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# Cartilaginous fishes (Chondrichthyes)

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## Abstract

**Sharks, rays, chimaeras, and relatives (Class Chondrichthyes) comprise an important component of living vertebrate diversity, with two subclasses, 18 orders, ~55 families, and ~1200 species. Recent morphological studies have supported a position for rays deeply nested within sharks. Molecular analyses, however, support a basal divergence between rays and sharks. New molecular timing analyses presented here suggest that the earliest divergences in Chondrichthyes occurred deep in the Paleozoic, 460–300 million years ago (Ma), and that most living families originated before the end of the Cretaceous (66 Ma). If accurate, these dates imply large ghost ranges in the fossil record for many chondrichthyan groups.**

Living members of the Subclasses Holocephali (chimaeras, including ratfishes, spookfishes, and rabbitfishes, ~43 sp.) and Elasmobranchii (sharks, rays, skates, sawfishes, and guitarfishes, ~1125 sp.) together comprise the extant representatives of the Class Chondrichthyes (cartilaginous fishes) (1). Holocephali includes only a single living order with three families (1, 2). Elasmobranchs are more diverse, with ~17 orders and ~52 families (there is some disagreement in ordinal and familial limits, especially among rays) (1, 3–5). Chondrichthyans can be differentiated from their closest living relatives, Osteichthyes (bony vertebrates), by possession of a skeleton of prismatic cartilage and internal fertilization via modified male pelvic fins (claspers). Other characters common to the group are possession of placoid (tooth-like) scales and, in many lineages, a heterocercal tail fin. While most sharks and chimaeras have a generally cylindrical “fishlike” body form (Fig. 1), some sharks and all batoids (rays, skates, sawfishes, and guitarfishes) are

dorsoventrally flattened and benthic in habit. Although early chondrichthyans included many freshwater forms, living species are overwhelmingly marine in distribution, excluding a few euryhaline sharks and rays and some freshwater stingrays. Here, we review the relationships of the subclasses, orders, and families of cartilaginous fishes. Additionally, molecular divergence times of these groups are estimated from publicly available sequence data and presented.

The fossil record of Chondrichthyes has been considered excellent, based largely on rich deposits of dental material (6). The cartilaginous skeleton of Chondrichthyes fossilizes poorly; therefore, skeletal fossil material is much rarer (7). The earliest fossils assigned to Chondrichthyes are from the Silurian (444–416 Ma) (8). Fossils become more common in the Devonian (416–359 Ma), including many representatives of extinct groups. Based on these fossils, the Subclasses Holocephali and Elasmobranchii are estimated to have diverged by 410 Ma (8). Fossil evidence for modern representatives of these subclasses—Suborder Chimaeroidei (chimaeras) and Infraclass Neoselachii (sharks and rays)—does not occur until the Mesozoic (251–66 Ma) (9, 10). Living orders and families can be identified from the Jurassic (200–146 Ma) onward, with fossil evidence of most families before the end of the Mesozoic (7, 10).



