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Authors: Claeson, Kerin M., O'Leary, Maureen A., Roberts, Eric M., Sissoko, Famory, Bouaré, Mamadou, et al.

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First Mesozoic record of the stingray *Myliobatis wurnoensis* from Mali and a phylogenetic analysis of Myliobatidae incorporating dental characters

KERIN M. CLAESON, MAUREEN A. O'LEARY, ERIC M. ROBERTS, FAMORY SISSOKO, MAMADOU BOUARÉ, LEIF TAPANILA, DAVID GOODWIN, and MICHAEL D. GOTTFRIED



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New specimens, including the first record of lower dental plates, of the extinct myliobatid *Myliobatis wurnoensis* were recovered from the Maastrichtian (Late Cretaceous) of the Iullemmeden Basin, Mali, and are the oldest record of the taxon. We evaluated the phylogenetic position of this taxon with reference to other myliobatids (extinct and extant) using osteology and dentition. Our results indicate that Myliobatinae and *Myliobatis* are each paraphyletic, and that *Aetobatus* and *Rhinoptera* are monophyletic. We also found that taxa known only from the Cretaceous, *Brachyrhizodus* and *Igdabatis*, are highly nested within Myliobatidae. The phylogenetic position of these taxa unambiguously extends the origin of Myliobatidae and most of its representative taxa into the Mesozoic.

Key words: Chondrichthyes, Myliobatidae, Myliobatiformes, dentition, batoid, ghost lineage, phylogeny, Cretaceous, Maastrichtian, Mali.

Kerin M. Claeson [kclaeson@mail.utexas.edu], Department of Geological Sciences, The University of Texas, Austin, Texas 78712-0254, USA;
Maureen A. O'Leary [maureen.oleary@stonybrook.edu], Department of Anatomical Sciences, Stony Brook University, Stony Brook, New York 11794, USA;
Eric M. Roberts [eric.roberts@jcu.edu.au] School of Earth and Environmental Sciences, James Cook University, Townsville, Queensland 4811, Australia;
Famory Sissoko, Institut des Sciences Humaines, Bamako, Mali (passed away);
Mamadou Bouaré [bouamala@yahoo.fr], École Nationale des Ingénieurs, Bamako, Mali;
Leif Tapanila [tapaleif@isu.edu], Department of Geosciences, Idaho State University, Pocatello, Idaho 83209-8072, USA;
David Goodwin [goodwind@denison.edu], Department of Geosciences, Denison University, Granville, Ohio 43023, USA;
Michael D. Gottfried [gottfrie@msu.edu], Department of Geological Sciences and Museum, Michigan State University, East Lansing, Michigan 48824, USA.

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Introduction

Myliobatiformes (stingrays) is a derived clade of batoid fishes known for having a characteristic serrated caudal spine. They are found worldwide and most species are living near the coast (Nelson 2006). Extant members of Myliobatiformes have been studied extensively and relationships among the derived taxa in the clade are well resolved based on morphology (Compagno 1973, 1977; Heemstra and Smith 1980; Maisey 1984; Nishida 1990; Lovejoy 1996; McEachran et al. 1996; Compagno 1999; Carvalho et al. 2004; González-Isáis and Domínguez 2004). Myliobatidae is a highly nested clade within Myliobatiformes. Its members consist of pelagic and sometimes coastal stingrays that are widely dispersed in modern oceans (e.g., Lovejoy 1996; Nelson 2006). The presence of powerful crushing jaws with several rows of pavement-like teeth is characteristic of these durophagous fishes (Summers 2000; Dean et al. 2005). There are seven extant myliobatid genera (*Myliobatis*, *Aetobatus*, *Aetomylaeus*, *Manta*, *Mobula*, *Pteromylaeus*, and *Rhinoptera*) containing approximately 37 species (Nelson 2006). Myliobatinae (sensu Nelson 2006) is a subset of taxa within Myliobatidae including *Myliobatis*, *Aetobatus*, *Aetomylaeus*, and *Pteromylaeus*. Evidence from phylogenetic analyses indicates that Myliobatinae is paraphyletic (Lovejoy 1996; Carvalho et al. 2004).

The myliobatid fossil record is extensive, with taxa known primarily from isolated dentitions. Approximately 150 extinct species have been identified and several have first appearances in the Late Cretaceous (Berg 1940; Cappetta 1987). To investigate further the phylogeny of Myliobatidae and the survivorship of the clade across the Cretaceous–Paleogene (K/T) boundary we expand upon previously published studies

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of extant Myliobatiformes and Myliobatidae by including fossilized dentitions and new characters derived from dental morphology.

Our survey of museum collections and the literature reveals that thousands of isolated dentitions have been attributed to *Myliobatis* for over a century (Woodward 1888); however, the monophyly of this expanded concept of *Myliobatis* has never been tested phylogenetically. To test the monophyly of *Myliobatis*, it is necessary to integrate taxa known exclusively on the basis of dentitions into a phylogenetic matrix that includes characters from the entire skeletal system (e.g., Carvalho et al. 2004). Such a taxon sample introduces both new data and missing data (empty cells) into the phylogenetic analysis, but the inclusion of data from previously unsampled species is essential for completing a total phylogeny of the clade (Kearney 2002; Wiens 2003, 2006; Kearney and Clark 2003; Shimada 2005). Furthermore, the inclusion of fossils facilitates the study of ghost lineages, which is critical for constructing phylogenetically informed hypotheses of species diversity in any given time horizon (Smith 1994).

Ours is the first examination of a diverse assemblage of extinct species of *Myliobatis* and their impact on relationships of all myliobatid taxa. We describe new fossil myliobatid dentitions from three Maastrichtian (Late Cretaceous) localities in the Iullemmeden Basin of Mali that were collected by a Centre Nationale de la Recherche Scientifique et Technologique-Stony Brook University expedition in 1999. We test relationships of Myliobatidae by adding these specimens as well as other fragmentary specimens to the published phylogenetic matrix of Carvalho et al. (2004). In contrast to prior investigations, we use species as operational taxonomic units (OTUs) to test the monophyly of myliobatid genera. By investigating the placement of the Malian and other fossil taxa within Myliobatidae we further examine the survivorship of the clade across the K/T boundary. By working at the species level our study can also be readily expanded upon by future systematists (see discussion by Prendini 2001).

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; ANSP, Academy of Natural Sciences, Philadelphia, USA; CNRST-SUNY, Centre Nationale de la Recherche Scientifique et Technologique, Bamako, Republic of Mali-Stony Brook University, Stony Brook, USA; FMNH, Field Museum of Natural History, Chicago, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; NHM, The Natural History Museum, London, UK; SMF, Senkenberg Museum, Frankfurt, Germany; SMNS Staatliches Museum für Naturkunde, Stuttgart, Germany; TNHC, Texas Natural History Collection, Austin, USA; YPM, Yale Peabody Museum, New Haven, USA; YPM-PU, Yale Peabody Museum, Princeton Collection, New Haven, USA; ZMB, Museum für Naturkunde, Berlin, Germany.

Other abbreviation.—CI, consistency index; HI, homoplasy index; OTU, operational taxonomic unit; RC, rescaled consistency index; RI, retention index; TL, tree length.

Geological setting

The Iullemmeden Basin of northern Mali and Niger (Fig. 1) preserves Cretaceous and Paleogene marine and continental strata deposited in and along the shores of the epeiric Trans-Saharan Seaway. This seaway inundated parts of central West Africa in the Early Cretaceous, and then again from the Late Cretaceous to middle Eocene (Petters 1979; Reyment and Dingle 1987; Tapanila et al. 2004, 2008). Relatively thin sedimentary packages derived from each of these two cycles are found in northern Mali, along the margin of the Adrar des Iforas Mountains (Radier 1959; Bellion et al. 1989; Moody and Sutcliffe 1991; Tapanila et al. 2004, 2008). The strata occur in fining-upward sequences (Fig. 2) associated with transgressive-regressive cycles of the Trans-Saharan Seaway, and they preserve diverse invertebrate and vertebrate faunas that demonstrate the seaway periodically served as a faunal conduit between the Tethys and South Atlantic Ocean (Moody and Sutcliffe 1993).

Several fossiliferous sections (localities Mali-7, -8, and -10) spanning the K/T boundary in the vicinity of Ménaka were measured and placed within a rigorous stratigraphic and sedimentological framework (Tapanila et al. 2004, 2008; Gaffney et al. 2007; Hill et al. 2008). Detailed facies analysis of the Ménaka area and other localities revealed the presence of five repeated facies, including sandstone and siltstone (Fa-

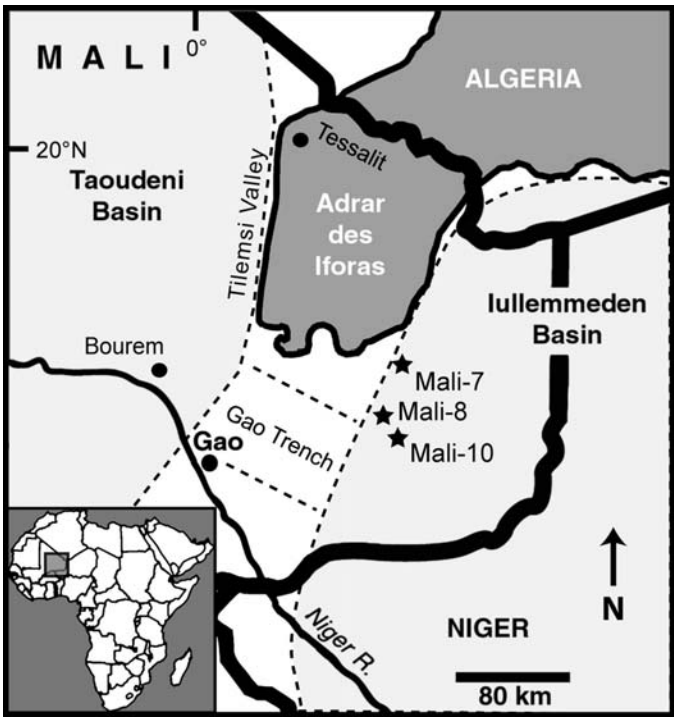


Fig. 1. Map of Mali indicating three localities discovered in the 1999 CNRST-SUNY expedition. Boundary between the Illummeden and Tauodeni basins in northern Mali is outlined in light gray. Mali-8 marks localities yielding fossils of Myliobatidae. Dark Gray marks exposed basement rocks in the Adrar des Iforas Mountains; white marks Proterozoic structure that connected the two light gray basin periodically during the Cretaceous–Paleogene.

