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## **Manta-like planktivorous sharks in Late Cretaceous oceans**

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### **Abstract:**

**The ecomorphological diversity of extinct elasmobranchs is incompletely known. Here, we describe *Aquilolamna milarcae*, a bizarre probable planktivorous shark from early Late Cretaceous open marine deposits in Mexico. *Aquilolamna*, tentatively assigned to Lamniformes, is characterized by hypertrophied, slender pectoral fins. This previously unknown body plan represents an unexpected evolutionary experimentation with underwater flight among sharks, more than 30 million years before the rise of manta and devil rays (Mobulidae), and shows that winglike pectoral fins have evolved independently in two distantly related clades of filter-feeding elasmobranchs. This newly described group of highly specialized long-winged sharks (Aquilolamnidae) displays an aquilopelagic-like**

**ecomorphotype and may have occupied, in late Mesozoic seas, the ecological niche filled by mobulids and other batoids after the Cretaceous–Paleogene boundary.**

Elasmobranchs—the group of cartilaginous fishes including sharks, skates, and rays—are a successful group of ecomorphologically diverse cartilaginous fishes that first appeared around 380 million years ago, during the Late Devonian period (1). Modern plankton-feeding elasmobranchs are represented by two main ecomorphotypes corresponding, on one hand, to the whale shark (Rhincodontidae), the basking shark (Cetorhinidae) and the megamouth shark (Megachasmidae) (i.e., a macrooceanic–tachypelagic morphotype characterized by a large fusiform body) and, on the other hand, to manta and devil rays (Mobulidae) (i.e., an aquilopelagic morphotype characterized by a dorsoventrally flattened body and winglike pectoral fins with a narrowly angular shape) (1-3). Whereas the former ecomorphotype convergently evolved during the Mesozoic in giant pachycormid bony fishes (4), the latter ecomorphotype has not been identified so far in the pre-Cenozoic fossil record (3, 5, 6). We report here a new, bizarre fossil shark showing a previously unknown bauplan and morphological features indicative of filter-feeding habits. This complete specimen from the early Late Cretaceous (Turonian) of Mexico offers important insights into the Mesozoic evolution of medium- to large-sized planktivorous fishes and the rise of “winged” pelagic elasmobranchs, long before the Paleogene origin and opportunistic radiation of mobulid rays (4-6).

*Aquilolamna milarcae* gen. et sp. nov. (formal taxonomic description is provided in the supplementary materials; Figs. 1 and 2 and figs. S3 to S6) stands out among both living and fossil elasmobranchs, with a body plan characterized by the acquisition of unusually hypertrophied pectoral fins combined with the persistence of a powerful tail showing a well-

developed caudal fin (mosaic evolution). Among selachimorphs (modern sharks), narrow, distally expanded bladelike pectoral fins are known in various macroceanic sharks (1, 7), but these predatory (e.g., *Isurus paucus* and *Carcharhinus longimanus*) or planktivorous (e.g., *Megachasma pelagios*) forms are less specialized than *Aquilolamna*. Another notable feature of *Aquilolamna* is its apparent lack of dorsal and pelvic fins, although a taphonomic cause cannot be ruled out. Among neoselachians (modern elasmobranchs), dorsal fins are absent in the enigmatic Early Jurassic eel-shaped shark *Ostenoselache* (8) as well as in various rajiform and myliobatiform rays (9, 10). The assumed dorsal fin secondary loss (or reduction) in *Aquilolamna* could be interpreted as a direct consequence of the acquisition of hypertrophied pectoral fins. In contrast, pelvic fins were lost only in a few extinct chondrichthyan taxa, including eugeneodontiforms (10) and possibly *Squatinactis*, a small-sized Paleozoic cladodont shark with enlarged pectoral fins (11).

*Aquilolamna* is tentatively assigned to Lamniformes (mackerel sharks) on the basis of features such as the radial asterospondylic-type vertebrae (12) and the caudal fin skeleton showing a high hypochordal ray angle (i.e., ventrally directed hypochordal rays) (13). The discovery of *Aquilolamna* provides further insight into the Late Cretaceous diversification of neoselachians (14, 15) and likely represents another example of the ecomorphological plasticity and disparity of lamniform sharks, a group that appeared during the Early Cretaceous and today comprises mainly highly autapomorphic taxa that share relatively few synapomorphies (16-18). Living lamniforms show an impressive variety of morphologies, habitats, behaviors, and diets, with forms ranging from filter-feeders (Cetorhinidae and Megachasmidae) to top predators (Lamnidae) (1, 16, 17). *Aquilolamnids* would reinforce the view that lamniforms achieved high

levels of ecomorphological disparity precociously in their evolutionary history, as early as the mid-Cretaceous (15, 18, 19).

