directly from the main stingray evolutionary branch, without any intervening node (fig. 51; note that this is also the case in the analysis presented in appendix 2, in which potamotrygonids would be at least as old as †''*Dasyatis*'' *muricata*, but not necessarily as old as †*Promyliobatis*). Potamotrygonids are consequently as old as the main evolutionary stem of stingrays, which is at least 50 million years old as inferred by the Monte Bolca stingrays.

In his overview of the temporal context for the origin and diversification of Neotropical fishes, Lundberg (1998: 55) posed the question, ''[c]ould the Potamotrygonidae be that [Late Cretaceous] old?'' According to our study, this certainly seems possible. Our phylogeny supports a divergence age for potamotrygonids that is considerably older than previous estimates—at least 12 million years older than the most generous timeframe allowed by Marques (2000), and at least some 27 million years older than Lovejoy et al.'s (1998) hypothesis. A 50 million-year-old Potamotrygonidae is clearly feasible when the morphological similarities between fossil and living elasmobranchs, including stingrays, are taken into account. A conservative morphology per se is not necessarily evidence that a particular lineage is very ancient, but given that the oldest stingrays known from skeletal remains (52 mya) are morphologically very similar to modern ones (a circumstance present in many elasmobranch groups known from even older fossils, e.g., †*Pseudorhina* from Late Jurassic of Solnhofen and modern *Squatina*; †*Asterodermus* from Solnhofen and modern rhinobatids; Woodward, 1889; Saint-Seine, 1949), a significant correlation between age and degree of morphological conservativeness in stingrays, as evidenced by their fossil record, cannot be discarded.

Certain components of the Neotropical ichthyofauna have pre-Miocene remains in South America, and it is believed that by middle or late Miocene the Neotropical fish fauna was essentially modern (Lundberg, 1998). Some of the more ancient groups mentioned below have a historical association with Africa (predating its Late Jurassic to Early Cretaceous separation from South America, some 150 to 110 mya), and therefore present a pattern of area relationships different from that of potamotrygonids, which are clearly not more closely related to a clade of African stingrays. Late Cretaceous (Maastrichtian) Neotropical fossils, mostly isolated fragments, include relatives of *Lepidosiren* (Schultze, 1991; Gayet and Meunier, 1998), osteoglossids (possibly Aptian; Lundberg, 1998; Gayet and Meunier, 1998), characiforms (Erythrinidae, Serrasalminae; Roberts, 1975; Gayet, 1991; Vari, 1995; Lundberg, 1998; Gayet et al., 2003), and siluriforms (overview in Lundberg, 1998). Callichthyid catfishes (Cockerell, 1925) and a variety of different characiforms (Gayet and Meunier, 1998) from the late Paleocene, and fossils related to *Lepidosiren* and to the Percichthyidae (a percomorph family) from the Eocene, are also reported from South America (Arratia and Cione, 1996; Lundberg, 1998; cf. Patterson, 1993). These groups are therefore older than 50 million