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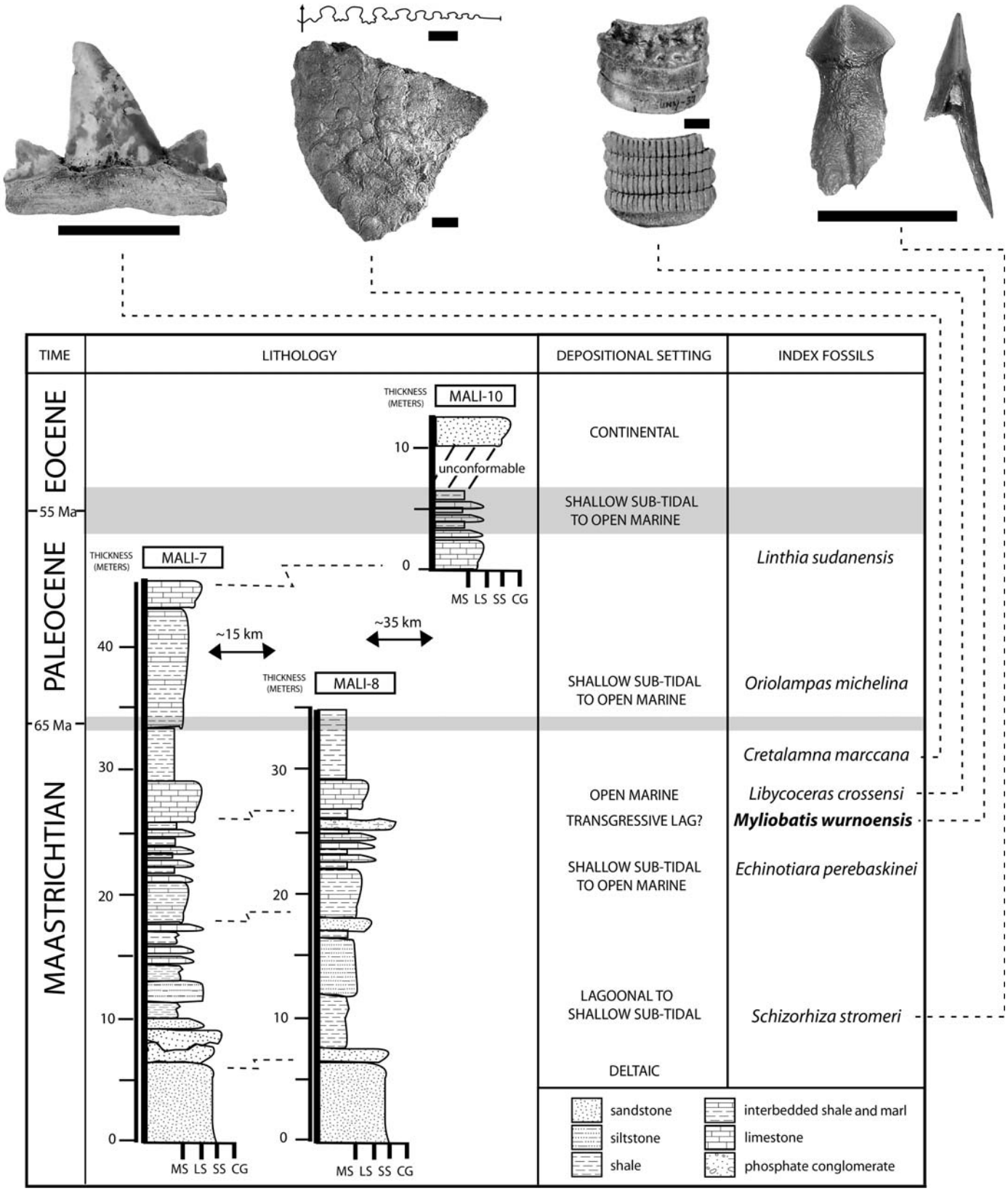


Fig. 2. Composite stratigraphic sections of localities Mali-7, -8, and -10. Relative stratigraphic positions of index fossils and inferred depositional settings supporting age of *Myliobatis wurnoensis* (Mali-8). Index fossils from Mali-7, -8, and -10. Lower gray line is the inferred KT boundary in this section and the upper gray line is the inferred position of the Paleocene–Eocene boundary in this section. Abbreviations: CG, conglomerate; LS, limestone; MS, shale; SS, sandstone.

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cies 1), paper shale (Facies 2), mollusk and echinoderm packstone (Facies 3), mudstone and wackestone (Facies 4), and phosphate conglomerate (Facies 5; Tapanila et al. 2008). Those facies associations are interpreted respectively as tidally-influenced shoreline and deltaic environments (Facies 1); shallow, normal-to-restricted marine lagoons and open platform settings (Facies 2); small patch oyster reefs and storm beds associated with shallow, sublittoral marine settings under normal salinity (Facies 3); low-energy shallow, sublittoral open marine settings with water depths <50 m (Facies 4); and shallow marine-to-brackish water phosphorites associated with periods of amalgamation and concentration by storm activity during periods of marine transgression (Facies 5; Tapanila et al. 2008).

The section at Mali-8 in particular (Figs. 1 and 2) consists of approximately 35 m of interbedded sandstones (Facies 1), shales (Facies 2), marly limestones (Facies 3 and 4), and a thick phosphate conglomerate (Facies 5), which were deposited as part of at least one complete sea level cycle (T5 Cyclothem of Greigert [1966]) in the Trans-Saharan Seaway (see Tapanila et al. [2008] for complete discussion). The Mali-8 section was well-correlated with another section located approximately 15 km away (~45 m thick), designated as Mali-7 (see also Hill et al. [2008: fig. 2] for detailed stratigraphic correlations). The base of each section is defined by Facies 1, characterized by large, inclined, fine-grained sandstone beds with glauconite and petrified wood of delta front origin. The next 20 m of each section represents deposits of the T5 transgressive systems tract, dominated by thinly laminated shales and marls of Facies 2 and 3, which are overlain by phosphatic limestones and a distinctive phosphate conglomerate (Facies 5) representing the maximum flooding surface (condensed section) of the T5 cyclothem. Above that level are open marine, quiet water mudstones and wackestones (Facies 4) and storm generated molluscan and echinoderm packstones (Facies 3) associated with the overlying T5 highstand systems tract (Tapanila et al. 2008: fig. 3).

Several myliobatid specimens were found in these sections, which also contain a variety of index fossils allowing us to use biostratigraphy to make a biochronological age assessment of the section. The base of the section (Fig. 2) contains latest Cretaceous index fossils, including the sawfish shark, *Schizorhiza stromeri* (which occurs in Maastrichtian deposits in Africa, Iraq, and North and South America; Cappetta [1987]), and the regular sea urchin, *Echinotiara perebaskinei* (Smith and Jeffery 2000). Furthermore, specimens of another Maastrichtian index fossil, *Cretalamna maroccana*, a lamniform shark (Case and Cappetta 1997; Shimada 2007) were also recovered from shale beds stratigraphically above the ray specimens. Approximately 10 meters higher in the section, specimens of the Paleogene echinoderm *Oriolampas michelini* bracket the approximate K/T contact in northern Mali.

Myliobatid specimens described here were collected at Mali-8 from a distinctive bone, pebble, and coprolite phosphatic conglomerate (Facies 5) at the 26 m level. Immediately above this interval, multiple specimens of the pseudoceratitic ammonite *Libycoceras crossensi* (Fig. 2) were recovered from Facies 4 mudstones and wackestones at localities Mali-7 and -8 demonstrating a Maastrichtian age for this part of the sequence, and establishing the first Mesozoic record of the morphologically characteristic myliobatid dentition. The ammonite-bearing mudstones and wackestones are interpreted as low-energy marine depositional environments, indicating that these fossils are in situ and have not been reworked from older deposits. Sequence stratigraphic analysis by Tapanila et al. (2008) also indicated that deposits at Mali-7 and -8 sections correspond to the second *Libycoceras* transgression (T5) documented throughout the Trans-Saharan Seaway. This stratigraphic interpretation is comparable with other sequence stratigraphic investigations by Greigert (1966) in the Iullemmeden Basin to the southeast and by Bellion et al. (1989) to the west in the Taoudeni Basin. A wealth of other faunal and geologic investigations on the Maastrichtian transgressive sequence (T5 Cyclothem) directly below the K/T boundary, also support the stratigraphic interpretations for Mali-7 and-8 (Radier 1959; Moody and Sutcliffe 1993; Dikouma et al. 1994; Colin et al. 1996; Zaborski and Morris 1998).

Systematic paleontology

Myliobatiformes Compagno, 1973

Myliobatidae Bonaparte, 1838

Myliobatis Cuvier, 1816

Myliobatis wurnoensis White, 1934

Fig. 3.

1934 *Myliobatis wurnoensis* White, 1934: 30–33, pl. 4: 2, 3.

Type material: Holotype, upper dental plate: NHM-P 18752; paratype, upper dental plate: NHM-P 18753, from Maastrichtian, locality Mali-8, Samit region in the northeast of the Republic of Mali.

Material.—Partial lower dental plates: CNRST-SUNY-2; CNRST-SUNY-3; partial upper dental plates: CNRST--SUNY-4; CNRST-SUNY-5; CNRST-SUNY-6; CNRST-SUNY-10; CNRST-SUNY-13; CNRST-SUNY-37; CNRST-SUNY-14; CNRST-SUNY-38; CNRST-SUNY-39.

Emended diagnosis.—Species of Myliobatidae with high crowns on upper and lower dental plates. Crowns of median teeth with steep lateral slopes and pinched margins (Fig. $3A_1$, B_1). Wide roots with irregular, block-like laminae and shallow, narrow grooves between laminae (Fig. $3A_3$, B_3, C_1). Supplements original diagnosis of White (1934: 30–31): "… massive teeth; coronal contour of upper dentition strongly arched transversely. Length of upper median teeth in adult exceeding one-fifth breadth; crown very thick and root shallow with exceptionally few (twenty-four) longitudinal grooves. Lateral teeth very narrow. (Lower dentition unknown)." Similar to extinct taxon *Myliobatis dixoni*, differentiated from *M. dixoni* in exhibiting a pinched lateral-margin of median teeth. Crown (viewed anteriorly or posteriorly) of *Myliobatis wurnoensis* with steep lateral slopes, absent in *M. dixoni*. Shape of individ-

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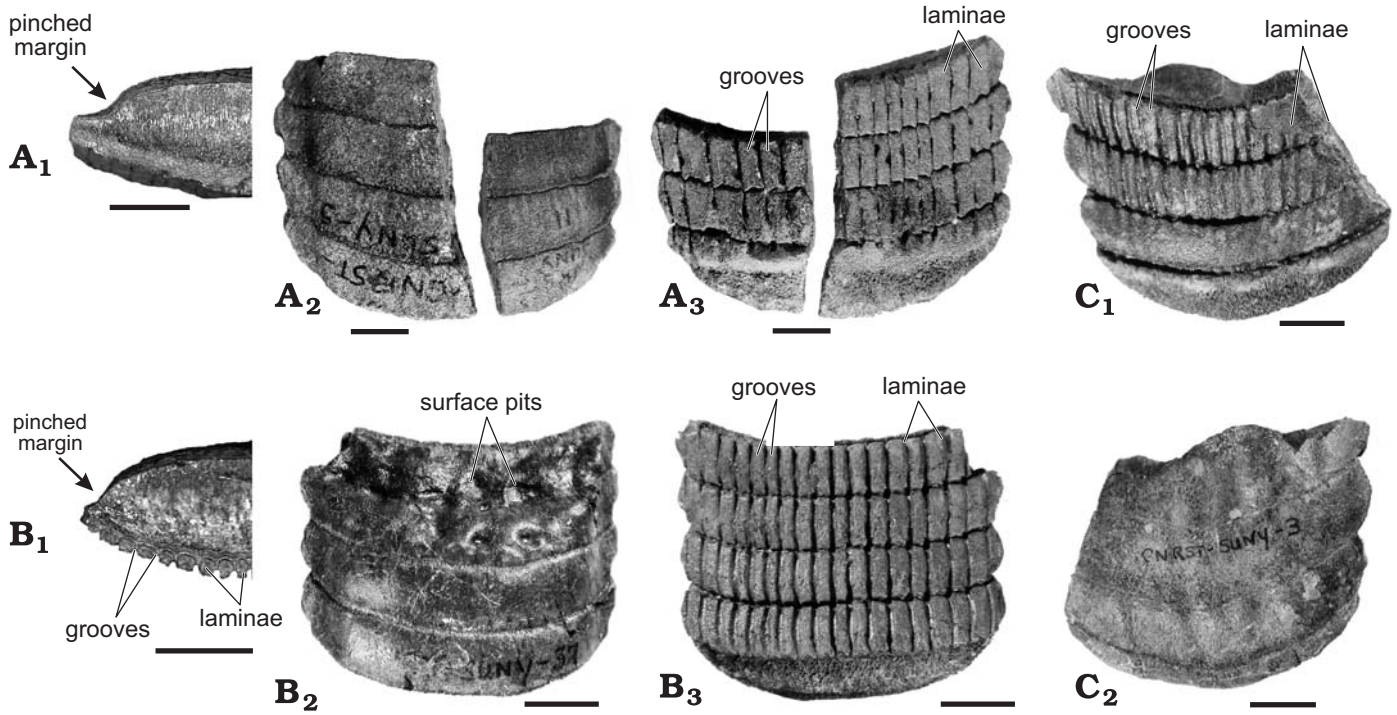


Fig. 3. The fossil stingray *Myliobatis wurnoensis* White, 1934 from Maastrichtian of Mali. **A**, **B**. Partial upper dental plates. **A**. CNRST-SUNY-5 in posterior (A_1), occlusal (A2), and basal (A_3) views. **B**. CNRST-SUNY-37 in posterior (B_1), occlusal (B_2), and basal (B_3) views. **C**. Partial lower dental plate, CNRST-SUNY-3 in occlusal (C_1) and basal (C_2) views. Anterior is to top of page for all images except A_1 and B_1, which are in posterior view. Scale bars 10 mm.

ual root laminae irregular and blocky in *M. wurnoensis*, uniform and narrow in *M. dixoni*.