The overall morphology and peculiar features of *Aquilolamna* (i.e., broad head with wide and near-terminal mouth, dentition most likely consisting of minute teeth, wing-shaped pectoral fins; see supplementary materials) strongly suggest that this shark was a suspension feeder, more closely related to the aquilopelagic than to the macrooceanic–tachypelagic ecomorphotype category (Fig. 3 and figs. S10 and S11). *Aquilolamna* was probably a relatively slow swimmer, comparable to other suspension-feeding elasmobranchs (20). The long and slender pectoral fins of *Aquilolamna* most likely acted as stabilizers, but they may also have been used for propulsion by slow flapping movements. In addition, *Aquilolamna* had a typical, well-developed heterocercal caudal fin, similar to that of most macrooceanic sharks (e.g., *Megachasma*) (1). Therefore, *Aquilolamna* probably used a combination of axial-based undulation and pectoral-fin-based oscillation for its locomotion, with main thrust generated by the caudal fin and pectoral fins activated for increasing speed and for maneuvering. This contrasts with the strict pectoral fin-based locomotion of modern suspension-feeding aquilopelagic forms (i.e., mobulids), which are characterized by powerful enlarged pectoral fins (broad-based “wings” used for propulsion by oscillation) and a whiplike tail (21, 22). Among neoselachians, the combination of axial and pectoral locomotion is known only in guitarfishes (Rhinopristiformes) and some electric rays (Torpediniformes) (21, 22); however, these batoids are undulatory appendage propulsors (21, 22), unlike *Aquilolamna*.

The skeleton-based genus *Aquilolamna* may correspond to the enigmatic tooth-based genus *Cretomanta* (fig. S9), known from the Late Cretaceous (Cenomanian–Maastrichtian) of North America and North Africa (6). *Cretomanta* is especially common in the Eagle Ford Group

of Texas (23), a lateral equivalent of the Agua Nueva Formation that yielded the holotype of *Aquilolamna milarcae* (figs. S1 and S9). *Cretomanta* is characterized by simple, minute hooked teeth (less than 2 mm high) that are indicative of planktivory, like teeth of manta rays and whale and basking sharks. *Cretomanta* was originally described as an early member of Mobulidae (24) and subsequently regarded as a possible planktivorous lamniform shark (19, 25). The microstructure of *Cretomanta* teeth, characterized by the presence of parallel-bundled and tangled-bundled enameloid layers typical of selachimorphs, strongly favours the latter hypothesis (26). The interpretation of *Cretomanta* as a suspension-feeding lamniform is consistent with the taxonomic and trophic positions proposed here for *Aquilolamna*. Therefore, we tentatively assign the genus *Cretomanta* to Aquilolamnidae. *Platylithophycus* from the Niobrara Chalk (27) is another mysterious Late Cretaceous (Coniacian–Campanian) genus that might also belong to Aquilolamnidae. On the basis of a single incomplete specimen consisting of gill arches and associated cartilage fragments, *Platylithophycus* was recently recognized as a large, possible filter-feeding elasmobranch of uncertain affinities, characterized by the presence of gill rakers of unusual morphology (27). A third putative Late Cretaceous plankton-feeding shark is the tooth-based genus *Pseudomegachasma*, a lamniform restricted to the Cenomanian and interpreted as a specialized sand tiger shark (Odontaspidae) (28). Given its tooth morphology and systematic placement, it can be reasonably assumed that *Pseudomegachasma* had an *Odontaspis*-like or *Megachasma*-like general appearance, clearly distinct from that of *Aquilolamna*.