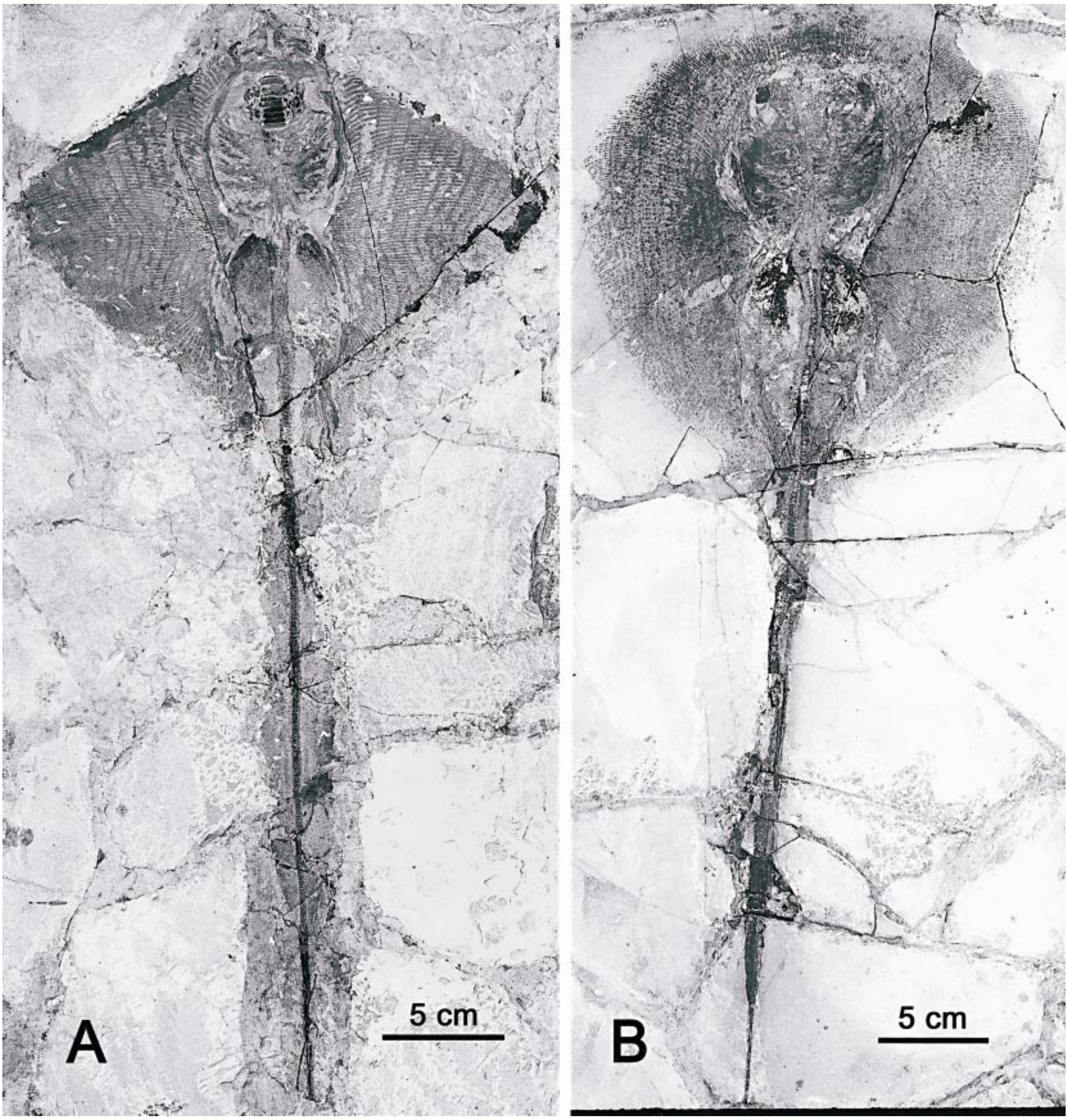


Fig. 49. Fossil stingrays from the marine early Eocene Monte Bolca deposits of northeastern Italy. **A.** †*Promyliobatis gazolae* (MCSNV VII B 90), a myliobatid. **B.** †''*Dasyatis*'' *muricata* (MCSNV VII B 92), a whiptailed stingray. The phylogenetic positions of both taxa are shown in figure 51.

years. The lack of a pre-Miocene fossil record for potamotrygonids should not be interpreted too decisively, as other Neotropical groups that are inferred to have originated much earlier than the Miocene, such as those with an historical African association, also lack a robust pre-Miocene fossil record (many characiforms, e.g., Roberts, 1975; Vari, 1995; doradoid and loricarioid catfishes; see summary in Lundberg, 1998). The Cretaceous stingray fossils that have been described from South America may even share a common ancestry with potamotrygonids, but this position is presently untenable as these fossils consist of very generalized isolated teeth (e.g., Schaeffer, 1963; see references in the Introduction), and the search for shared, derived dental features is

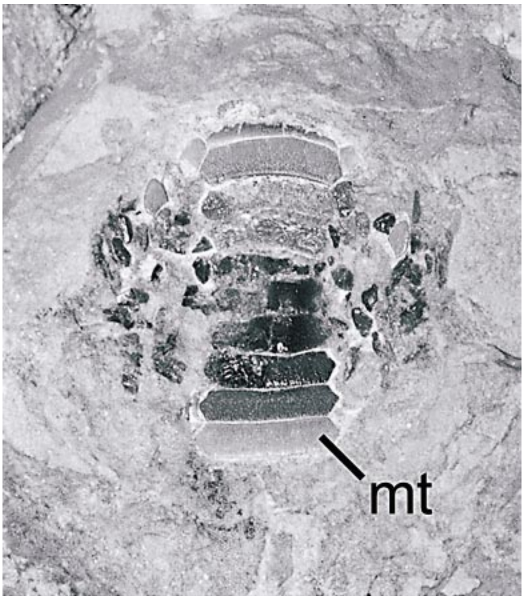


Fig. 50. Enlarged view of the dentition of †*Promyliobatis gazolae* (MCSNV VII B 90); entire specimen depicted in figure 49A. Individual lateral teeth are visible, scattered at both sides of the enlarged median tooth row (mt).

still not a standard employed by fossil teeth specialists (e.g., Cappetta, 1975, 1987).

Our stingray phylogeny (figs. 43, 51) and its implied area cladogram (fig. 48) do not permit the formulation of such a clearcut biogeographic scenario as that presented by Lovejoy (1996) and Lovejoy et al. (1998). Because potamotrygonids are the sister-group of a large clade that contains most of the modern stingray diversity, it is more difficult to accurately pinpoint or restrict to a small area the distribution of their common ancestor. This contrasts with Lovejoy's hypothesis (and to a lesser extent with the ''Pacific/urolophid'' theory forwarded by Brooks et al., 1981), in which the common ancestor of the amphi-American *Himantura* + Potamotrygonidae clade was candidly inferred to have been distributed in the proto-Caribbean Sea. Biogeographic hypotheses that deal with ''deeper'' phylogenetic divergence events, that is, those hypotheses based on relationships among higher level taxa or more inclusive monophyletic groups, will usually encounter this difficulty, especially regarding relatively widespread marine forms (our stingray phylogeny is a case in point). Of course, if the postulated phylogenetic relationships are inaccurate, then a specific area relationship is not more probable just because its biogeographic implications appear to be more alluring. Our phylogeny (fig. 43), in fact, is not at odds with the mechanism proposed by Lovejoy (1996) and Lovejoy et al. (1998) to explain the presence of the potamotrygonid common ancestor in South America (through a marine introgression). Although we refute that amphi-American *Himantura* is the sister-group to potamotrygonids, the common ancestor of the clade Potamotrygonidae + (''Dasyatidae'' + (Gymnuridae + Myliobatidae)) could also have inhabited the proto-Caribbean region (or the eastern Pacific realm, which was continuous with the proto-Caribbean until the completion of the Panamanian Isthmus in the Pliocene). Therefore, the ancestor of the Potamotrygonidae could still have invaded South America through a marine introgression from that area. This invasion is possible because, according to our phylogeny, there was already a large stingray lineage present in the Americas which eventually gave rise to the Urotrygonidae, †*Heliobatis*, and to the common ancestor of the large clade above (this component originally had a strong historical association with the Indo-Pacific region; see discussion above concerning the origin of the Green River stingrays).