Description.—Upper and lower dentitions were recovered at the same locality. These include the first specimens representing a lower dentition for this taxon. All plates possess six-sided and tightly interlocking teeth. Median teeth are approximately four to five times wider than they are anteroposteriorly long. In occlusal view, median teeth are straight to moderately arcuate but not distinctly chevron shaped. Lateral terminals of the median teeth are angled and pointed anteriorly so that the curvature of median teeth is concave. Lower median teeth are less arcuate than the upper median teeth. Lateral teeth are not preserved on any specimens, but the angular, interdigitating lateral margins are retained on the median teeth for several specimens. The crown of the median teeth is thickest in the center and slopes steeply towards the lateral margins that are thin and pointed or pinched. Roots are polyaulacorhizous with 14–24 laminae. Laminae are rectangular and block-like. Individual laminae vary in width, from 1.0–3.2 mm, but all are wider than the adjacent grooves between them (Fig. $3A_3$, B_3, C_1). Laminae are narrow and uniform medially, with some wider and irregular laminae occurring laterally.

Variation in attributed specimens.—CNRST-SUNY-2 is a lower dental plate that is significantly worn posteriorly and on the basal surface. Four medial teeth are present and the posteriormost tooth is narrower than the anteriormost tooth at 42 mm and 48 mm respectively. Margins of the median teeth that interlock with lateral teeth have a short posterior edge and a long anterior edge. In basal view, the lateral margin of the root row is pointed anteriorly. CNRST-SUNY-3 is also a lower dental plate, and is approximately 65 mm across at the posteriormost median tooth: the left anterior portion is broken. Five ridges cross the occlusal surface in the anteroposterior direction (Fig. $3C_2$). Unlike CNRST-SUNY-2, lateral margins of median teeth in CNRST-SUNY-3 possess a short anterior edge and slightly longer posterior edge.

In certain specimens, toothwear, an important indicator of diet, is recognizable. CNRST-SUNY-4 and -14 both have occlusal and basal surfaces that are rough, unpitted and porous. The occlusal surfaces on CNRST-SUNY-13 and -37 are irregularly pitted and suggest a grinding surface (Fig. $3B_2$). We observed pronounced increase in crown height, along the tooth row from anterior to posterior, in CNRST-SUNY-13 (4 mm high anteriorly to 20 mm high posteriorly) and in CNRST-SUNY-37 (4 mm high anteriorly to 22 mm high posteriorly). In all other specimens crown height among individual median tooth plates is uniform along the tooth row from anterior to posterior.

Stratigraphic and geographic range.—Maastrichtian, locality Mali-8, interbedded shales and limestones. Samit region in the northeast of the Republic of Mali.

Phylogenetic analysis

Taxonomic sample.—Roughly 90 fossil dentitions, some fragmentary, representing extinct species were examined and compared with dentitions of 25 specimens of extant

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myliobatids (Appendix 1). The data matrix expands on that presented by Carvalho et al. (2004), which included 23 taxa that were scored at the genus-level. Our final combined matrix includes 40 terminal taxa. Thirty-eight are myliobatiform ingroup taxa and two, *Raja* and *Rhinobatos*, are outgroup taxa (Appendix 2). We retained the genus level OTUs of the Carvalho et al. (2004) analysis with the exception of species in Myliobatidae. We decompose *Myliobatis* into eight species-level OTUs (four extant and four extinct), and *Aetobatus* and *Rhinoptera* into three species-level OTUs each, so that we might assess the monophyly of *Myliobatis*, *Aetobatus*, *Rhinoptera*, and Myliobatidae. For the 13 taxa represented by dentition only, initial identifications made for this study were based on criteria detailed by Cappetta (1987). Most taxa were examined from original material; however, original material could not be accessed for all characters. In those cases information was scored from the literature.

Character sample.—We compiled a total of 65 morphological characters (Appendices 2 and 3) using Mesquite 2.0 (Maddison and Maddison 2006) and MorphoBank (O'Leary and Kaufman 2007). The entire data matrix is retrievable with supporting images at MorphoBank.org. The data matrix includes 43 unmodified characters from Carvalho et al. (2004). An additional 22 new characters (numbers 44–65) are exclusively dental and are described in this text. Characters and states for the entire matrix are listed in Appendix 3.

Phylogenetic methods.—We treated all characters as unordered and equally weighted. Multistate characters were treated as uncertain. The character matrix was analyzed using PAUP* 4.0b10 (Swofford 2002) using the maximum parsimony optimality criterion. We employed heuristic searches with 1000 replicates of random stepwise addition (branch swapping: tree-bisection-reconnection) holding one tree at each step. Branches were collapsed to create soft polytomies if the minimum branch length was equal to zero (amb- option); afterwards, we explored agreement subtrees (Cole and Hariharan 1996). We calculated Bremer support (Bremer 1994) for nodes retained in the strict consensus tree. This was done manually in PAUP* using constraint trees generated in MacClade 4.08 for OS X (Maddison and Maddison 2005) from the Decay Index PAUP* File command. We report unambiguous optimizations for particular nodes of interest retained in the strict consensus (optimizations were performed on individual most parsimonious trees). We calculated ghost lineages (Norell 1992; Cavin and Forey 2007) by mapping part of our tree onto the stratigraphic record, using First Appearance Data as described in Cappetta (1987) and the new Cretaceous record of *M. wurnoensis* as described in our study.

Results

All characters were parsimony informative and the matrix had 27.6% missing data. The heuristic search resulted in eight most parsimonious trees. The strict consensus tree is depicted in Fig. 4 with Bremer support values given for all nodes. Unambiguous character changes are mapped for Myliobatidae in Fig. 5. Ghost lineages are drawn in Fig. 6. The strict consensus tree depicts a paraphyletic Myliobatinae (Fig. 4). *Myliobatis* is also paraphyletic. A revision of the taxonomy of the species of *Myliobatis* is outside the scope of this paper.

The strict consensus tree topology (Fig. 4) is congruent with the consensus tree recovered by Carvalho et al. (2004) and the non-Myliobatidae portion of our consensus tree is identical to that portion in theirs (Fig. 4A). The optimal agreement subtree removed only five (*Plesiobatis*, "*Himantura*", *Dasyatis*, *Pteroplatytrygon*, and the extinct taxon *Asterotrygon*) of 40 taxa, all of which were outside the ingroup, Myliobatidae. From here on we describe in detail only the hypothesized relationships within Myliobatidae (Figs. 4B, 6). These differ from the relationships hypothesized by Carvalho et al. (2004).

Hypolophites is the immediate sister taxon to a monophyletic Myliobatidae (Figs. 4B and 5: node-A); these clades share broad, six sided, pavement-like teeth. The majority of extinct taxa we studied are interspersed among extant myliobatids. *Apocopodon* is the sister taxon to all remaining taxa within Myliobatidae (Figs. 4B and 5: node-B). Myliobatidae is distinguished from outgroup taxa by their expanded median teeth with a polyaulacorhizous root morphology that interlock by a tongue and groove mechanism. There is a polytomy at node-C (Figs. 4B and 5) consisting of *Myliobatis freminvillii*, *Myliobatis goodei*, and the unnamed clade including node-D. No unambiguous character changes were mapped to the polytomy at node-C. No unambiguous character changes could be mapped to the polytomy at node-D, comprising the extinct taxon *Myliobatis striatus*, *Myliobatis aguila*, *Myliobatis californica*, and the unnamed clade including node-E (Figs. 4B, 5). These two polytomies were present in all eight most parsimonious trees as an effect of the amb- option during tree searches.

There were no unambiguous character changes mapped for the clade including node-E. This clade, including node-E, consists of the extinct taxon *Myliobatis toliapicus*, which is sister to the clade including node-F (Figs. 4B, 5). The clade including node-F is distinguished from *M. toliapicus* by possessing upper teeth that are curved. At node-F, the extinct taxon, *Weissobatus micklichi* is sister taxon to the clade including node-G. Node-G is distinguished from *W. micklichi* by non-dental morphology, a pelvic girdle that is arched.

At node-G, an *Aetobatus*-clade splits from the remainder of Myliobatidae (Fig. 4B). Node-H includes five extinct taxa and leads towards *Rhinoptera*, *Mobula*, and *Manta*. That clade is distinguished from *Aetobatus* by possessing domed tooth crowns, as opposed to deep crowns. At node-H, the extinct taxon *Myliobatis dixoni* is sister taxon to the clade including node-I. The clade including node-I possesses wide, blocky, and irregularly spaced root laminae. The extinct taxon *Myliobatis wurnoensis* possesses a single autapomorphy, pinched lateral margins of the median teeth, distinguishing it from the clade including node-J. Node-J is further dis-

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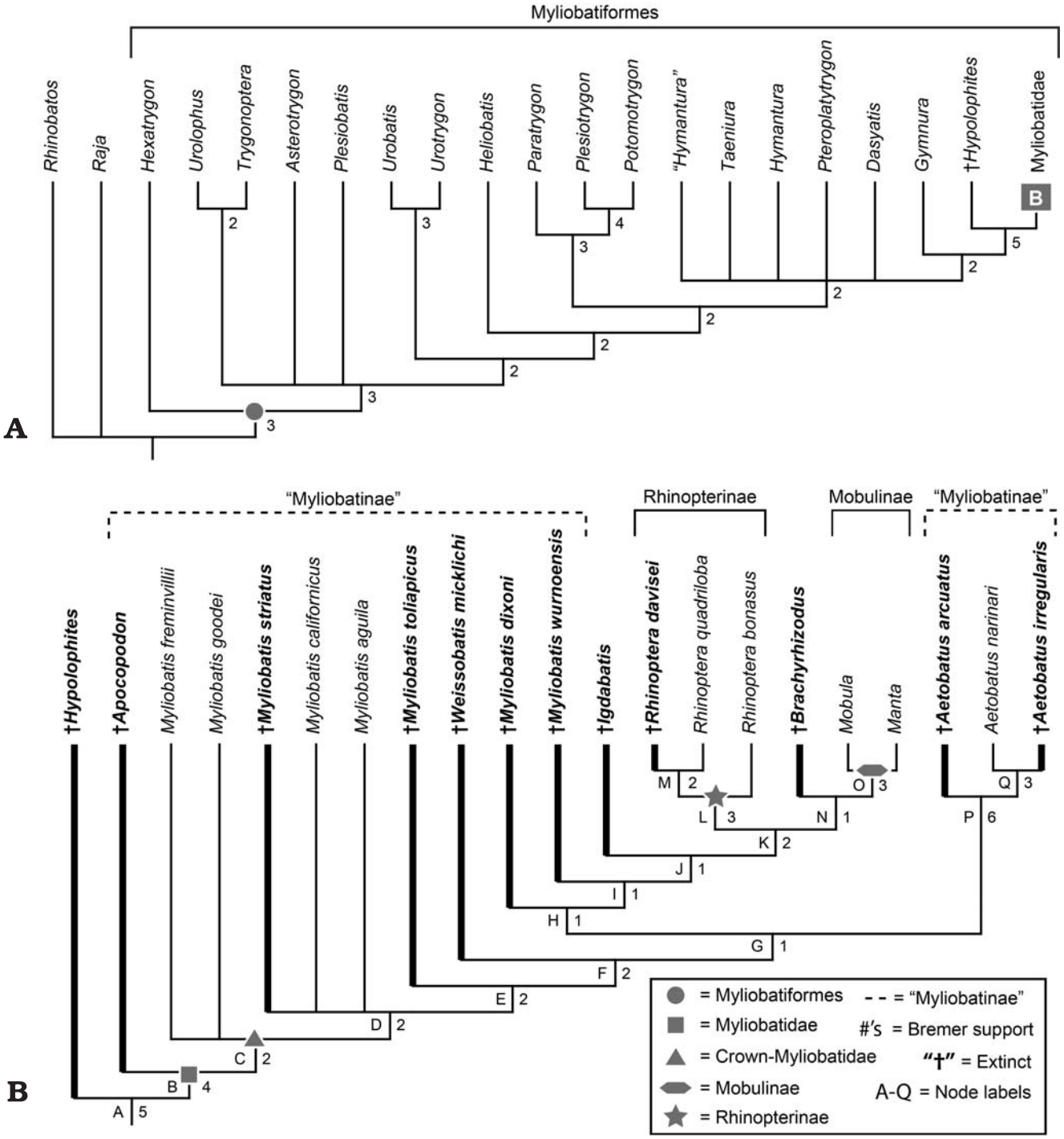