Late Cretaceous aquilolamnoid sharks (*Aquilolamna* and possibly *Cretomanta* and *Platylithophycus*) and giant suspension-feeding pachycormid bony fishes (*Bonnerichthys* and *Rhinconichthys*) (4) may have been directly affected by the severe end-Cretaceous extinction of calcifying planktonic organisms resulting from an extreme acidification of surface oceans (29-

31). Aquilolamnids and giant pachycormids all became extinct at the Cretaceous–Paleogene (K–Pg) event and were ecologically replaced during the early Paleogene (Paleocene) by pelagic planktivorous batoids (*Archaeomanta*, *Sulcidens*, and the stem mobulid *Burnhamia*) (4–6) and rhincodontid sharks (*Palaeorhincodon*) (4), respectively (Fig. 4). The discovery of aquilolamnids suggests that the guild of large filter-feeding fishes changed in composition but not in structure after the end-Cretaceous mass extinction event, with both aquilopelagic and macroceanic–tachypelagic convergent forms being represented in pre- and post-K–Pg open marine ecosystems.

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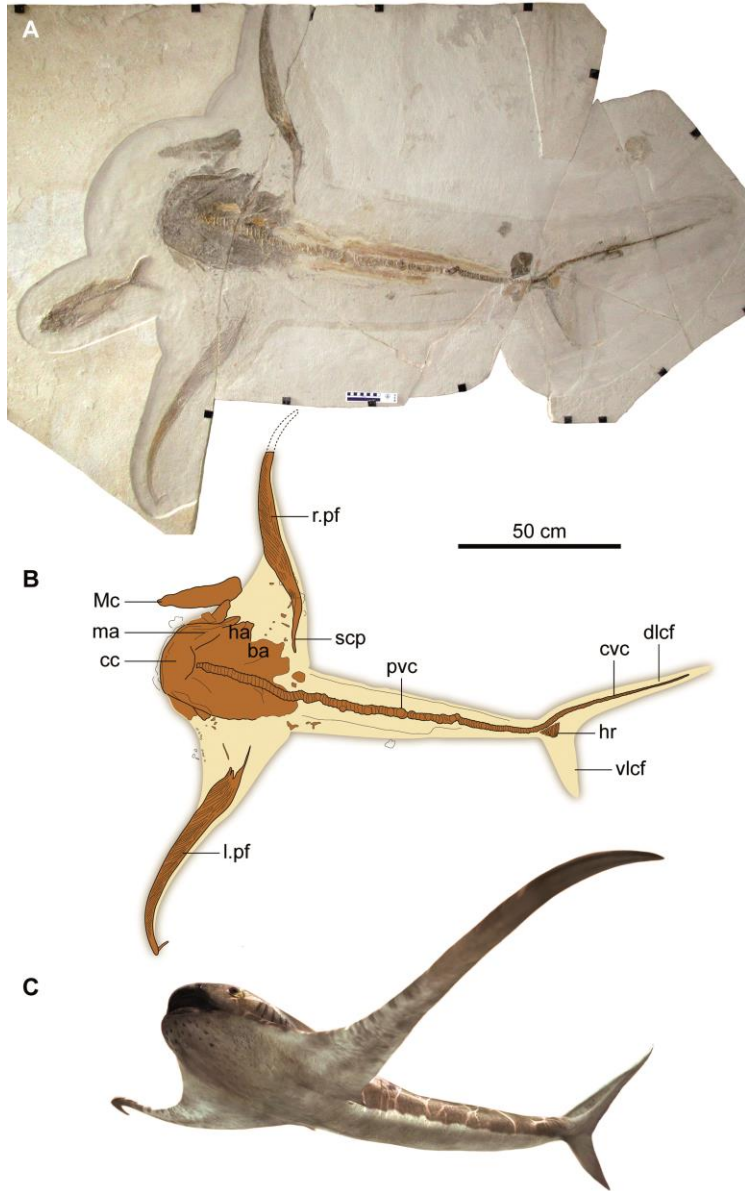