We disagree, however, with Lovejoy et al.'s (1998) hypothesis in relation to the timing of the vicariant event that allowed for the introduction of the potamotrygonid ancestor into South America. A Miocene epicontinental seaway (such as the Pebasian Seaway of Lundberg et al., 1998) occurred far too recently according to our phylogeny, but earlier marine incursions are also known from the proto-Caribbean region (i.e., from the north; Hoorn, 1993; Hoorn et al., 1995; Smith et al., 1994; Lundberg et al., 1998). According to Smith et al. (1994) and Lundberg et al. (1998), extensive marine transgressions over northern South America occurred frequently (at least four times) from the Late Cretaceous (Maastrichtian) to the late Miocene, and the duration of each incursion and its resulting seaway lasted for millions of years. Two epicontinental incur-

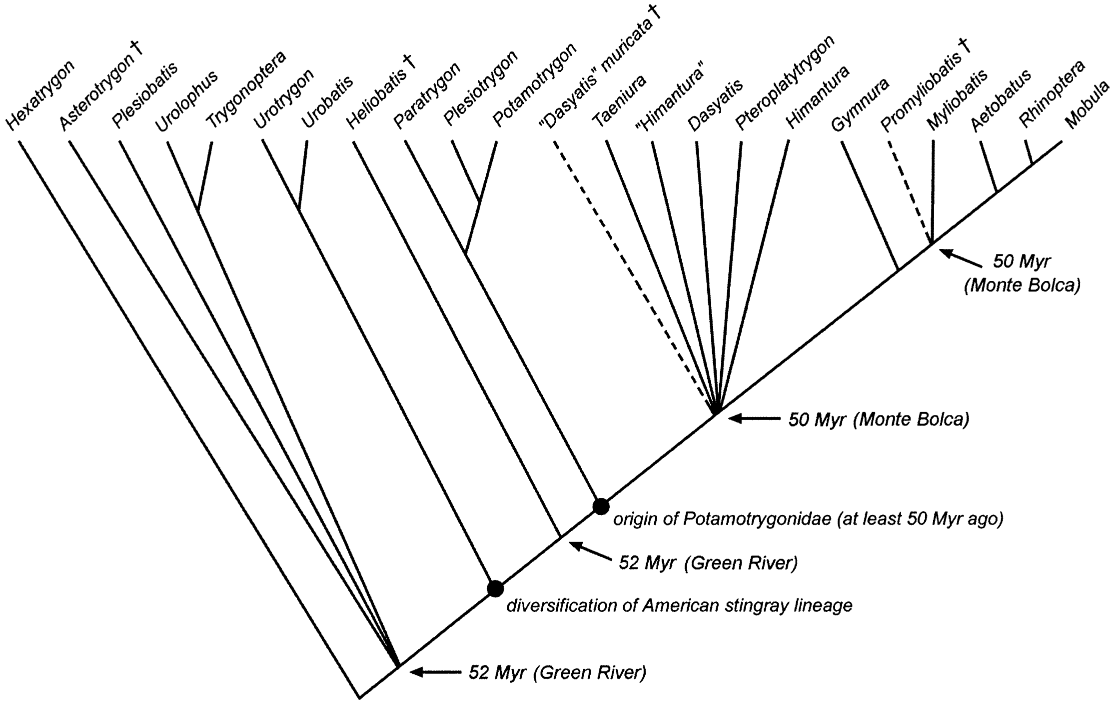


Fig. 51. Tree resulting from our phylogenetic analysis of myliobatiforms, showing placement of two early Eocene stingray taxa from the Monte Bolca Formation of northeastern Italy (fossils presented in fig. 49). These taxa allow for the timing of divergence events between the node that gives rise to †*Heliobatis* and the node that contains gymnurids and myliobatids; the groups derived directly from the main stem of the phylogeny between these nodes must have originated at least by the early Eocene (roughly 50 mya). See figure 48 for geographical distribution of terminal taxa.

sion episodes in particular are congruent with the minimum age of the potamotrygonid lineage (50 mya) derived from our phylogeny: a Late Cretaceous seaway, and another one that lasted from the late Paleocene to the very early Eocene (fig. 52). Either incursion may have trapped the potamotrygonid ancestor in the neotropics, where it slowly adapted to a progressively more freshwater environment.