**Fig. 1** A Great White Shark (*Carcharodon carcharias*) from near Isla Guadalupe, Mexico. Credit: T. Goss.

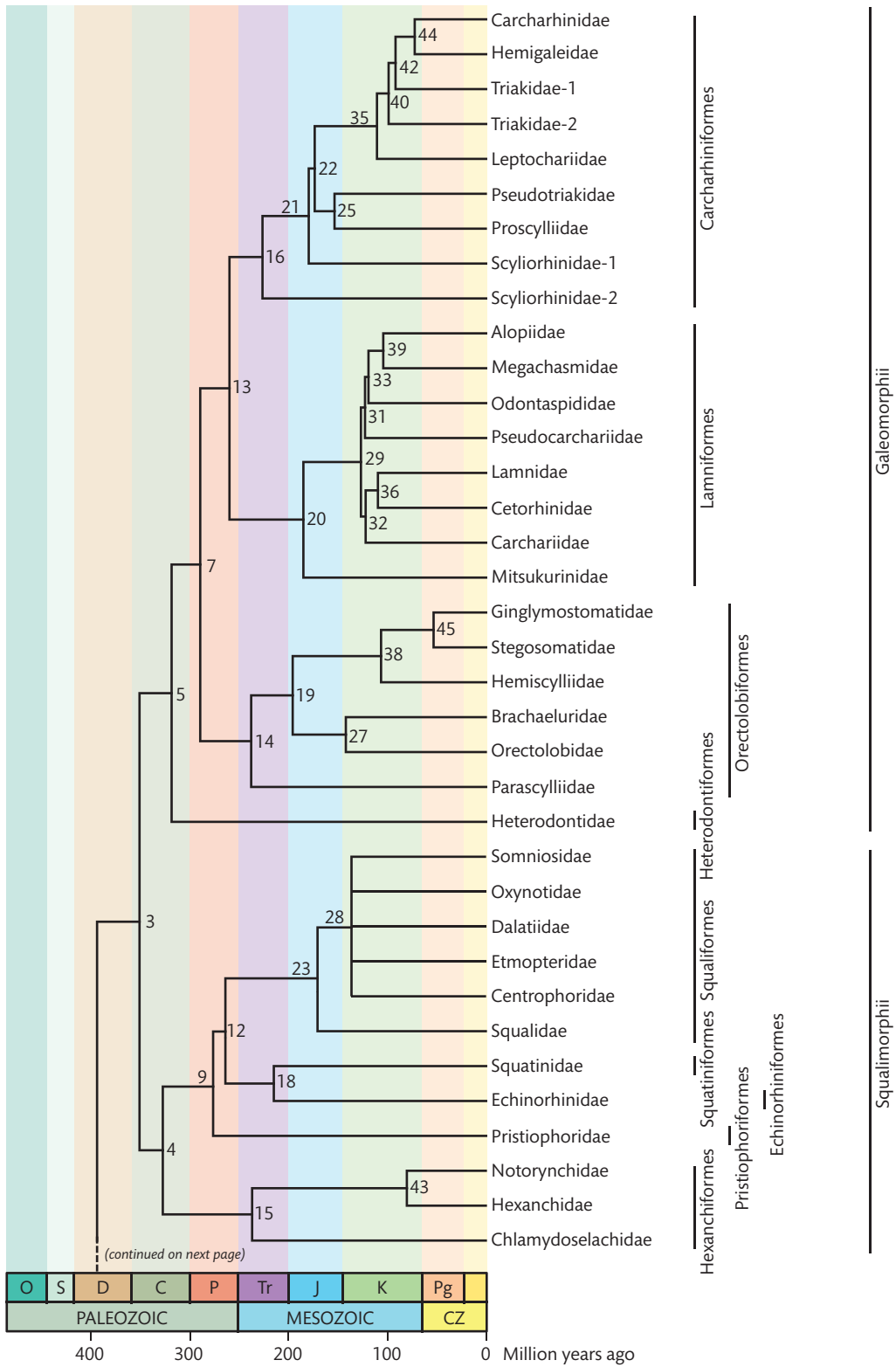
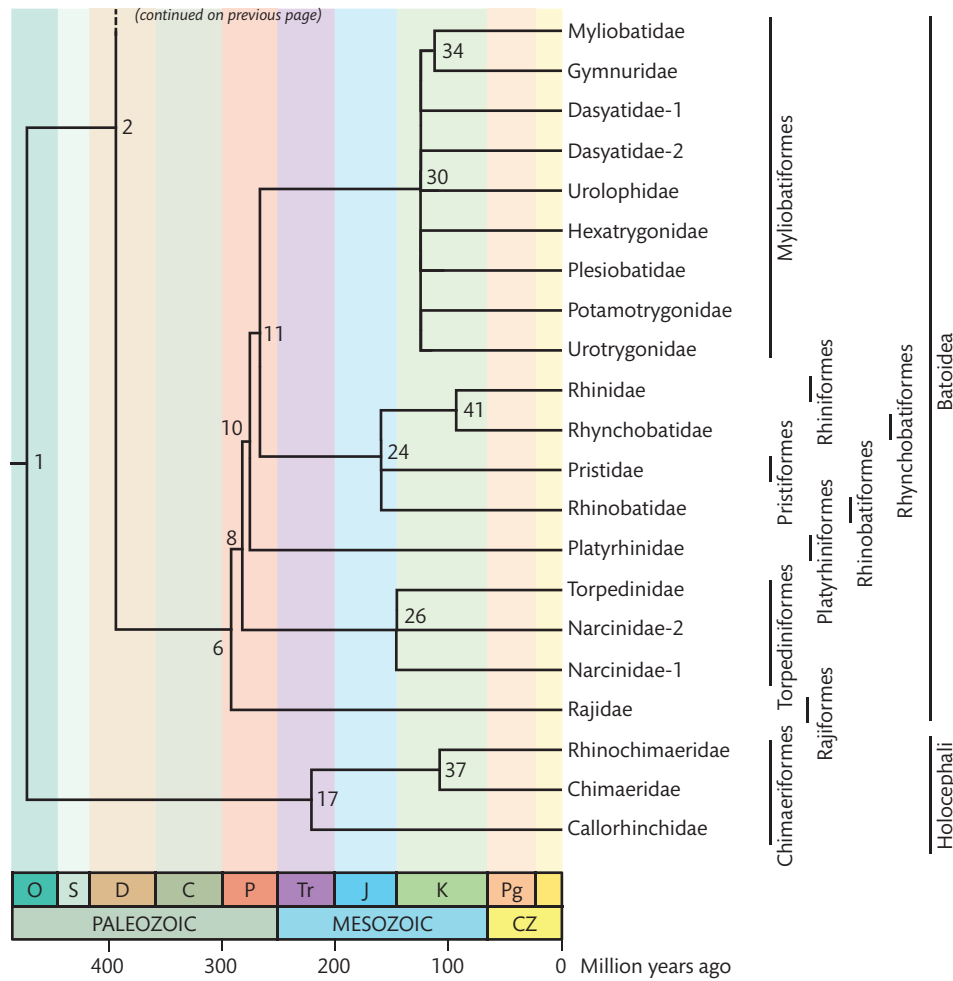