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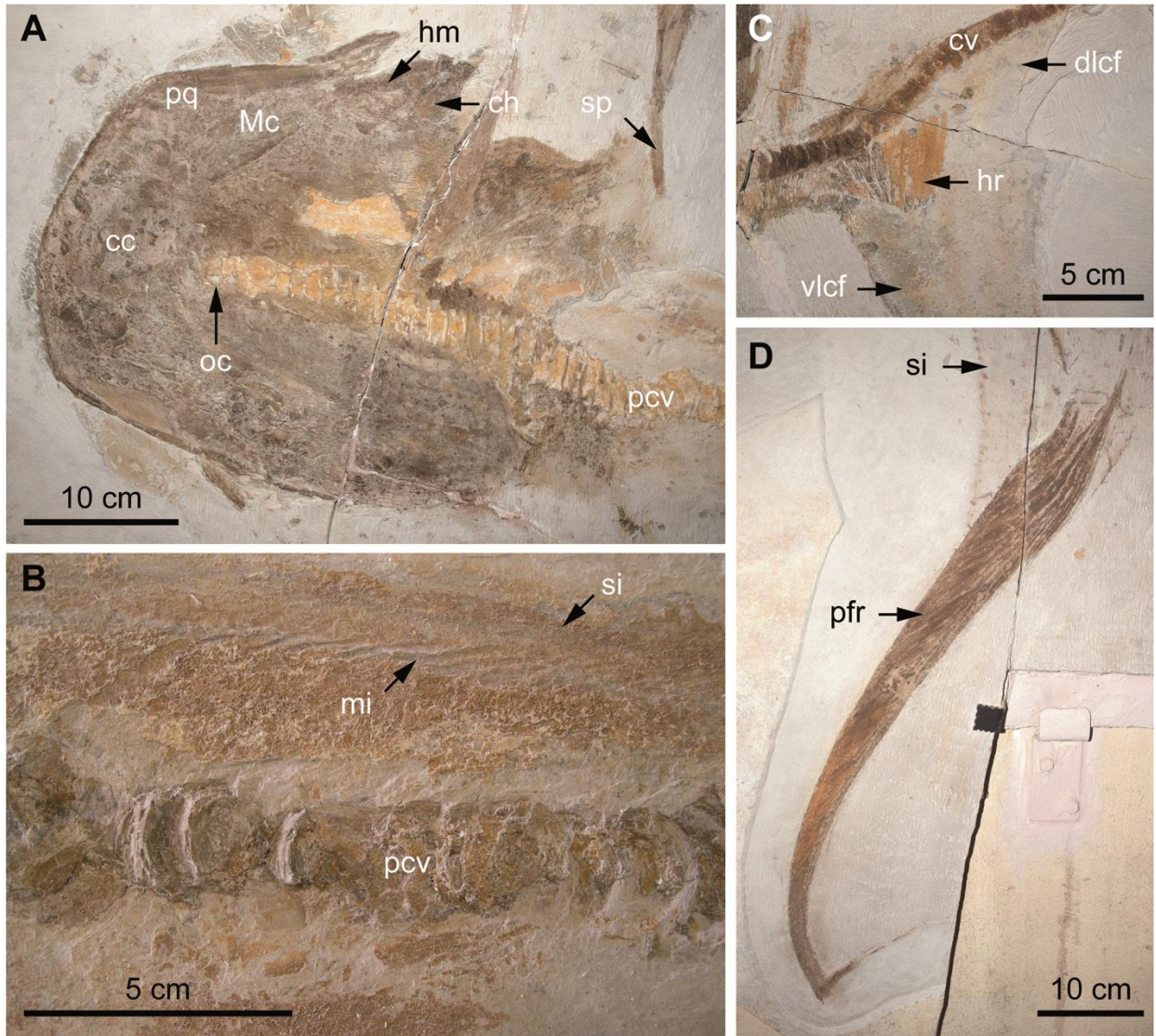
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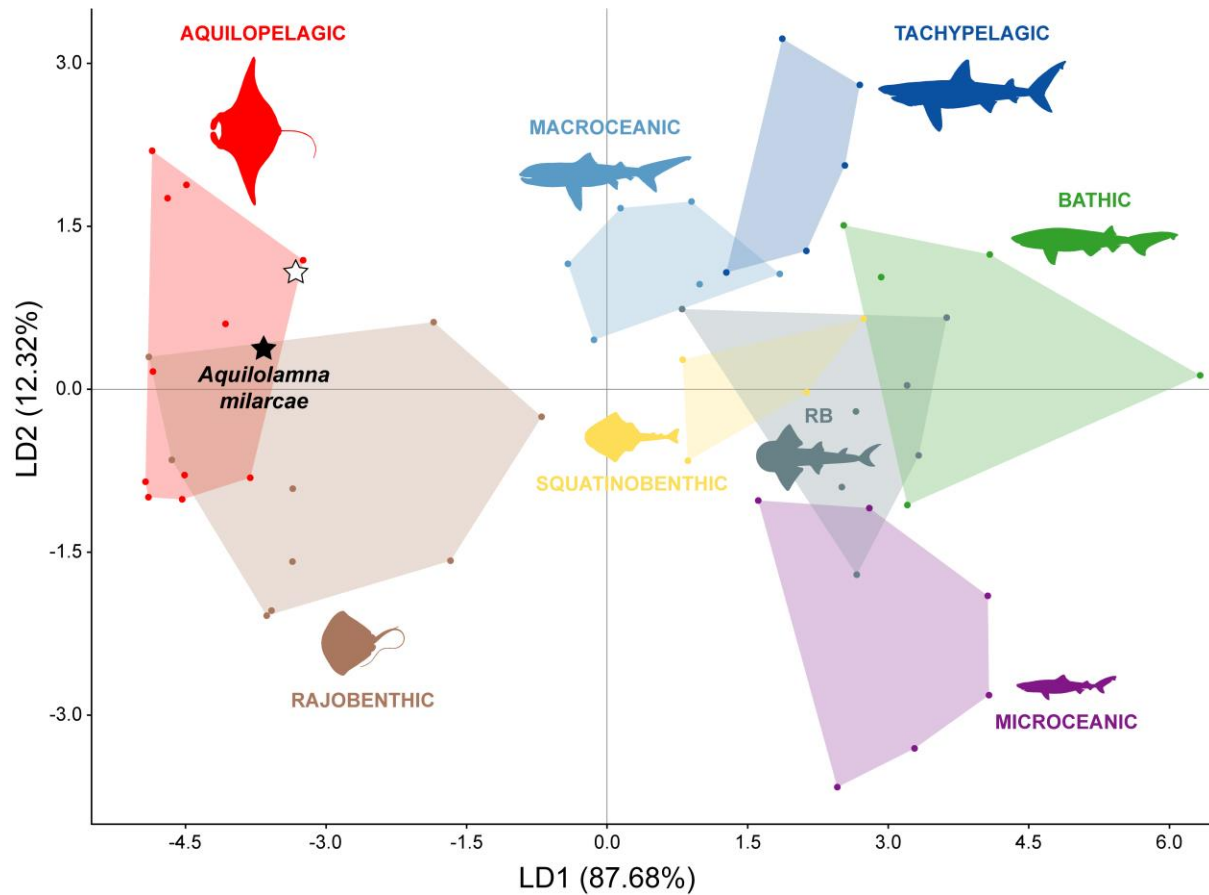
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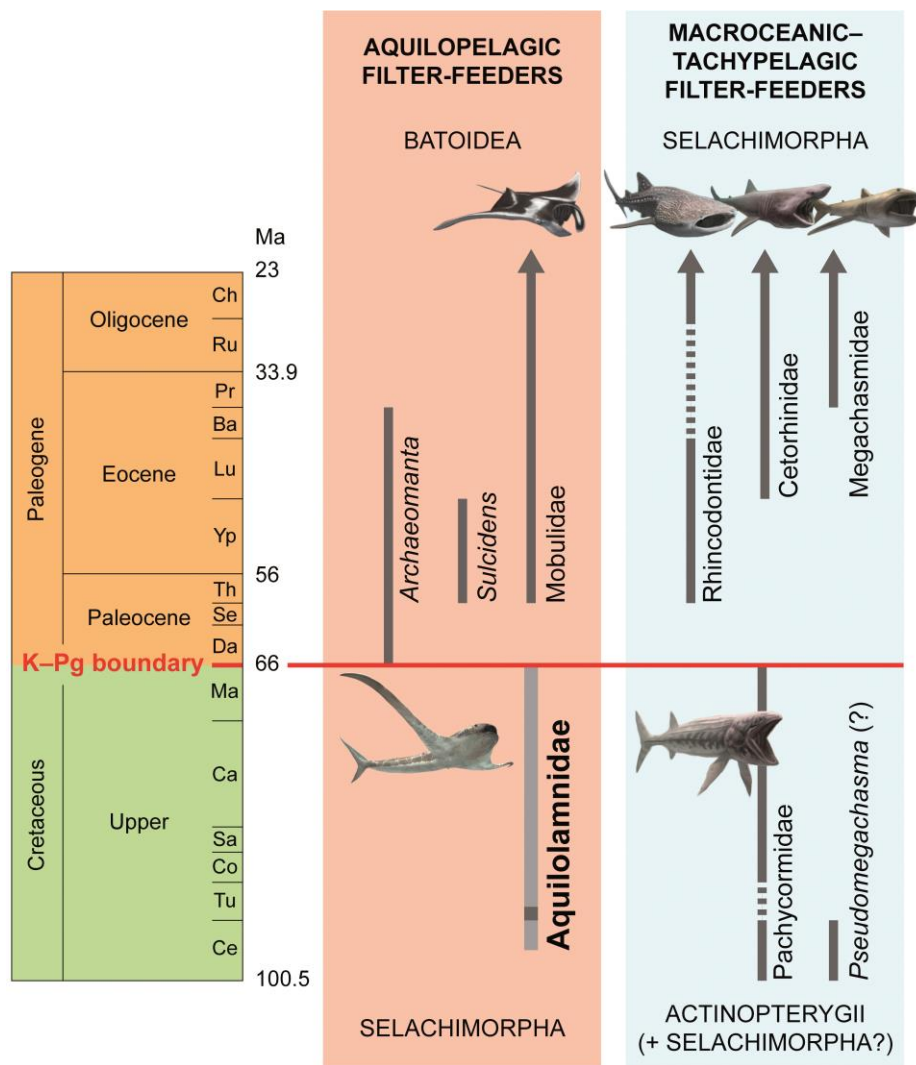
**Fig. 1. The holotype and reconstruction of *Aquilolamna milarcae*.** (A) Photograph and (B) interpretative line drawing of the holotype of *A. milarcae* (INAH 2544 P.F.17). Cartilaginous skeletal elements are shown in brown, and outline based on preserved soft tissue imprints in beige. ba, branchial arches; cc, chondrocranium; cvc, caudal vertebral column; dlc, dorsal lobe of the caudal fin; ha, hyoid arch; hr, hypochochordal rays; l.pf, left pectoral fin; ma, mandibular arch; Mc, Meckel's cartilage; r.pf, right pectoral fin; pvc, precaudal vertebral column; scp, scapular process; vlcf, ventral lobe of the caudal fin. (C) Life reconstruction of *A. milarcae*.