Fig. 4. Strict consensus of eight most parsimonious trees (MPT). **A**. Tree from full analysis with Myliobatidae condensed as single terminal taxon in gray box labeled "B". **B**. Expanded Myliobatidae portion of tree, which is identical on all eight MPTs. TL = 141, CI = 0.6312, HI = 0.3688, RI = 0.8844, RC = 0.5583. Bold face in B denotes extinct taxa.

tinguished from *Myliobatis wurnoensis* by possession of teeth that are differentially expanded, loosely interlocking, and connected by a bulbous tongue and groove joint. At node-J, the extinct taxon *Igdabatis* is the sister taxon to *Rhinoptera* + (*Brachyrhizodus* + [*Mobula* + *Manta*]) (Figs. 4B and 5: node-K).

Rhinoptera is monophyletic (Figs. 4B and 5: node-L, Rhinopterinae sensu Nelson 2006). *Rhinoptera davisei* is more closely related to *Rhinoptera quadriloba* than either taxon is to *Rhinoptera bonasus* (Fig. 5: node-M). The relative position of these species of *Rhinoptera* in the consensus tree and the morphological variation reported for each species (Appendix 3) is consistent with *R. quadriloba* being a valid species.

Brachyrhizodus is the sister taxon to *Mobula* + *Manta* (Fig. 5: node-L), contrary to the hypothesis proposed by

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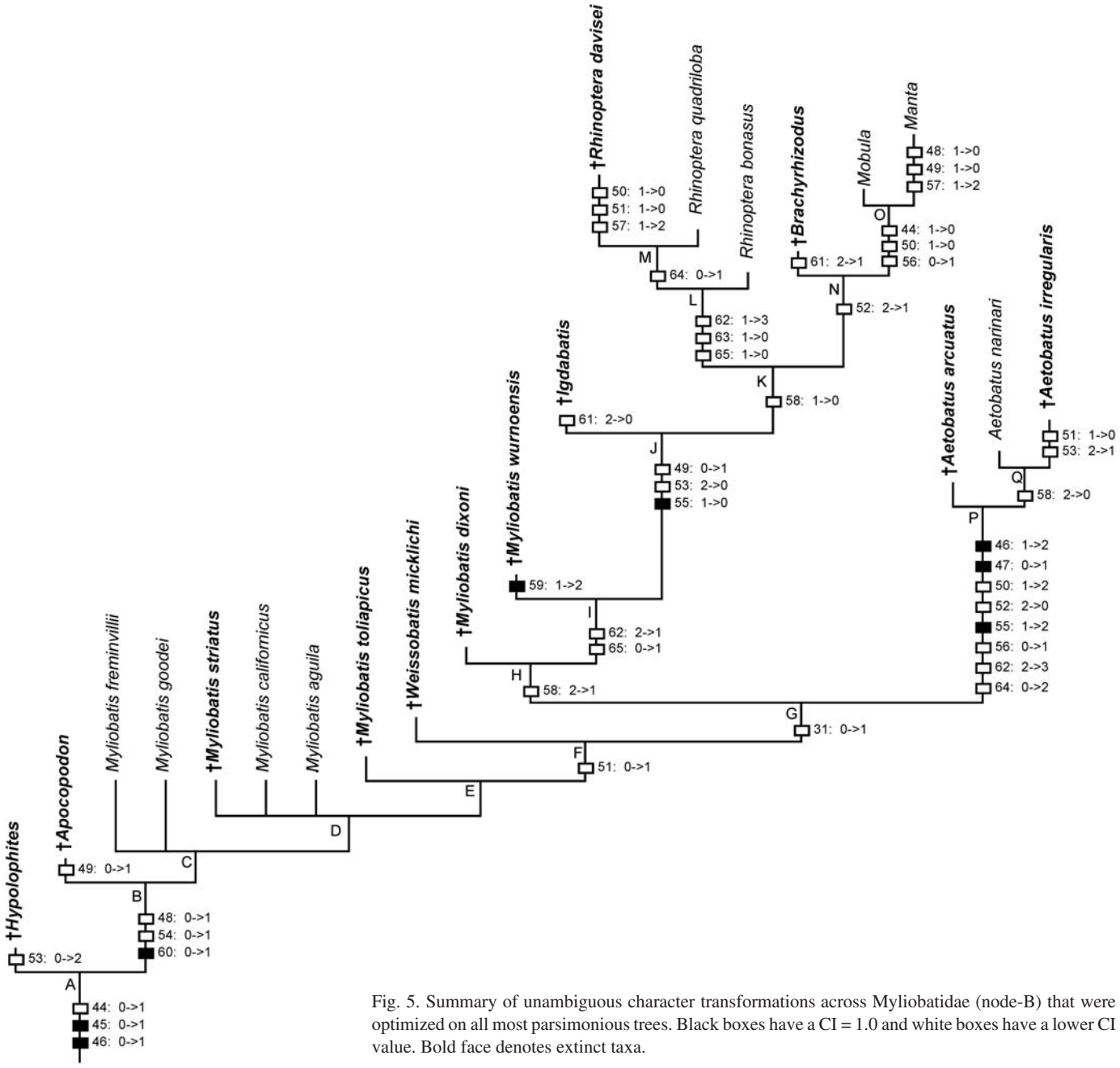


Fig. 5. Summary of unambiguous character transformations across Myliobatidae (node-B) that were optimized on all most parsimonious trees. Black boxes have a CI = 1.0 and white boxes have a lower CI value. Bold face denotes extinct taxa.

Cappetta (1987) that *Brachyrhizodus* is closely related to *Rhinoptera*. We recover Mobulinae (Fig. 4B; node-O, Mobulinae sensu Nelson 2006): *Rhinoptera* as the sister taxon of *Brachyrhizodus* + (*Mobula* + *Manta*). *Rhinoptera* is distinguished from Mobulinae by possessing regularly spaced, fine edged root laminae, which are narrower than the grooves dividing them, while Mobulinae lack any curvature to their teeth. *Brachyrhizodus* is a stem-mobuline and *Mobula* + *Manta* represent crown-Mobulinae (Fig. 4B: node-O). *Rhinoptera* + Mobulinae share a straight tooth crown. *Mobula* + *Manta* reversed their tooth morphology to possess minute teeth with a low crown. At node-P, *Aetobatus* is monophyletic. *Aetobatus irregularis* + *Aetobatus narinari* are more closely related to one another than either is to *Aetobatus arcuatus.* *Aetobatus* is distinguished from the clade including node-H by eight unambiguous character changes (Fig. 5).

Considering both tree topology and the first appearances of a clade and its sister taxon, we can make inferences about ghost lineages (Norell 1992). New fossils of *Myliobatis wurnoensis* demonstrate for the first time that this taxon occurred on both sides of the K/T boundary (Fig. 6). The new *M. wurnoensis* material recovered from lagoonal/shallow subtidal deposits of the Cretaceous of Iullemmeden Basin represents a temporal extension for the species of several million years. At least two other genera within Myliobatidae have a fossil record prior to the K/T boundary, *Igdabatis* and *Brachyrhizodus* (Romer 1942; Cappetta 1972; 1987; Cappetta and Case 1975; Prasad and Cappetta 1993).

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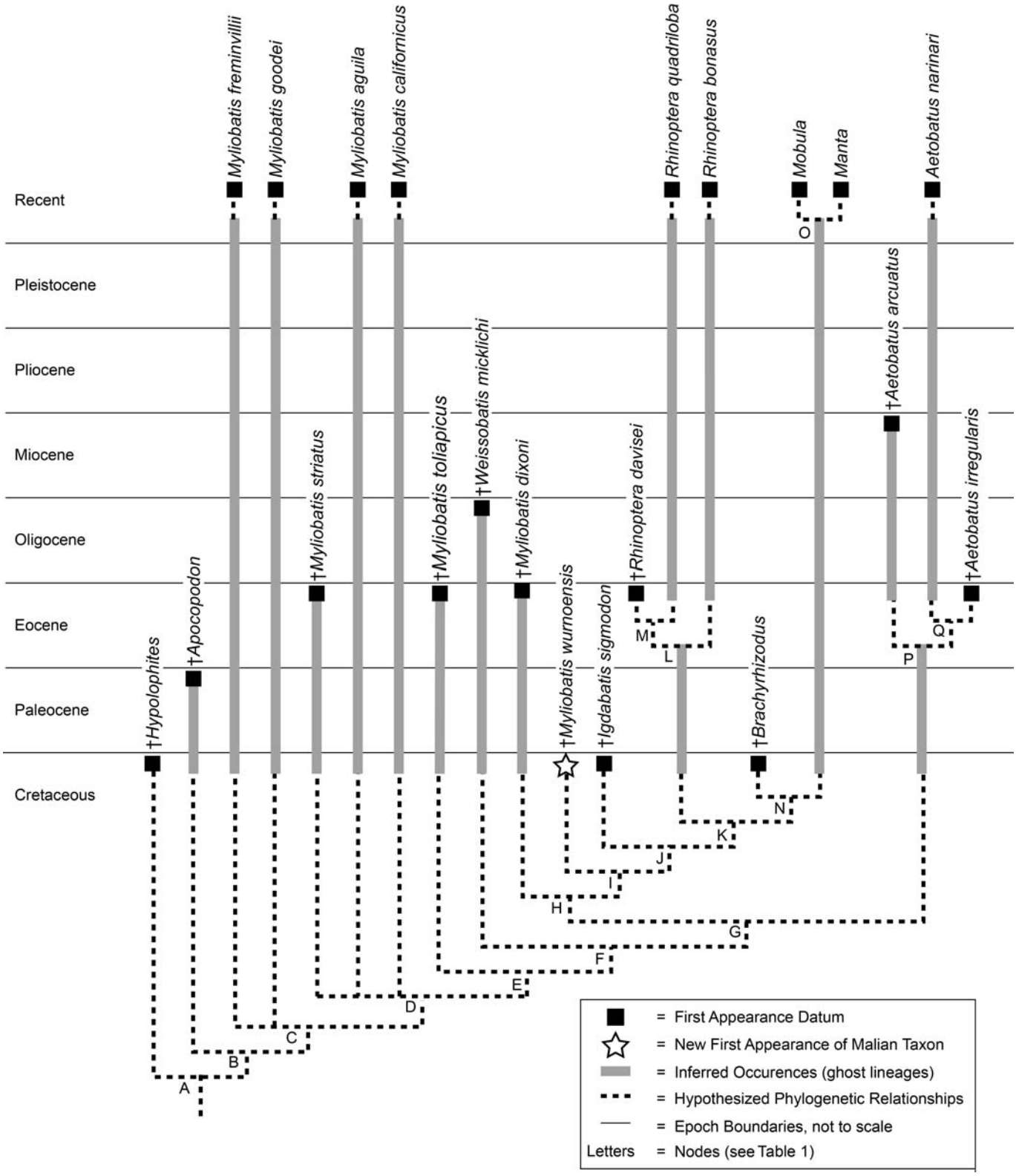


Fig. 6. Phylogenetic relationships and stratigraphic distribution of Myliobatidae. Epochs are not drawn to scale.