The biogeographic hypothesis presented here for the origin of the Potamotrygonidae (a pre-early Eocene marine incursion from the north) does not refute the area relationships of other taxa mentioned by Lovejoy (1996) in support of his theory (the ''proto-Caribbean/*Himantura*'' hypothesis). Our hypothesis (cf. fig. 48) is congruent with the area cladogram presented by Lovejoy (1997: fig. 4a): Indo-west Pacific + (South American freshwater + (eastern Pacific + Caribbean/northern West Atlantic)). We simply think that a further area relationship (the American component) should be added after the Indo-west Pacific region (the basalmost area). These area relationships largely apply to other groups in which there is a basal Neotropical freshwater species that is the sister-group to an eastern Pacific/Caribbean species pair (such as anchovies of the genera *Cetengraulis* and *Anchovia*; Nelson, 1984) or other taxa that may have undergone vicariance and subsequent diversification due to the formation of the Panamanian Isthmus (such as amphi-American *Himantura*). These historical associations are still possible under our hypothesis; the only adjustment is that their ancestors may have invaded the Neotropical freshwater system much earlier than the Miocene (but not necessarily, at least regarding the engraulids). Without robust dating (i.e., strong fossil evidence), it is not possible to precisely determine which marine transgression (or other mechanism) was responsible for the invasion of the ancestral taxon; it could have been the same epicontinental seaway that carried the potamotrygonid ancestor (or other primitively marine groups), but this event could also have occurred much later. Although amphi-American *Himantura* is placed in a polytomy with other ''dasyatid'' genera and Gymnuridae + Myliobatidae, it may eventually prove to be basal to these taxa (as indicated when analyzing our matrix with the weighting schemes of Farris, 1969 and Goloboff, 1993; see above and fig. 47). In addition, our biogeographic theory does not contradict the northwest–southeast derivation sequence or vicariant pattern that has been reported for some Neotropical fishes distributed in northern South America (e.g., the curimatid *Potamorhina*, Vari, 1984; to a lesser extent *Steindachnerina* and *Creagutus*, Vari, 1991; Vari and Harold, 2001; for summaries, see Vari, 1988; Vari and Weitzman, 1990; Lundberg and Chernoff, 1992). In these cases, according to the above authors, basal species are distributed in northern South America and, through vicariance, more derived species have been pushed progressively farther south or southeast from the ancestral area.

CONCLUSIONS

(1) The new monotypic genus †*Asterotrygon* is distinguished from all stingrays, both fossil and extant, on the basis of its unique plesodic dorsal fin covered by denticles, and by a combination of features including an intense covering of minute hooklike denticles over most of dorsal disc and tail regions and stout tail at base. The new genus has many characters present in selected Recent stingray genera, such as well-developed hyomandibulae connected to Meckel's cartilage by robust ligaments containing an angular cartilage; separate vertebral elements extending to tip of tail (instead of a continuous cartilaginous rod); postorbital processes separated from triangular outgrowth (the supraorbital process) of the supraorbital crest by a notch; and both dorsal and ventral tail-folds supported by rudimentary radial elements. Primitively, both Green River stingray taxa (†*Asterotrygon* and †*Heliobatis*) retain a keyhole-shaped dorsal fontanelle, posteriorly directed antorbital cartilages, elongated iliac processes on the pelvic girdle, and many other features present in most benthic stingrays. The new genus is morphologically very similar to many extant nongymnurid and nonmyliobatid stingrays.

(2) †*Asterotrygon* and †*Heliobatis* present many of the characters unique to stingrays (Order Myliobatiformes), such as caudal stings, laterally expanded shelflike postorbital processes, second synarcual cartilage, absence of jugal arches, and absence of thoracic ribs. †*Asterotrygon* also presents an anterior expansion of the medial (basibranchial) plate, a small transverse basihyal element, and the first pair of hypobranchials relatively straight and obliquely oriented from the ventral pseudohyoid bar to articulate with the basihyal; these features are considered herein to be additional stingray synapomorphies.

(3) Our phylogenetic analysis resulted in 35 equally most parsimonious trees, which are reduced to five subgroups of topologies once the uncertainty concerning the affinities of dasyatid genera are removed. Both Green River stingray genera are systematically positioned far apart in all minimum-length trees obtained. †*Asterotrygon* is resolved as a basal stingray either in a polytomy with *Plesiobatis* and urolophids (as in the strict consensus tree), or as sister-group to urolophids (in 21 of the 35 minimum-length trees obtained). †*Heliobatis* is unequivocally placed as sister-group to a large clade that includes potamotrygonids, dasyatids, gymnurids, and myliobatids.

(4) Results from our phylogenetic study are as follows: *Hexatrygon* is basal to all other stingray taxa, urolophids (*Trygonoptera* + *Urolophus*) are monophyletic, urotrygonids (*Urotrygon* + *Urobatis*) are monophyletic, potamotryonids are monophyletic and *Paratrygon* is the most basal genus within the family, potamotrygonids are sister-group to a large node comprising dasyatid genera (in a polytomy) and Gymnuridae + Myliobatidae, and the Dasyatidae is not monophyletic on any of the equally most parsimonious trees obtained. *Himantura* should be divided into two genera, one for amphi-American species and *Himantura* sensu stricto exclusive for