Fig. 2 Continues



**Fig. 2** A timetree of cartilaginous fishes (Chondrichthyes). Divergence times are from Table 1. Galeomorphii, Squalimorphii, and Batoidea comprise the Subclass Elasmobranchii. *Abbreviations:* C (Carboniferous), CZ (Cenozoic), D (Devonian), J (Jurassic), K (Cretaceous), O (Ordovician), P (Permian), Pg (Paleogene), S (Silurian), and Tr (Triassic). Codes

for paraphyletic and/or polyphyletic groups are as follows: Triakidae-1 (*Mustelus*), Triakidae-2 (*Triakis*), Scyliorhinidae-1 (Pentanchinae), Scyliorhinidae-2 (Scyliorhininae), Dasyatidae-1 (*Dasyatis*), Dasyatidae-2 (*Himantura*), Narcinidae-1 (Narcininae), and Narcinidae-2 (Narkinae).

Division of living cartilaginous fishes into Elasmobranchii and Holocephali is strongly supported by morphological analyses, as is uniting these groups to form Chondrichthyes (6, 9, 11). Within Holocephali, it is believed that Rhinochimaeridae and Chimaeridae form a group to the exclusion of Callorhynchidae (12). The relationships of the more species-rich elasmobranchs are more contentious. Early studies suggested a basal split between sharks and rays (13, 14). In 1992, Shirai published an extensive and influential analysis of morphological variation among sharks and rays in which he proposed a “Hypnosqualean hypothesis” wherein the batoids fall together with the dorsoventrally

compressed sawsharks (Pristiophoriformes) and angel sharks (Squatiniiformes) (15). These in turn group with the Orders Squaliformes, Hexanchiformes, and Echinorhiniformes in the Hypnosqualean clade. The Orders Lamniformes, Carcharhiniformes, Orectolobiformes, and Heterodontiformes are grouped as Galea (3, 4). Minor modifications to Shirai’s original 1992 hypothesis of elasmobranch interrelationships were made by de Carvalho in 1996 (4). This hypothesis remains the consensus from morphological data.

Because the monophyly of Chondrichthyes and reciprocal monophyly of Elasmobranchii and Holocephali have not been controversial and are supported by

**Table 1.** Divergence times (Ma) and their confidence/credibility intervals (CI) among cartilaginous fishes (Chondrichthyes), based on analyses presented here.