**Fig. 2. Anatomical details of *Aquilolamna milarcae*.** (A) Cephalic region. (B) Trunk region. (C) Caudal region. (D) Left pectoral fin. ch, ceratohyal; cv, caudal vertebrae; hm, hyomandibula; mi, muscle imprint; oc, occipital centrum; pcv, precaudal vertebrae; pfr, pectoral fin radials; pq, palatoquadrate; si, skin imprint; sp, scapular process.



**Fig. 3. Ecomorphotype of *Aquilolamna milarcae*.** Linear discriminant (LD) analysis based on log-transformed precaudal length (or disc length) and pectoral fin span (or disc width) measurements for 53 living elasmobranch species belonging to eight specialized ecomorphotypes, with *Aquilolamna milarcae* added. Note the position of *A. milarcae* (black star), clearly separated from other selachimorph taxa and suggesting an aquilopelagic-like ecomorphotype for this distinctive shark; this is confirmed when a 250-cm hypothetical maximum total length is used for *A. milarcae* (white star) (see supplementary materials). RB, rhinobenthic; light-blue silhouette, *Megachasma pelagios*; dark-blue silhouette, *Cetorhinus maximus*; green silhouette, *Hexanchus griseus*; purple silhouette, *Pseudocarcharias kamoharai*; yellow silhouette, *Squatina japonica*; gray silhouette, *Rhina ancylostoma*; red silhouette, *Mobula birostris*; brown silhouette, *Pteroplatytrygon violacea*.



**Fig. 4. Aquilopelagic and macroceanic–tachypelagic planktivorous fishes (Neoselachii and Actinopterygii) before and after the Cretaceous–Paleogene boundary.** The stratigraphic distribution (Cenomanian–Maastrichtian) of Aquilolamnidae is based on *Aquilolamna* (dark gray) and known occurrences of the enigmatic genera *Cretomanta* and *Platylithophycus* (light gray), two other possible members of the family; arrowed lineages represent still-living groups. Ba, Bartonian; Ca, Campanian; Ce, Cenomanian; Ch, Chattian; Co, Coniacian; Da, Danian; Lu, Lutetian; Ma, Maastrichtian; Pr, Priabonian; Ru, Rupelian; Sa, Santonian; Se, Selandian; Th, Thanetian; Tu, Turonian; Yp, Ypresian.