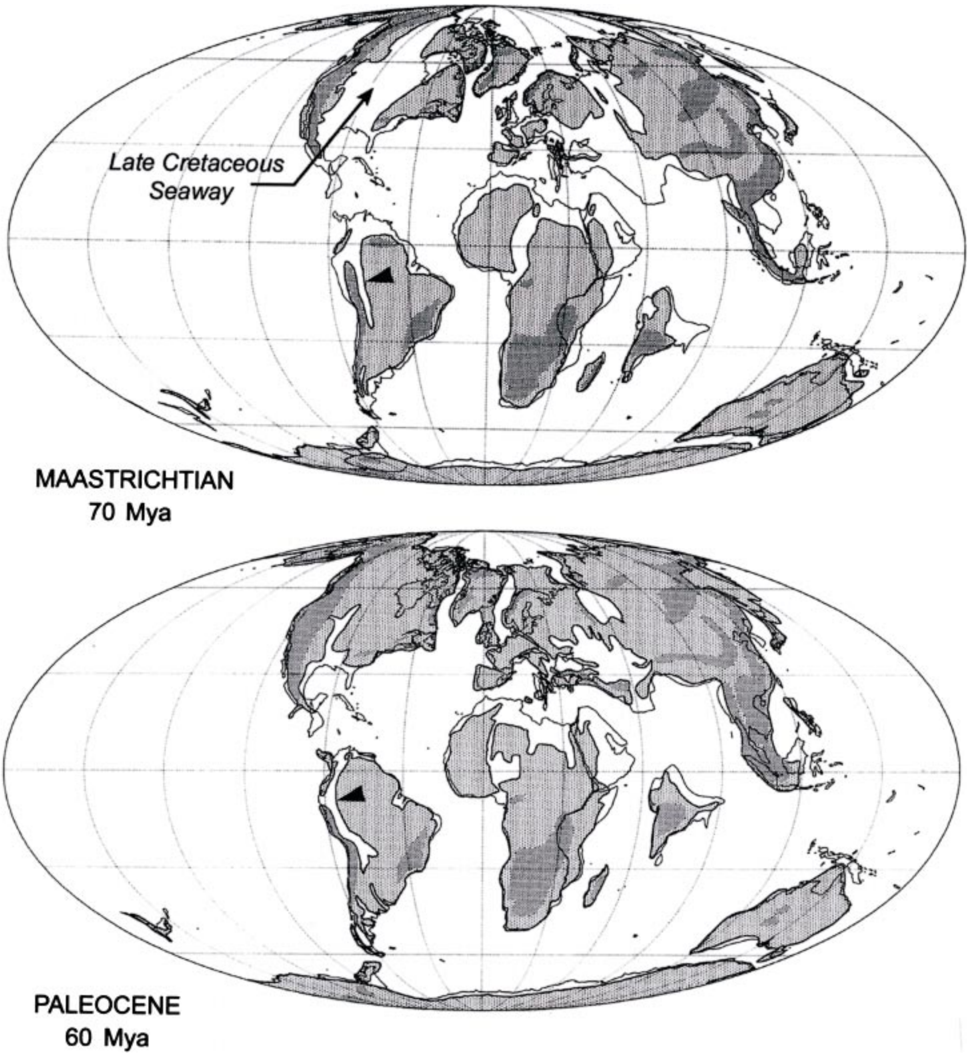
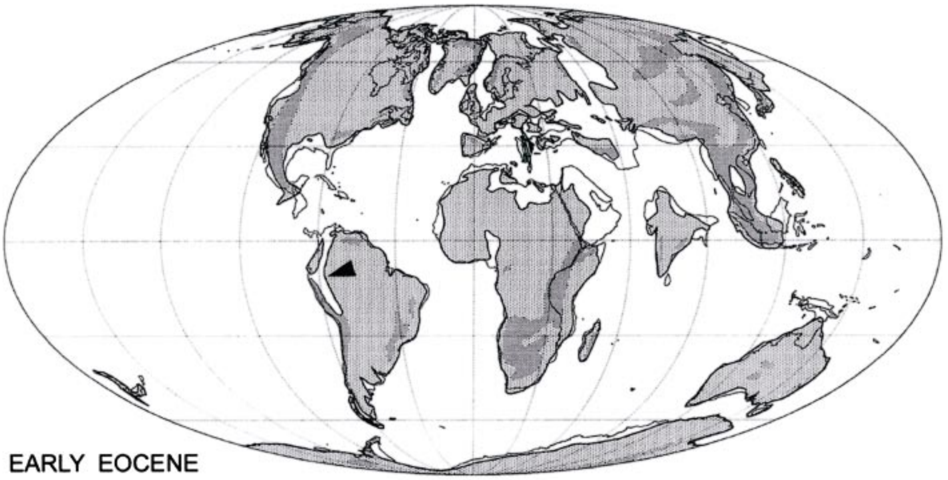


Fig. 52. Maps showing the distribution of the continents and the extent of their coastlines (in darker line) from Late Cretaceous (Maastrichtian) to middle Eocene, spanning some 25 million years (modified from Smith et al., 1994). Arrowheads indicate the extent of marine incursions (epicontinental seaways) into South America from the north (the proto-Caribbean/eastern Pacific region) during these intervals. Mya = million years ago.

west Indo-west Pacific species. *Taeniura* is putatively monophyletic based on the unique morphology of their first hypobranchial (and possibly the anterior expansion of the hyomandibulae).

(5) Phylogenetic relationships among certain stingray genera are problematic due to lack of information concerning many of their component species. A species-level phylogeny is necessary to adequately understand the true systematic relevance of many features, such as the configuration of tail-folds, fusion of ceratobranchial elements, and even the hyomandibular-Meckelian ligament. Morphological variation among component species of familial-level stingray terminal taxa may lead to elevated polymorphisms, but more data for most stingray species are still needed before a comprehensive species-level phylogeny can be accomplished.



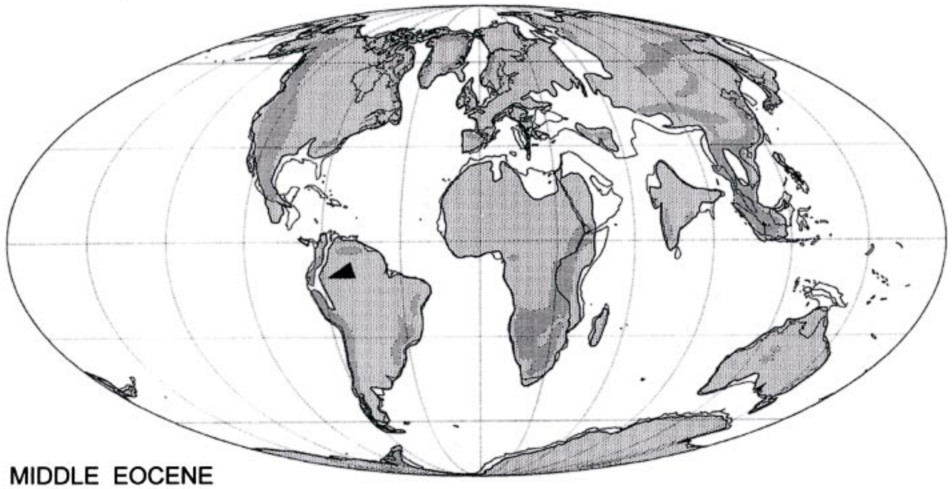


Fig. 52. Continued.