These taxa are more highly nested than all species of *Myliobatis*. Thus, the relative positions of all Cretaceous taxa within Myliobatidae unambiguously extend the record of the clade across a major extinction boundary. The present phylogeny shows that all major lineages of Myliobatidae examined existed in the Mesozoic, making the Mesozoic diversity count much greater than a direct tally of stratigraphic occurrences alone.

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Dental character analysis and polarity

The characters that are new or modified for this study are described here with reference to figures illustrating these states (Figs. 7, 8). A complete character list is available in Appendix 3 and at Morphobank.org. Characters 44–46 are modified from character 19 by Carvalho et al. (2004: 84), which described "Arrangement of teeth in both upper and lower jaws" as a combination of tooth type, shape, and relative position. We split this character because tooth type, shape, and position do not vary together.

(44) Tooth type in both upper and lower jaws: (0) minute; (1) broad; (modified from character 19, Carvalho et al. [2004]). In outgroup taxa and most non-myliobatid stingrays, teeth are usually minute (state 0; Fig. 7A, B). The derived mobuline taxa *Mobula* and *Manta*, have secondarily minute cusps (Fig. 7E–G). The alternative tooth type is a broad, flattened one (state 1; Figs. 7C, D, H, 8B–F). The extinct *Hypolophites*, which has enormous individual teeth, demonstrates the derived state (Fig. 8A).

(45) Arrangement of teeth in both upper and lower jaws: (0) arranged in separate diagonal rows or ribbons; (1) horizontal conveyor or pavement-like arrangement; (modified from character 19, Carvalho et al. [2004]). The many individual teeth in non-myliobatid taxa are lined up in separate, diagonal rows or criss-crossing ribbons (state 0; Figs. 7A, B, 8A). In all myliobatid taxa, however, a more horizontal conveyor or pavement-like arrangement is present (state 1; Figs. 7C–H, 8C–F). The horizontal alignment of the teeth is retained in *Mobula* and *Manta*, despite their relatively minute size (Fig. 7F_2, G_2).

(46) Tooth shape: (0) square to rounded; (1) hexagonal, six distinct sides; (2) rectangular with posteriorly deflected lateral margins; (modified from character 19, Carvalho et al. [2004]). The minute teeth of non-myliobatid taxa are square to round and they may slightly overlap one another (state 0; Fig. 7A, B). Teeth with six recognizable sides are present in the extinct, non-myliobatid taxon, *Hypolophites*, as well as all myliobatids except for *Aetobatus* (state 1; Figs. 7C–G, 8A). *Aetobatus*, which almost always consists only of a single row of tooth plates, has teeth that are more rectangular and not six-sided (state 2; Fig. 7H). The appearance of six-sided teeth co-occurs with the appearance of broad and flattened teeth. These states are retained in the secondarily minute-toothed taxa, *Mobula* and *Manta*, and lost in the greatly expanded-toothed taxon, *Aetobatus*.

(47) Lateral teeth: (0) present; (1) absent. Lateral teeth are present in most taxa examined (state 0; Figs. 7A–G, 8A–E). Lateral teeth were observed to be absent from almost all specimens of *Aetobatus* (state 1; Figs. 7H, 8F). In a single specimen of *Aetobatus narinari* (TMM-M-7010) five lateral tooth plates were present among all 19 intact median tooth plates. We chose to score *Aetobatus* with the derived state, because this observation was isolated to a single specimen.

(48) Differentiation of median teeth from lateral teeth: (0) median and lateral teeth are similar; (1) median teeth relatively expanded. Median teeth can be similar to laterally adjacent teeth as they are in all non-myliobatid taxa and in *Manta* (state 0; Figs. 7A, B, G, 8A). Median teeth can otherwise be expanded in the lateral direction, i.e., they are broader than they are anteroposteriorly long (state 1; Figs. 7C, D, F, 8B–E). *Mobula* is the only taxon examined to possess expanded median teeth despite having small teeth. *Aetobatus* is scored as not applicable (-) because it possesses no lateral teeth.

(49) Differentiation among lateral teeth: (0) lateral teeth unexpanded; (1) some lateral teeth expanded. Lateral teeth are primitively unexpanded relative to median teeth and other lateral teeth (state 0; Figs. 7A, B, 8A). In *Rhinoptera*, *Mobula*, *Brachyrhizodus*, and *Igdabatis*, some lateral teeth are expanded, and resemble the longer teeth of the median tooth row (state 1; Fig. 7C, F). Lateral teeth in *Manta* are considered secondarily unexpanded (Fig. 7G) *Aetobatus* is scored as not applicable (-) because it possesses no lateral teeth.

(50) Relative amount of curvature in expanded lower teeth: (0) straight and uncurved; (1) moderately curved; (2) strongly curved into distinct chevron. Individual teeth are often straight, or uncurved in the extant myliobatid taxa (Fig. 7B–G) *Rhinoptera*, *Myliobatis freminvillii*, *Myliobatis goodei*, *Myliobatis aguila*, *Myliobatis californica*, *Mobula*, and *Manta* and the extinct taxon *Myliobatis striatus* (state 0; Fig. 8E). Median and sometimes lateral teeth (when expanded) may be slightly curved (state 1). This state is observed in the majority of extinct taxa examined, namely, *Myliobatis toliapicus*, *Myliobatis dixoni*, *Myliobatis wurnoensis*, *Weissobatis*, *Brachyrhizodus*, and *Igdabatis* (Figs. 3C, 8B–D). A third condition is a strongly curved chevron-shaped tooth plate, which is present only in *Aetobatus* (state 2; Figs. 7H, 8F). Non-myliobatid taxa were scored as not applicable (-) because they possessed no expanded teeth.

(51) Upper tooth curvature: (0) uncurved; (1) curved. The amount of curvature in upper median teeth is always less than in the lower median teeth, even in *Aetobatus*. We observed only two states for upper median teeth: uncurved (state 0) or curved (state 1). Curved upper teeth were present in the extinct taxa *Myliobatis dixoni*, *Myliobatis wurnoensis*, *Weissobatis*, *Igdabatis*, and *Aetobatus arcuatus* (Figs. 3A, B, 8D). All other myliobatid taxa had no distinct curvature to their expanded teeth. Non-myliobatid taxa were scored as not applicable (-) because they possessed no expanded teeth. *Brachyrhizodus* was scored as missing (?) because we consider the teeth we sampled to be lower dentition.

(52) Direction of tooth curvature: (0) concave; (1) horizontal; (2) convex. This character is observable on upper and lower dental plates and is distinct from characters 50 and 51. A concave curvature occurs in the taxa that have median teeth with lateral margins that are directed anteriorly or out of the mouth when articulated with the jaw, i.e., extinct taxa *Brachyrhizodus*, *Myliobatis wurnoensis* (state 2; Figs. 3, 8B). In taxa without expanded tooth curvature, the condition is scored as horizontal (state 1). The third condition, a convex

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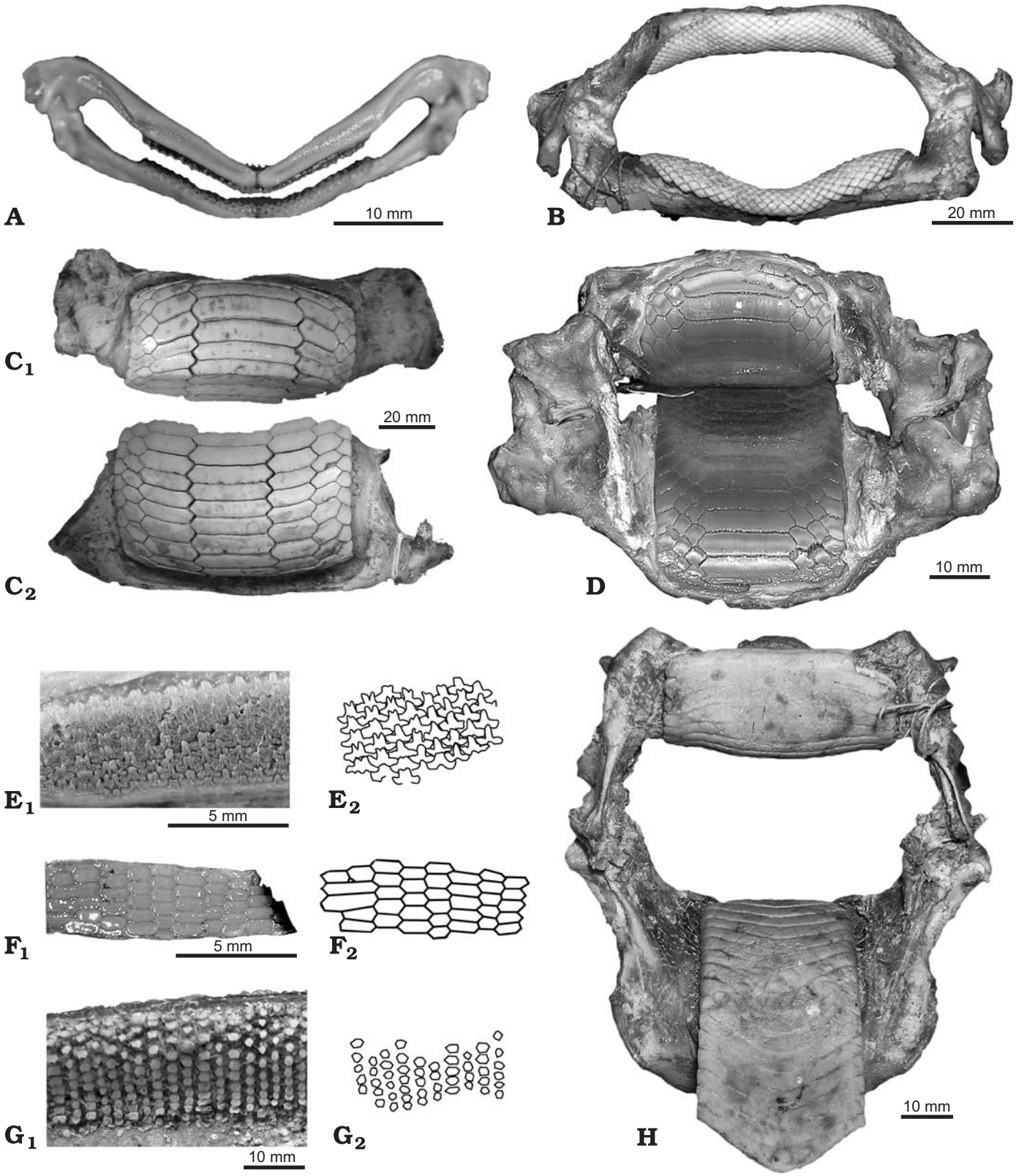


Fig. 7. Comparative extant taxa of Myliobatidae. **A**, **B**, **D**. Articulated jaws and tooth rows. **C**. Disarticulated jaws and articulated tooth rows. **E–G**. Articulated tooth rows. **A**. *Raja* sp., AMNH 92321b, in labial view. **B**. *Dasyatis* sp., FMNH 15625, in labial view. **C**. *Rhinoptera quadriloba* (LeSueur, 1817), FMNH 82986, in occlusal view. **D**. *Myliobatis californica* Gill, 1865, MCZ 424, in lingual view. **E**. *Mobula hypostoma* (Bancroft, 1831), AMNH 44124, in occlusal view, photograph (E_1), line drawing (E_2); **F**. *Mobula rochebruni* (Vaillant, 1879), FMNH 38450, in occlusal view, photograph (F_1), line drawing (F_2). **G**. *Manta hamiltoni* (Walbaum, 1792), FMNH 41385, in occlusal view, photograph (G_1), line drawing (G_2). **H**. *Aetobatus narinari* (Euphrasen, 1790), FMNH 10985, in labial view.