Timetree		Estimates					
Node	Time	This study (a)		This study (b)		This study (c)	
		Time	CI	Time	CI	Time	CI
		1	471	471	494-434	486	495-463
2	393	393	431-354	440	471-403	357	402-319
3	350	350	392-309	419	452-380	273	319-235
4	327	327	372-283	392	431-345	256	304-214
5	318	318	359-279	374	414-330	258	301-222
6	291	291	333-250	308	368-248	308	357-262
7	289	289	329-252	344	386-300	234	276-201
8	281	281	324-241	-	-	294	344-249
9	276	276	323-232	329	385-265	219	269-178
10	274	274	318-235	-	-	285	334-240
11	265	265	307-227	283	341-228	273	321-228
12	263	263	311-220	312	370-247	207	256-165
13	259	259	297-226	304	346-262	220	260-190
14	237	237	287-186	280	338-215	-	-
15	236	236	295-183	285	353-202	-	-
16	226	226	261-195	269	310-228	189	227-166
17	220	220	320-125	248	351-128	-	-
18	214	214	269-163	252	324-176	-	-
19	195	195	249-139	231	296-160	-	-
20	185	185	224-148	222	270-175	-	-
21	179	179	210-153	213	251-177	155	194-124
22	173	173	204-149	205	242-171	141	179-111
23	170	170	218-128	190	268-121	142	188-106
24	159	159	219-105	-	-	169	233-110
25	153	153	183-127	183	222-147	114	156-77
26	145	145	205-98	-	-	154	215-101
27	142	142	201-84	169	243-97	-	-
28	135	135	184-93	154	229-91	108	155-73
29	126	126	160-104	167	217-125	120	154-102
30	124	124	159-98	-	-	127	166-99
31	122	122	155-100	140	193-93	-	-
32	122	122	154-101	122	167-100	117	150-100
33	119	119	151-97	120	172-74	117	151-98
34	111	111	139-97	115	148-100	115	149-98
35	110	110	133-96	112	140-96	-	-
36	109	109	142-83	93.4	139-59	109	142-86
37	107	107	182-51	-	-	123	197-65
38	106	106	162-60	127	196-69	-	-
39	104	104	139-73	103	157-58	-	-

Table 1. Continued

Timetree		Estimates					
Node	Time	This study (a)		This study (b)		This study (c)	
		Time	CI	Time	CI	Time	CI
40	98.6	98.6	118–90	99	123–90	107	139–90
41	92.4	92.4	150–47	–	–	99.6	164–49
42	91.6	91.6	111–77	91	116–73	94.8	127–73
43	79.7	79.7	150–29	98.6	185–34	–	–
44	72.1	72.1	94–53	70.9	97–50	–	–
45	53.1	53.1	97–23	64.6	119–27	–	–

Note: Node times for the timetree are from the combined analysis of *RAG1*, *12S*, and *16S* alignments [shown with CI in column (a)]. Columns (b) and (c) present estimates from *RAG1* and *12S/16S* analyses, respectively.

numerous morphological characters, molecular studies have not been designed to specifically address these relationships. However, recent molecular studies that have included a broad enough sample of taxa to draw conclusions have supported the monophyly of these groups (16, 17). The interrelationships among the holocephalan families have not yet been addressed with molecular data. However, one mitochondrial gene study, using several holocephalan species as outgroups, has suggested that *Rhinochimaeridae* is embedded within *Chimaeridae* (18).

Most molecular studies have focused on elasmobranch interrelationships. Studies in the early to mid-1990s included too few taxa or sites to infer strong conclusions (19–21). Since 2003, elasmobranch relationships have been inferred with more comprehensive data sets of both nuclear and mitochondrial data, including most orders and families (7, 17, 18, 22, 23). These studies consistently (but weakly) reject the *Hypnosqualea* hypothesis, and instead suggest a basal divergence between sharks and batoids. Within the batoids, skates (*Rajiformes*) appear basal, followed by electric rays (*Torpediniformes*), then sawfishes and guitarfishes (*Pristiformes*, *Rhinobatiformes*), with stingrays (including butterfly, eagle, and manta rays; *Myliobatiformes*) being the most derived (7, 17, 21, 24). In these studies, most of the batoid orders were represented by only one or a few families, but there are numerous myliobatiform families. Analyses including these families have not found significantly supported relationships, although it appears that the butterfly rays and manta/eagle rays (*Gymnuridae* and *Myliobatidae*) form a group (24). No studies have yet

determined the relationships among the families of guitarfishes (*Rhinidae*, *Rhynchobatidae*), thornback rays (*Platyrrhinidae*), or panrays (*Zanobatidae*). Based on analysis of mitochondrial *12S ribosomal RNA (rRNA)* gene sequences available in GenBank, however, it appears that *Rhinidae* and *Rhynchobatidae* form a sawfish/guitarfish group with *Pristidae* and *Rhinobatidae*, while the position of thornback rays remains unresolved (results not shown).