(6) Our phylogenetic study led to the following biogeographic implications: †*Asterotrygon* displays a strong historical association with the Indo-west Pacific region (and possibly with Australia); a large American stingray component was established before the early Eocene, which eventually gave rise to the Urotrygonidae and †*Heliobatis*; the origin of the Neotropical freshwater stingrays (Potamotrygonidae), which is completely independent of the origin of the Green River stingrays, occurred before the early Eocene, much earlier than previous Miocene estimates; the potamotrygonid ancestor could have entered South America through an epicontinental seaway from the north (from the proto-Caribbean/eastern Pacific region), during the period ranging from the Late Cretaceous or Paleocene to the early Eocene.

ACKNOWLEDGMENTS

Numerous collection managers and curators have provided invaluable assistance in furnishing stingray specimens for dissection and/or work space in their collections: G. Nelson (retired), Scott A. Schaefer, Melanie L. J. Stiassny, Barbara A. Brown, Norma R.

Feinberg, and Radford Arrindell (AMNH); Peter R. Last, John D. Stevens, Alastair Graham, and Gordon Yearsley (CSIRO); Barry Chernoff, Mary-Anne Rogers, and Kevin Swagel (FMNH); the late Lorenzo Sorbini, Alessandra Aspes, Roberto Zorzin, Anna Vaccari, and Francesca Buttorini (MCSNV); Karsten Hartel and Karel Liem (MCZ); Françoise Meunier, Bernard Séret, Guy Duhamel, Patrice Pruvost, and Pascal Deynat (MNHN); José Lima de Figueiredo, Osvaldo Oyakawa, and Alberto Akama (MZUSP); Peter Forey, Anthony C. Gill, Darrel J. Siebert, Oliver Crimmen, and Sean Davidson (NHM); Bruce Erickson (SMMP); Ulisses L. Gomes (UERJ); Luca Altichieri (UP); Lynne R. Parenti, Susan Jewett, Leslie Knapp, and Jerry Finan (USNM); Hans Joachim-Paepke and Gloria Arratia (ZMB). Most of the Green River stingrays examined for this paper were prepared by the staff of the Department of Geology of the FMNH and the Division of Paleontology of the AMNH. Special thanks are due to Peter Last, Gus Yearsley, and Al Graham of CSIRO in Hobart who were very generous in allowing the first author to examine numerous radiographs and slides of stingrays in their collections, and for discussions concerning stingaree systematics. The first author has benefited a great deal from discussions with Nathan R. Lovejoy and especially John D. McEachran concerning stingray evolution. For a productive exchange of ideas regarding reproductive symmetry in stingrays, we sincerely thank Nick K. Dulvy, Buck Snelson, Wade D. Smith, and Henry Mollet. For assistance with technical matters and discussions regarding systematics and biogeography in general, thanks are due to Robert C. Schelly and W. Leo Smith (AMNH). Carl Mehling (AMNH) provided assistance with PhotoShop. The superb artistic rendering of the skeleton of the potamotrygonid stingray in figure 16 was illustrated by Lorraine Meeker (AMNH), who also mounted the figures of the Green River stingrays and many others in this paper; along with Chester Tarka (AMNH), Lorraine is sincerely thanked for her efforts and patience. Most of the excellent photographs of the cleared-and-stained stingrays depicted in the color plates were taken by John Weinstein (FMNH), including those of the full specimens. We thank our two reviewers for pointing out mistakes and omissions, for their careful reading of the manuscript, and for their insightful comments. Preliminary presentations on different parts of the research presented in this paper were given at ASIH 96 (New Orleans) and at the Symposium on the Phylogeny and Classification of Neotropical Fishes in 1997 (Porto Alegre); funding for the first author to attend those meetings was provided by the Donn Rosen Fund of the Department of Ichthyology (AMNH) and by Roberto Reis, Luiz Malabarba, and other symposium organizers, respectively. The final version of this paper was presented at ASIH 2003 (Manaus) through the financial support provided by the Fundação de Amparo à Pesquisa do Estado de São Paulo (Fapesp proc. no. 02/06459–0) to M.R.C. Major funding to the first author in relation to this project was largely provided by the American Museum of Natural History (as part of an Axelrod Postdoctoral Fellowship in the Division of Paleontology) and Field Museum of Natural History, and both institutions are sincerely thanked. We also gratefully acknowledge the generosity of Thomas (deceased) and Hilda Maloney for the donation of the AMNH paratype of *Asterotrygon*, and of Dr. Herbert R. and Evelyn Axelrod for their constant and invaluable support of paleoichthyological research at the AMNH.

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APPENDIX 1

COMPARATIVE BATOID (NONSTINGRAY) MATERIAL EXAMINED

Abbreviations: C&S, cleared and stained; XR, x-ray radiograph; D, dissected; SW, wet skeleton (maintained in diluted ethanol); SD, dry skeleton (prepared with dermestid beetles).