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curvature, occurs when the lateral margins of median teeth are directed posteriorly, or into the mouth (state 2 as it is in *Aetobatus* (Figs. 7H, 8F).

(53) Tooth association: (0) loosely interlocking; (1) sometimes loosely interlocking or tightly interlocking; (2) tightly interlocking. Fossilized myliobatid dentitions are found in isolation or as whole dental plates. Isolated teeth imply a loosely interlocking association among articulated teeth (state 0). Multiple teeth found in articulation that must be forcibly disarticulated in order to observe them in isolation are considered derived (state 2). We observed a third state in one taxon, *Aetobatus irregularis*, which we tentatively consider an intermediate state (state 1). Occasionally dentitions were present as loosely interlocking isolated teeth or as tightly interlocking teeth as indicated by two or more plates associated with each other. It was usually the case that upper teeth of *A. irregularis* were found disarticulated while lower teeth were in articulation.

(54) Tooth interlocking mechanism: (0) overlapping; (1) tongue and groove; (2) no direct contact. The way that teeth interlock anteroposteriorly is not a direct indication of how tightly those teeth interlock and therefore it is scored separately. Teeth may overlap as is the case for non-myliobatid stingrays (state 0). In most myliobatid stingrays, they may fit together by means of a tongue and groove (state 1). Teeth in *Mobula* and *Manta*, which are secondarily minute, as well as the extinct taxon, *Brachyrhizodus*, have no direct contact (state 2).

(55) Shape of interlocking mechanism: (0) bulbous; (1) short shelf; (2) long shelf. The tongue of the tongue-and-groove interlocking mechanism may exist as a bulbous ridge, which is the condition in *Rhinoptera* and the extinct taxon *Igdabatis* (state 0; Fig. $8D_2$, D_4). In *Myliobatis* and *Weissobatis*, there is a short posteriorly directed shelf (state 1; Fig. $8C_2$, E_4). In *Aetobatus*, there is a long, posteriorly directed shelf created by the roots that begins slightly anterior to the posterior margin of the tooth crown and extends far posteriorly, past the posterior margin of the tooth crown (state 2; Fig. $7F_4$). Taxa without a tongue and groove articulation were scored as not applicable (-) in the data matrix.

(56) Crown height: (0) crown height exceeds root depth on unworn teeth; (1) crown height does not exceed root depth on unworn teeth. Crown height was scored using median teeth for Myliobatidae. Although crown height is variable within many batoid species seasonally, the relative height of the crown compared to the depth of the underlying roots is consistent in specimens observed. In most taxa, the crown height is high, exceeding the root depth in unworn teeth (state 0; Figs. $3A_1$, B_1, $8E_3$). *Aetobatus*, *Mobula*, and *Manta*, all have a relatively low crown, where the height does not exceed root depth on unworn teeth (state 1; Fig. $7F_3$).

(57) Occlusal surface: (0) cusped; (1) smooth; (2) depressed. The occlusal surface of teeth, prior to wear, is cusped with one or more peaks ancestrally (state 0; Fig 7A). The surface is otherwise smooth, with no cusps or depressions in most taxa (state 1: Figs. $3B_2$, C_2, 7B–H, $8A_1$, B_1, C_1, D_1, F_1). In the extinct taxon, *Rhinoptera davisei*, and *Manta*, the occlusal surface is depressed in the center (state 2). *Dasyatis* is polymorphic for smooth and depressed occlusal surfaces. *Mobula* is polymorphic for smooth and cusped occlusal surfaces (Fig. 7E, F).

(58) Crown shape in anterior or posterior view: (0) straight; (1) domed; (2) deep. Crown shape was scored using median teeth for Myliobatidae. The occlusal surface of a tooth is not a good indication of the overall morphology of the tooth crown. When viewed anteriorly or posteriorly, the crown may be straight or uniformly thick (state 0), as it is in the extinct taxon, *Brachyrhizodus*, as well as *Myliobatis freminvillii*, *Myliobatis goodei*, *Aetobatus narinari, Aetobatus irregularis*, *Rhinoptera*, *Mobula*, and *Manta*. The crown may also be domed with a bulbous, outward or lingually curving surface (state 1), as is the condition in *Myliobatis aguila*, *Myliobatis dixoni*, *Myliobatis wurnoensis*, and *Igdabatis* (Figs. $3A_1$, $8D_2$). The third observed condition is a deep crown, where the surface is not greatly domed, but the contact with the roots bulges towards the jaw cartilages (state 2), as it does in *Myliobatis californica*, *Myliobatis striatus*, *Myliobatis toliapicus*, and *Aetobatus arcuatus* (Fig. $8E_3$, F_3).

(59) Lateral margins: (0) not pinched; (1) pinched. When viewed anteriorly or posteriorly, the lateral margins of the median teeth are often the same height as middle of the tooth or gradually-sloped so that the distal ends of the teeth form a peak, much lower than the middle of the tooth (state 0). In the extinct taxon, *Myliobatis wurnoensis*, lateral margins were pinched relative to the center of the tooth (state 1; Fig. $3A_1$, B_1). This character state is autapomorphic for *M. wurnoensis*.

(60) Root type: (0) holaulacorhizous; (1) polyaulacorhizous. Roots in the stingrays are either holaulacorhizous (state 0; Fig. $8A_3$) or polyaulacorhizous (state 1; Figs. $3A_3$, B_3, C_1, $8B_2$, C_3, D_3, E_2, F_2); see Cappetta (1987) for review.

(61) Number of roots: (0) 2 roots; (1) 3 to 4 roots; (2) 5 roots or greater. Number of root laminae in non-myliobatid stingrays is 2 (state 0; Fig. $8A_3$). In *Brachyrhizodus* there are 3 or 4 roots (state 1; Fig. $8B_2$). All other taxa examined from Myliobatidae have 5 or more roots (state 2; Figs. $3A_3$, B_3, C_1, $8C_3$, D_3, E_2, F_2).

(62) Roots in basal view: (0) triangles; (1) wide blocks; (2) narrow blocks; (3) fine edges. The shape of the root laminae in basal view is triangular in non-myliobatid stingrays (state 0; Fig. $8A_3$). The extinct taxa, *Apocopodon*, *Brachyrhizodus*, *Igdabatis*, and *Myliobatis wurnoensis* possess wide blocks (state 1; Figs. $3A_3$, B_3, C_1, $8B_2$, C_3, D_3). *Myliobatis striatus*, *Myliobatis freminvillii*, *Myliobatis aguilla*, *Myliobatis toliapicus*, *Myliobatis goodei*, and *Weissobatis* have narrow blocks (state 2; Fig. $8E_2$). *Rhinoptera* and *Aetobatus* have extremely thin, fine, comb-like edges to their laminae (state 3; Fig. $8F_2$). The condition of this character is unknown in *Manta* and *Mobula* and scored as "?" in the data matrix.

(63) Distance between root laminae: (0) narrower than root laminae; (1) broad, groove wider than root laminae. Ancestrally, the grooves dividing each lamina are narrower than the root itself (state 0). In *Rhinoptera*, *Myliobatis cali-*

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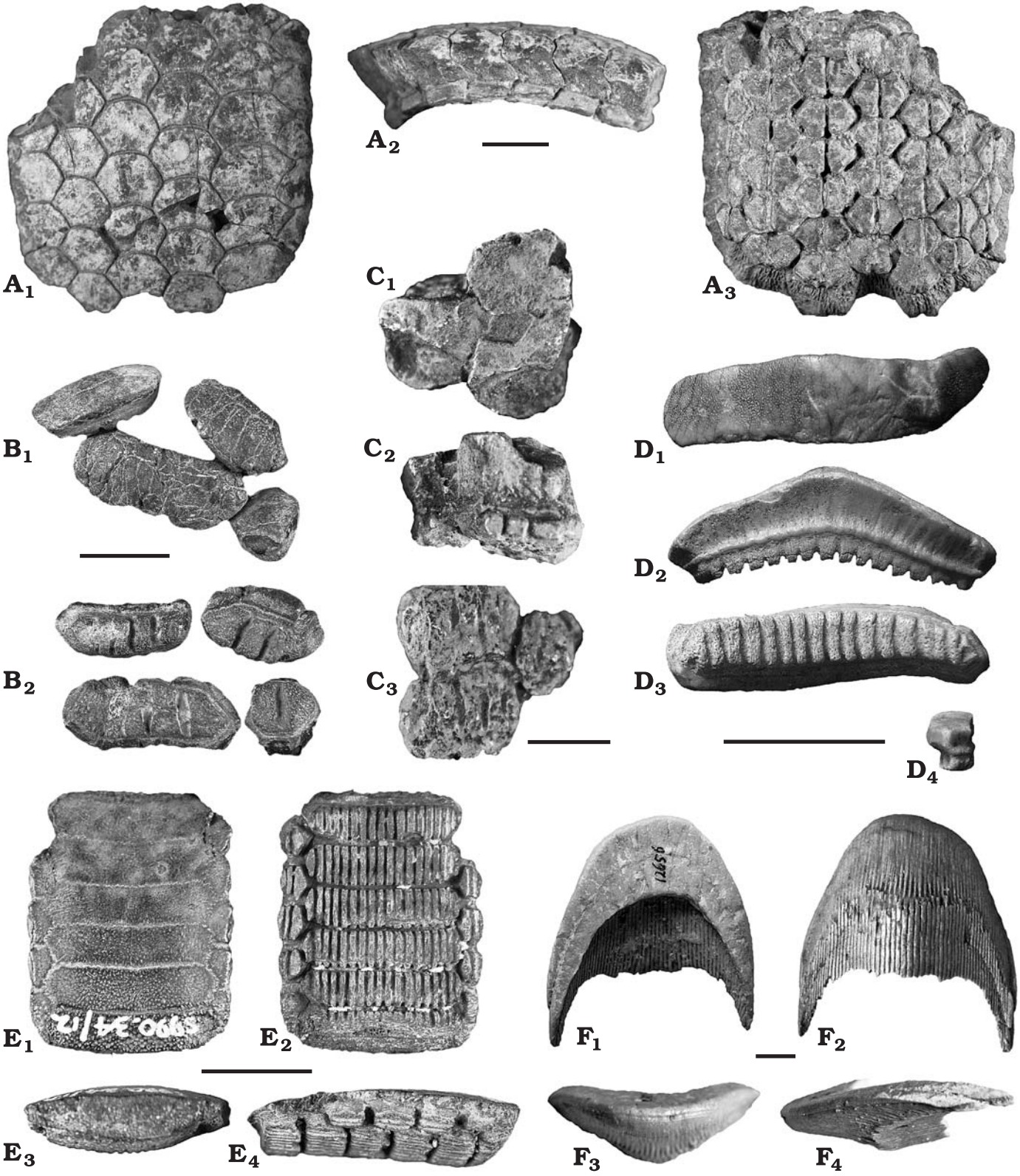


Fig. 8. Comparative extinct taxa of Myliobatiformes; known ages mapped onto Fig. 6. **A**. *Hypolophites myliobatoides* Stromer, 1910, NHM P18781; A_1, occlusal view, anterior to top; A_2, lateral view, anterior to left; A_3, root view, anterior to top. **B**. *Brachyrhizodus wichitaensis* Romer, 1942, NHM P89095; B_1, occlusal view; anterior undetermined; B_2, root view; anterior undetermined. **C**. *Apocopodon sericius*, NHM P24670, C_1, occlusal view, anterior to top; C_2, lateral view, anterior to left; C_3, root view, anterior to top. **D**. *Igdabatis sigmodon*, TMM 45892-1; D_1, occlusal view, anterior to top; D_2, posterior view; D_3, root view, anterior to bottom; D_4, lateral view, anterior to left. **E**. *Myliobatis striatus*, NHM P.66859; E_1, occlusal view, anterior to top; E_2, root view, anterior to top; E_3, posterior view; E_4, lateral view, anterior to left. **F**. *Aetobatus arcuatus*, SMNH 12656-3; F_1, occlusal view, anterior to top; F_2, root view, anterior to top; F_3, anterior view; F_4, lateral view, anterior to left. Scale bars 10 mm.