Pristidae

Anoxypristis cuspidata: AMNH 3268 (C&S).

Pristis pectinata: AMNH 44010 (XR), AMNH 2540 (XR).
Pristis perotteti: AMNH 55624 (C&S).
Pristis pristis: AMNH 44011 (C&S, gill arches only).
Pristis zijsron: AMNH 44048 (C&S, gill arches only).

Rhinidae
Rhina ancylostoma: AMNH 44015 (XR).

Rhynchobatidae
Rhynchobatus djiddensis: AMNH 44066 (XR).

Rhinobatidae
Rhinobatos albomaculatus: AMNH 44068 (XR).
Rhinobatos annulatus: AMNH 53081 (XR).
Rhinobatos irvinei: AMNH 53080 (XR).
Rhinobatos lentiginosus: AMNH 8913 (C&S), AMNH 44043 (XR), AMNH 44044(XR), AMNH 44045 (XR), AMNH 44046 (XR).
Rhinobatos percellens: AMNH 3938 (XR), AMNH 55621 (C&S), AMNH 55622 (C&S).
Rhinobatos rhinobatos: AMNH 40994 (XR).
Trygonorhina fasciata: AMNH 44104 (XR).
Zapteryx exasperata: OSU 3954 (XR).
Zanobatus schoenleinii: MNHN 1989–1528 (D; XR), MNHN uncataloged (XR).

Rajidae
Bathyraja albomaculata: AMNH 44109 (XR).
Bathyraja kincaidii: AMNH uncataloged (XR).
Leucoraja erinacea: AMNH 43158 (XR).
Leucoraja ocellata: AMNH 43158 (XR).
Okamejei kenojei: AMNH 44058 (XR).
Psammobatis bergi: AMNH 44020 (XR).
Psammobatis lentiginosa: AMNH 44019 (XR).
Psammobatis cf. *scobina*: AMNH 44044 (XR).
Raja binoculata: AMNH 38156 (C&S).
Raja clavata: AMNH 1510 (XR).
Raja texana: AMNH 16350 (C&S).
Rajella fyllae: AMNH 49510 (XR).

Platyrhinidae
Platyrhina limboonkengi: MNHN uncataloged (XR).
Platyrhina sinensis: AMNH 44055 (C&S, XR), AMNH 26413 (XR), MNHN 1307 (holotype, XR).
Platyrhinoidis triseriata: OSU 40 (XR).

Torpedinidae
Torpedo fuscomaculata: AMNH uncataloged (D).
Torpedo torpedo: AMNH 1509 (XR), AMNH 4128 (C&S).
Torpedo sp.: OSU 37 (XR).

Fig. 53. Strict consensus tree (length = 57 steps, CI = 0.63, RI = 0.69) of 12 equally most parsimonious trees (length = 53 steps, CI = 0.65, RI = 0.72) obtained with phylogenetic analysis performed with matrix in table 7 (with pelagic stingrays experimentally coded as a single terminal, Myliobatidae). See appendix 2 for further details.

Narcinidae
Benthobatis marcida: AMNH 56011 (XR), MCZ 37130 (XR), TCWC 1903.01 (SW), USNM 157958 (C&S).
Diplobatis ommata: AMNH 44100 (XR).
Diplobatis pictus: TCWC 1900.01 (SW).
Narcine bancroftii: AMNH 2488 (C&S); AMNH 218276 (SD).
Narcine brasiliensis: UERJ 776.3 (C&S), UERJ 1157 (C&S), USNM 216829 (C&S).
Narcine entemedor: AMNH 15695 (XR), AMNH 11800 (XR).
Narcine leoparda: USNM 222198 (C&S), 222198 (D).
Narcine oculifera: CAS 66838 (C&S).
Narcine rierai: RUSI 48256 (C&S).
Narcine tasmaniensis: AMNH uncataloged (XR).

Narkidae
Narke capensis: AMNH 44031 (XR).
Narke impennis: AMNH 44054 (XR).
Temera hardwickii: RMNH 7431 (C&S).
Typhlonarke aysoni: AMNH 44047 (XR).

APPENDIX 2

Experimental Phylogenetic Analysis

Pelagic stingrays are coded as a single terminal (Myliobatidae). Matrix is presented in table 7 (note that the basihyal is coded more simplistically in this matrix and that a single outgroup is used). This analysis is not a substitute for the phylogenetic study of the Green River stingrays presented in this paper, which is based on the matrix in table 5 (with pelagic stingray genera coded individually) and summarized in the cladogram in figure 43 (see text for further discussion). This phylogeny is included here to highlight how sensitive stingray topologies may be to the differential treatment of characters and/or the inclusion of taxa, a reflection of their high levels of character conflict.

Parsimony analysis of the matrix in table 7 with Hennig86 (using an exact algorithm, *ie) resulted in 12 equally most parsimonious trees (length = 55 steps, CI = 0.55, RI = 0.72); the strict consensus (length = 57 steps, CI = 0.63, RI = 0.69) is shown in figure 53. The consensus includes a few original clades, such as the component including all stingrays except *Hexatrygon* + (Gymnuridae + Myliobatidae) and, somewhat suprisingly, the monophyly of the Dasyatidae (i.e., without including potamotrygonids). Both clades are not present in the phylogenetic analyses of Nishida (1990), Lovejoy (1996), McEachran et al. (1996), or our own analysis presented above (matrix in table 5, phylogeny in fig. 43). †*Heliobatis* is resolved as the sister-group of the node uniting Potamotrygonidae and Dasyatidae in all minimum-length trees. The monophyly of the clade Dasyatidae + Potamotrygonidae in the strict consensus is supported by a single homoplastic character (number 34 in table 7): cartilaginous rod in the tail as opposed to complete, individual vertebral centra (occurs independently for Myliobatidae). The Dasyatidae is supported as monophyletic due to the dorsal fossa on the scapular process (character 26), which is homoplastic (but unambiguous). The resulting 12 minimum-length trees vary only in the relationships within Dasyatidae and whether †*Asterotrygon* pairs with Urolophidae or is placed in a basal polytomy with it. *Plesiobatis* is nested well within the cladogram, as opposed to being basal to all or almost all stingrays (Nishida, 1990; Lovejoy, 1996; McEachran et al., 1996), due in part to our treatment of characters 33 (dorsal fin) and 13 (hyomandibular-Meckelian ligament), and because it has a nasal curtain extending posteriorly to the mouth opening (character 44).

Overall, these results are significantly at odds with the phylogenetic results derived from the more comprehensive matrix presented in this pa-

TABLE 7

Matrix Summarizing Character-States Used for Phylogenetic Analysis with Myliobatidae and Gymnuridae Each Scored as Single Terminal (cf. table 5)

Characters numbered as in matrix in table 5 and text. Characters that varied solely within Myliobatidae were excluded. *Himantura* represent Indo-west Pacific species (*Himantura* sensu stricto); "*Himantura*" represent amphi-American species (*H. schmardae* and *H. pacifica*). See text for further description and information for each character.

	1	1 1 1 1 2	2 2 2 2 2 2 2 2 3	3 3 3 3 3 4	4 4 4
	1 2 3 4 8 9 0	2 3 4 5 0	1 2 3 5 6 7 8 9 0	1 3 4 5 7 0	1 2 4
Outgroup	0 0 0 0 0 0 0	0 0 0 0 0	0 0 0 0 0 0 0 0 0	0 0 0 0 0 0	0 0 0
†*Heliobatis*	? ? ? ? ? 0 0	? 1 0 0 ?	? ? ? ? 0 0 0 0 0	0 1 0 1 ? ?	? ? ?
†*Asterotrygon*	? ? ? ? ? 0 0	? 1 1 0 1	? ? 1 ? 0 0 0 0 0	0 0 0 1 ? ?	? ? ?
Hexatrygon	0 0 0 ? 0 1 0	0 0 0 0 0	? 0 1 0 0 0 0 0 0	0 1 0 0 ? 0	0 0 0
Plesiobatis	0 0 0 1 0 1 0	1 1 0 0 0	1 1 0 2 0 0 0 0 0	0 1 0 0 0 0	0 0 1
Urolophus	0 0 0 1 1 0 0	1 1 0 1 0	1 1 1 0 0 0 0 0 1	0 ? 0 0 0 0	0 0 1
Trygonoptera	0 0 0 1 1 0 0	1 1 0 0 0	1 1 1 0 1 0 0 0 1	0 0 0 0 ? 0	0 0 1
Urobatis	1 0 0 1 0 0 0	1 1 0 0 1	1 1 1 ? 1 0 0 0 0	0 1 0 0 0 0	0 1 1
Urotrygon	1 0 0 1 0 0 0	1 1 0 0 2	1 1 1 0 1 0 0 0 0	0 1 0 0 0 0	0 1 1
Paratrygon	0 0 2 1 0 0 0	1 1 0 0 1	1 1 1 0 0 0 0 0 0	1 1 1 2 0 1	1 0 1
Potamotrygon	0 0 1 1 0 0 0	1 1 1 0 1	1 1 1 1 0 1 0 0 0	1 1 1 1 2 1	1 0 1
Plesiotrygon	0 0 1 1 0 0 0	1 1 1 0 1	1 1 1 1 0 1 0 0 0	1 1 1 1 2 1	1 0 1
"*Himantura*"	0 0 0 1 0 0 0	1 1 1 0 1	1 1 1 0 1 0 0 0 0	0 1 1 2 2 0	0 0 1
Taeniura	0 0 0 1 0 0 0	1 1 0 0 1	1 1 1 0 1 0 0 0 0	0 1 1 1 1 0	0 0 1
Himantura	0 1 ? 1 0 0 0	1 1 0 0 1	1 1 1 0 1 0 0 0 0	0 1 1 2 0 0	0 0 1
Pteroplatytrygon	0 1 0 1 0 1 0	1 1 0 0 1	1 1 1 0 1 0 0 0 0	0 1 1 1 0 0	0 0 1
Dasyatis	0 1 ? 1 0 0 0	1 1 0 0 1	1 1 1 0 1 0 ? 0 0	0 1 1 1 0 0	0 0 1
Gymnuridae	0 1 0 1 0 0 1	1 0 0 0 0	1 1 1 0 0 0 1 1 0	0 ? 0 2 0 0	0 0 1
Myliobatidae	0 2 0 1 0 ? 1	1 ? 0 1 2	1 1 0 ? 1 0 ? 1 0	0 0 1 2 ? 0	0 0 1

per (table 5), but the resulting systematic positions of both Green River stingrays are similar to that analysis. Successive approximations weighting resulted in six trees (length = 279 steps, CI = 0.88, RI = 0.89), the strict consensus of which has one additional node in relation to the strict consensus obtained without weighting: *Pteroplatytrygon* + *Himantura* sensu stricto + *Dasyatis*.

INDEX OF STINGRAY GENERA AND SPECIES

(f = figure, t = table)