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fornicus, and *Dasyatis*, however, the groove between each lamina is wider than the lamina itself (state 1).

(64) Inclination of roots: (0) no inclination; (1) offset and step-like; (2) long and strongly inclined. When viewed from the side, the laminae of the root in the majority of taxa have a vertical slope, with no posterior offset or inclination (state 0; Fig. $8C_2$, D_4). In some taxa, the roots are slightly offset and step like as in *Myliobatis striatus*, *Myliobatis toliapicus*, *Rhinoptera quadriloba*, and *R. davisei* (state 1; Fig. $8E_4$). Autapomorphic to *Aetobatus* is the presence of long and strongly posteriorly inclined roots (state 2; Fig. $8F_4$).

(65) Root groove position: (0) regularly spaced between laminae; (1) irregularly spaced between laminae. The spacing of grooves between laminae is often at regular intervals (state 0). However, in *Brachyrhizodus*, *Igdabatis*, and *Myliobatis wurnoensis* those grooves can be irregularly spaced (state 1; Figs. $3A_2$, B_3, C_1, $8B_2$, D_3).

Discussion

The comprehensive phylogenetic study of Myliobatiformes by Carvalho et al. (2004) was based on several extant taxa and a number of relatively complete and exquisitely preserved fossils from the late early Eocene Green River Formation of Wyoming. Those authors found that the Eocene fossils were relatively basal among Myliobatiformes and that including those fossils in their analysis helped to resolve relationships among all Myliobatiformes. Not studied, however, were the less complete fossil specimens of taxa within Myliobatidae that include a plethora of fragmentary, although characteristic, pavement-like dentitions.

Here we test for the first time the relationships of several extinct taxa within Myliobatidae. We integrate taxa known from fossilized dental plates, including specimens recovered from the Cretaceous of Mali, into a phylogenetic analysis that combines data from prior studies, including non-dental character systems scored for extinct and extant taxa. We redescribe through the character analysis dental morphology for Myliobatiformes and offer new characters and states for distinguishing and relating species in Myliobatidae. The results of the phylogenetic analyses here corroborate the topologies of several genus-level morphological analyses that were conducted for the Myliobatidae (e.g., Nishida 1990; Lovejoy 1996; McEachran et al. 1996; Shirai 1996; Carvalho et al. 2004). We also find that synapomorphies for major nodes within Myliobatidae are often dental features, which has not been previously observed (Fig. 5).

Extinct taxa are widely distributed across the tree presented here (Fig. 4B). *Hypolophites* is not most closely related to other members of "Dasyatidae" (such as *Dasyatis*) as was previously hypothesized (Cappetta 1987), but is instead the immediate sister taxon to a monophyletic Myliobatidae (Fig. 4). Our results, however, are consistent with those from previous studies (Carvalho et al. 2004) that demonstrate that "Dasyatidae" is not monophyletic. *Apocopodon* is sister to all remaining taxa within Myliobatidae (Fig. 5: node-B) and shares the pavement-like dentition characteristic of the clade. *Igdabatis* also shares the elongate median teeth characteristic of Myliobatidae, and is the sister taxon to Mobulinae + *Rhinoptera*. The relative position of the extinct species in *Rhinoptera* is interesting because *R. davisei* is more closely related to *R. quadriloba* than either is to *R. bonasus* (Fig. 5: node-P). Previously *R. quadriloba* was considered a junior synonym of *R. bonasus* (Eschmeyer 1998), therefore, we would have predicted that these species would be sister taxa. The variation recognized in the specimens examined for this study (Appendix 3), however, provides evidence that *R. quadriloba* is a valid species. *Brachyrhizodus* is the sister taxon to *Mobula* + *Manta* (Fig. 5: node-L), contrary to the hypothesis proposed by Cappetta (1987) that *Brachyrhizodus* is closely related to *Rhinoptera*.

The new Malian *Myliobatis wurnoensis* material represents the first well-preserved upper and lower dentitions of this species. In addition, the new fossils demonstrate for the first time that *Myliobatis wurnoensis* occurred on both sides of the K/T boundary. Previously, the earliest documented occurrence of the species was the Paleocene–Landenian (de Geyter et al. 2006; early Eocene, sensu White 1934). Several myliobatid taxa have Mesozoic ranges, including *Igdabatis* and *Brachyrhizodus*, and collectively, our strict consensus shows that there are a number of ghost myliobatid lineages that cross the K/T boundary. Thus a number of myliobatid taxa are inferred to have survived this mass extinction event and species counts of the Late Mesozoic myliobatids are much higher than a simple count of fossils recovered alone. *Aetobatus* and *Rhinoptera* are each monophyletic. *Aetobatus* is the sister taxon to a clade that includes *Rhinoptera* + Mobulinae. Our expanded character and taxon sample, however, does not support a monophyletic *Myliobatis*. The relative position of *Aetobatus* and *Myliobatis* on the strict consensus tree also indicates that "Myliobatinae" (sensu Nelson 2006) is paraphyletic (Fig. 4B). "Myliobatinae" was erected based on conventional phenetic similarities, and we have corroborated Nelson's (2006) prediction that the subfamily would be found to be paraphyletic if more species were included in a cladistic analysis. Based on our results, "Myliobatinae" amounts to members of Myliobatidae that are not part of Mobulinae, *Rhinoptera*, or *Aetobatus* (i.e., extinct and extant species of *Myliobatis*, *Apocopodon*, *Weissobatis*, and *Igdabatis*) supporting Nelson's hypothesis of paraphyly.

Examining dentitions comparatively, in the context of whole-body specimens, provides our only means of testing the phylogeny of the total clade (Shimada 1997). The present study is an example of how fragmentary or incomplete specimens, here dentitions, can possess an important suite of characters and states for phylogenetic analysis. This new information allows us to generate testable hypotheses of evolutionary relationships and morphological transformations among closely related taxa.

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Appendix 1

Comparative material

Extinct taxa: Exclusively fossil dentition

Aetobatus arcuatus: NHM P15213, NHM P15214, NHM P10249, MCZ 412, AMNH 28032, FMNH PF44, SMNS 12656-1, SMNS 12656-2, SMNS 12656-3, SMNS 87056; *Aetobatus irregularis*: YPM-PU 10334, YPM-PU 10336, YPM-PU 10322, NHM 990.68.5_PV330, NHM P66858, NHM P66734, NHM P66733, NHM P66732, NHM P10002, NHM P12915, NHM P60902; *Apocopodon sericius*: NHM P.24670, P.24671; *Brachyrhizodus wichitaensis*: YPM-PU 22382, NHM P58095-P58101, NHM P62012-P62021; *Hypolophites myliobatoides*: NHM P18781; *Igdabatis sigmodon*, TMM 45892-1; TMM 45892-2; TMM 45892-3; TMM 45892-4; TMM 45892-5; *Myliobatis tobijei*: AMNH 44146, AMNH 4736; *Myliobatis wurnoensis*: CNRST-SUNY 2-28, NHM P18452-P18453; *Myliobatis dixoni*: YPM PU 10320, NHM P66744, NHM P66859, NHM P66860, NHM P66861, NHM P66862, SMNS 87640; *Myliobatis toliapicus*: YPM PU 10335, NHM P528, FMNH P26042; *Rhinoptera sp*: MCZ 13191, YPM PU 21135; *Weissobatis micklichi*: SMNS 84752_2

Extant taxa: Dental and whole bodied specimens

Aetobatus flagellum: MCZ 158054; *Aetobatus narinari*: MCZ 865s, FMNH 10985, FMNH 10986, FMNH 10987, FMNH 51267, SMF 30673; *Aetomylaeus maculatus*: ANSP 60433; *Aetomylaeus nichofii*: MCZ 1393; *Dasyatis sabina*: AMNH 211610SW, AMNH 73869; *Dasyatis americanus*: FMNH 15625, FMNH 15624, FMNH 10957, FMNH 10958, FMNH 10959; *Dasyatis diptura*: FMNH 83720; *Gymnura micrura*: AMNH 086386, AMNH 73890, FMNH 89990, TNHC 10994; *Gymnura japonica*: FMNH 59307; *Gymnura sp*: MCZ 153675; *Himantura uamak*: AMNH 98730; *Himantura walga*: ZMB 21716 (x2); *Manta hamiltoni*: FMNH 41385; *Mobula coilloti*: MCZ -1111; *Mobula hypostoma*: AMNH 44124, AMNH 21660; *Mobula rochebruni*: FMNH 38648, FMNH 38649, FMNH 38450; *Myliobatis goodei*: MCZ 1343, MCZ -638; *Myliobatis freminvillii*: MCZ 40744, MCZ 400, AMNH 55863; *Myliobatis californicus*: MCZ 424, FMNH 59934; *Myliobatis aguila*: MCZ -828; *Myliobatis tenuicaudatus*: UF 81852; *Myliobatis australus*: UF 99858; *Paratrygon aiereba*: AMNH 59869, AMNH 59872, AMNH 59874; *Potamotrygon motoro*: FMNH 94503; *Potamotrygon orbigny*: AMNH 59870; *Potamotrygon sp*: ZMB 33206; *Potamotrygon hystrix*: ZMB 16863; *Pteromylaeus asperrimus*: MCZ 397, FMNH 41572; *Rhinoptera bonasus*: AMNH 1034, AMNH 098173, MCZ 418, UF 20030; *Rhinoptera quadriloba*: FMNH 82986; *Taeniura lymma*: ZMB 4657, ZMB 5718; Specimens absent from this list were observed only in the literature.

Appendix 2

Data Matrix. Symbols for polymorphic characters: # = (0 and 1); @ = (1 and 2). Unscored cells: – = not applicable; ? = missing.

	10	20	30	40
Rhinobatos	0000000000	0000000000	0000000000	0000000000
Raja	0000000000	0000000000	0000000000	0000000000
†*Heliobatis*	????00??00	0?1?0000??	????000000	0101??????
†*Asterotrygon*	????00??00	0?1100001?	?1??000000	0001??????
Hexatrygon	00??000000	000000001?	0100000000	01000?0?00
Plesiobatis	0001000010	0110000011	1002000000	0100000000
Urolophus	0001000110	0110100011	1100000020	0#00000000
Trygonoptera	0001000100	0110000011	1100100020	00000?0000
Urobatis	1001000000	0110000021	110#100000	0100000000
Urotrygon	1001000000	0110000031	1100100000	0100000000
Paratrygon	0021000000	0110000021	1100000001	0112000011
Plesiotrygon	0011000000	0111000021	1101010001	0111020011
Potamotrygon	0011000000	0111000021	1101010001	0111020011
"*Himantura*"	0001000000	0111000021	1100100000	0112020000
Taeniura	0001000000	0110000021	1100100000	0111010000
Himantura	01#1000000	0110000021	1100100000	0112000000
†*Hypolophites*	??????????	??????????	??????????	??????????
Dasyatis	01#1000000	0110000021	110010#000	0111000000
Pteroplatytrygon	0101000010	0110000021	1100100000	0111000000
Gymnura	0101000001	0100000011	1100001110	1102000000

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†*Apocopodon*	??????????	??????????	??????????	??????????
†*Igdabatis sigmodon*	??????????	??????????	??????????	??????????
†*Brachyrhizodus*	??????????	??????????	??????????	??????????
Myliobatis freminvillii	0201001001	11101?1131	2010101100	0012101100
Myliobatis goodei	0201001001	11101?1131	2010101100	0012101100
Myliobatis aguila	0201001001	11101?1131	2010101100	0012101100
Myliobatis californicus	0201001001	11101?1131	2010101100	0012101100
†*Myliobatis striatus*	??????????	??????????	??????????	??????????
†*Myliobatis toliapicus*	??????????	??????????	??????????	??????????
†*Myliobatis dixoni*	??????????	??????????	??????????	??????????
†*Myliobatis wurnoensis*	??????????	??????????	??????????	??????????
†*Weissobatis micklichi*	????0????1	?1????????	???????100	0012??????
Aetobatus narinari	0201001011	1110111131	20111?21?0	1012101100
†*Aetobatus arcuatus*	??????????	??????????	??????????	??????????
†*Aetobatus irregularis*	??????????	??????????	??????????	??????????
Rhinoptera quadriloba	0201111011	1110111131	201?1?20?0	1012101100
Rhinoptera bonasus	0201111011	1110111131	201?1?20?0	1012101100
†*Rhinopteradavisei*	??????????	??????????	??????????	??????????
Mobula	0201111011	1100110131	20111?20?0	1012101100
Manta	??????????	??????????	??????????	??????????
Rhinobatos	000000000-	--00?00000	0000?	
Raja	000000000-	--00?00000	0000?	
†*Heliobatis*	?0?000000-	--00?00000	0000?	
†*Asterotrygon*	?0?000000-	--00?00000	0000?	
Hexatrygon	000000000-	--00?00000	0000?	
Plesiobatis	001000000-	--00?00000	0000?	
Urolophus	001000000-	--00?00000	0000?	
Trygonoptera	001000000-	--00?00000	0000?	
Urobatis	101000000-	--00?00000	0000?	
Urotrygon	101000000-	--00?00000	0000?	
Paratrygon	001000000-	--00?00000	0000?	
Plesiotrygon	001000000-	--00?00000	0000?	
Potamotrygon	001000000-	--00?00000	0000?	
"*Himantura*"	001000000-	--00?00000	0000?	
Taeniura	001000000-	--00?00000	0000?	
Himantura	001000000-	--00?00000	0000?	
†*Hypolophites*	???111000-	--20?01000	0000?	
Dasyatis	001000000-	--00?0@000	0010?	
Pteroplatytrygon	001000000-	--00?00000	0000?	
Gymnura	001000000-	--00?00000	0000?	
†*Apocopodon*	???1110110	0101-01001	01000	
†*Igdabatis sigmodon*	???1110111	1201001101	01001	
†*Brachyrhizodus*	???1110111	?102-01001	11001	
Myliobatis freminvillii	0111110100	0101101001	22000	
Myliobatis goodei	0111110100	0101101001	22000	
Myliobatis aguila	0111110100	0121101101	22000	
Myliobatis californicus	0111110100	0121101201	22100	
†*Myliobatis striatus*	???1110100	0121101201	22010	

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†*Myliobatis toliapicus*	???1110101	0221101201	22010
†*Myliobatis dixoni*	???1110101	1221101101	22000
†*Myliobatis wurnoensis*	???1110101	1221101111	21001
†*Weissobatis micklichi*	?1?1110101	1221101?01	22000
Aetobatus narinari	0211121--2	1021211001	23020
†*Aetobatus arcuatus*	???1121--2	1021211201	23020
†*Aetobatus irregularis*	???1121--2	0011211001	23020
Rhinoptera quadriloba	0311110111	1201001001	23110
Rhinoptera bonasus	0311110111	1201001001	23100
†*Rhinoptera davisei*	???1110110	0201002001	23110
Mobula	0310110110	?101?1#001	2?00?
Manta	???0110000	?102?12001	2?00?

Appendix 3

Character List. CMG = character as presented by Carvalho et al. (2004).

1. (01, CMG) Tubules of subpleural components of hyomandibular lateral line canals: (0) not branched at extremities; (1) extremities dichotomously branched
2. (02, CMG) Subpleural components of the hyomandibular lateral line canals: (0) posterior branch extends caudally more or less parallel to longitudinal body axis; (1) posterior branch inflects towards midline to form a lateral hook; (2) posterior branch inflects to continue anteriorly almost parallel to anterior branch, forming a large indentation
3. (03, CMG) Suborbital components of infraorbital lateral line canals: (0) projecting posteriorly lateral to mouth; (1) projecting posteriorly lateral to mouth and anteriorly lateral to nasal openings; (2) forming a complex web-like pattern on lateral aspects of the anteroventral disc region
4. (04, CMG) Scapular loops formed by scapular components of trunk lateral line canals: (0) absence of loops; (1) presence of scapular loops
5. (05, CMG) Anterior process of neurocranium: (0) absent; (1) present
6. (06, CMG) Preorbital process: (0) present; (1) absent
7. (07, CMG) Preorbital canal for passage of superficial ophthalmic nerve: (0) dorsally located; (1) anteriorly located
8. (08, CMG) Foramen for the optic (II) nerve: (0) moderately sized; (1) very enlarged
9. (09, CMG) Postorbital process of neurocranium: (0) infraorbital lateral line canal separates postorbital process from small, anterior triangular outgrowth (supraorbital process) of the supraorbital crest; (1) postorbital process with small foramen for passage of infraorbital lateral line canal
10. (10, CMG) Extent of orbital region: (0) orbital region of neurocranium long; (1) shortened orbital region with more anteriorly placed supraorbital and postorbital process
11. (11, CMG) Postorbital process: (0) without ventrolateral projection; (1) continuing ventrolaterally to form a cylindrical projection
12. (12, CMG) Ventrolateral expansion of nasal capsules: (0) nasal capsules laterally expanded; (1) nasal capsules ventrolaterally expanded
13. (13, CMG) Articulation between hyomandibula and Meckel's cartilage: (0) hyomandibulae directly attached to lower jaws; (1) hyomandibulae articulating with lower jaws through strong, stout ligament (hyomandibular-Meckelian ligament) at distal tip
14. (14, CMG) Angular cartilages: (0) absence of angular cartilages within hyomandibular-Meckelian ligament; (1) presence of angular cartilages within ligament
15. (15, CMG) Secondary hyomandibular cartilages: (0) absent; (1) present
16. (16, CMG) Symphysial fusion of upper and lower jaws: (0) antimeres separate at symphysis; (1) both antimeres of jaws symphysially fused
17. (17, CMG) Mandibular width at symphysis: (0) lower jaws slender at symphysis; (1) lower jaws symphysially thickened
18. (18, CMG) Lateral projections of lower jaws: (0) absent; (1) present
19. (20, CMG) Basihyal cartilage: (0) basihyal laterally elongated, fused to first hypobranchialis; (1) basihyal a single element, but separate from first hypobranchials; (2) basihyal separate from first hypobranchials but fragmented into more than one component; (3) basihyal absent
20. (21, CMG) Fusion of ventral pseudohyoid and first ceratobranchial: (0) absent; (1) present
21. (22, CMG) Arrangement of posterior ceratobranchials: (0) separate from each other; (1) ankylosis between forth and fifth ceratobranchials; (2) fourth and fifth ceratobranchials fused to each other
22. (23, CMG) Median projection of the basibranchial medial plate: (0) absent; (1) present
23. (24, CMG) Articulation between fifth epi- and ceratobranchial elements to scapulocoracoid: (0) close together; (1) widely separated
24. (25, CMG) Lateral stay of synarcual: (0) originates ventral to spinal nerve foramina; (1) originates dorsal to spinal nerve foramina; (2) contacting synarcual both dorsally and ventrally to foramina

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25. (26, CMG) Fossa on dorsal scapular region: (0) absent; (1) present
26. (27, CMG) Contact between pro- and mesopterygium in the pectoral fin: (0) absent; (1) present
27. (28, CMG) Distinct components of the mesopterygium: (0) mesopterygium single element; (1) fragmented; (2) missing altogether
28. (29, CMG) Lateral expansion of radials in pectoral region: (0) absent; (1) present
29. (30, CMG) External margin of mesopterygium: (0) more or less straight, not fused to radials; (1) undulated, not fused to radials; (2) highly sinuous, appearing to be fused with articulating radial elements
30. (31, CMG) Median prepelvic process: (0) absent or weakly developed; (1) very elongated
31. (32, CMG) Pelvic girdle shape: (0) not arched or only moderately so; (1) greatly arched
32. (33, CMG) Dorsal fin: (0) present; (1) absent
33. (34, CMG) Cartilaginous rod in tail: (0) absent; (1) present
34. (35, CMG) Caudal fin: (0) present; (1) reduced to tail-folds; (2) absent
35. (36, CMG) Adductor mandibulae complex: (0) without posteromedial extension; (1) posteromedial extension present
36. (37, CMG) Spiracularis muscle: (0) projecting ventrally to insert on either palatoquadrate, Meckel's cartilage, and or hyomandibula; (1) projecting ventrally and posteriorly beyond hyomandibulae and both sets of jaws to insert dorsal to coracomandibularis; (2) projecting ventrally and posteriorly beyond hyomandibulae and both sets of jaws to insert ventral to coracomandibularis
37. (38, CMG) Depressor mandibularis muscle: (0) present; (1) absent
38. (39, CMG) Coracohyoideus muscle: (0) not connected at midline; (1) connected at midline
39. (40, CMG) Urea retention: (0) urea retained in blood; (1) urea excreted in urine
40. (41, CMG) Rectal gland: (0) present; (1) reduced
41. (42, CMG) Spiracular tentacle: (0) absent; (1) present
42. (43, CMG) Cephalic lobes: (0) absent; (1) single and continuous; (2) single with an indentation; (3) paired
43. (44, CMG) Nasal curtain: (0) not reaching mouth region; (1) extending posteriorly as far as mouth opening
44. (modified from 19, CMG) Tooth type in both upper and lower jaws: (0) minute; (1) broad
45. (modified from 19, CMG) Arrangement of teeth in both upper and lower jaws: (0) arranged in separate diagonal rows or ribbons; (1) horizontal conveyor or pavement-like arrangement
46. (modified from 19, CMG) Tooth shape: (0) square to rounded; (1) hexagonal, six distinct sides; (2) rectangular with posteriorly deflected lateral margins
47. Lateral teeth: (0) present; (1) absent
48. Differentiation of median teeth from lateral teeth: (0) median and lateral teeth are similar; (1) median teeth relatively expanded
49. Differentiation among lateral teeth: (0) lateral teeth unexpanded; (1) some lateral teeth expanded
50. Relative amount of curvature in expanded lower teeth: (0) straight and uncurved; (1) moderately curved; (2) strongly curved
51. Upper tooth curvature: (0) uncurved; (1) curved
52. Direction of tooth curvature: (0) concave; (1) flat; (2) convex
53. Tooth association: (0) loosely interlocking; (1) sometimes loosely interlocking or tightly interlocking; (2) tightly interlocking
54. Tooth Interlocking mechanism: (0) overlapping; (1) tongue and groove; (2) no direct contact
55. Shape of interlocking tongue: (0) bulbous; (1) short shelf; (2) long shelf
56. Crown height: (0) high - crown height exceeds root depth on unworn teeth; (1) low crown
57. Occlusal surface: (0) cusped; (1) smooth; (2) depressed
58. Crown shape in anterior or posterior view: (0) straight; (1) domed; (2) deep
59. Lateral margins: (0) not pinched; (1) pinched
60. Root type: (0) holaulacorhizous; (1) polyaulacorhizous
61. Number of roots: (0) 2 roots; (1) 3 to 4 roots; (2) 5 roots or greater
62. Roots in basal view: (0) triangles; (1) wide blocks; (2) narrow blocks; (3) fine edges
63. Distance between roots: (0) broad, groove wider than root; (1) narrow
64. Inclination of roots: (0) no inclination; (1) offset and step-like; (2) long and strongly inclined
65. Root groove position: (0) regularly spaced between laminae; (1) irregularly spaced between laminae

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