Molecular studies of shark orders and families have led to a somewhat better understanding of relationships. The two major groups of sharks, galeomorphs and squalimorphs, are supported in most molecular studies (7, 17, 18, 22, 23, 25). Although morphologically part of *Galeomorphii*, the horn sharks (*Heterodontiformes*) are in a basal position in molecular phylogenies, and cluster with both *Squalimorphii* and *Galeomorphii*, depending on the data set. Within the *Galeomorphii*, the orders *Lamniformes* and *Carcharhiniformes* are generally recovered as closest relatives (7, 18, 23). In the *Squalimorphii*, *Squatiniiformes* (angel sharks), and *Echinorhiniformes* (bramble sharks) are close relatives, while cow sharks (*Hexanchiformes*) are outside all other squalimorph orders (7, 17, 18, 22, 23, 25). At the family level, the nominal groups *Scyliorhinidae* and *Triakidae* are estimated to be paraphyletic (26, 27) while the position of the hammerhead sharks is seen to fall within the *Carcharhinidae*. Accordingly, they are not considered a distinct family herein (24). *Carchariidae* and *Odontaspidae* (often considered a single family) form divergent branches in *Lamniformes* (7, 28). The interfamilial relationships of *Squaliformes* remain unexplored.

Until now, no timing analyses have been performed at or above the family level using molecular sequence data. Martin *et al.* (29) calculated the rate of evolution in sharks for *cytochrome b* sequences, but did not use this rate to infer times of divergence among different families. Batoid divergence times have been calculated, but only within families (30, 31). However, divergence times of higher chondrichthyan taxa have been inferred using immunological distances (32). These data suggest a very old divergence between sharks and batoids (392 Ma), and show divergences among sharks beginning 300 Ma.

Because there is no study reporting molecular divergence times of chondrichthyan families, we report herein the results of an analysis using published sequence data employing methodology described elsewhere (33). Sequence data were obtained from the most comprehensive available studies, using the nuclear protein-coding *RAG1* gene and the mitochondrial *12S* and *16S rRNA* genes (7, 18, 26). Additional *12S* and *16S* sequences of 15 batoid families were included from GenBank, as only Rajidae and Urolophidae were included in the study of Douady *et al.* (18). Together these data encompass a patchwork of sequences for 53 of 55 families of Chondrichthyes, excluding only Zanobatidae (panrays) and Rhincodontidae (whale shark). We note that while 53 of 55 families are represented, relatively few families are represented by all three genes, as a consequence of concatenating the data from three different studies with few overlapping taxa. In total, eight batoid families are represented only by *12S* sequences, and 15 shark families by only *RAG1* sequences, while 17 families include all data and the remaining 13 families include data for two genes. Tree topology was based on the studies that reported the sequences, although branches that are not resolved or conflict among these and other published molecular phylogenies were collapsed to polytomies for the final timetree (Fig. 2). These polytomies mainly affect Squaliformes and the batoid orders, as molecular studies including squaliform families have very short, poorly supported internal branches, and relationships within batoid orders are similarly poorly supported (7, 17, 22, 24). An analysis of batoid *12S* sequences used in the timetree did not find any significantly supported relationships within batoid orders (results not shown).

For the timetree, a combined analysis of all data was used. Analyses were also performed for the separate *RAG1* and *12S/16S* data sets (Table 1). An amniote (*Homo*), amphibian (*Xenopus*), actinopterygian (*Danio*), cyclostome (*Petromyzon*), and echinoderm (*Strongylocentrotus*) were used as outgroups, but these

taxa are not presented in the timetree. A total of 14 minimum (min.) and three maximum (max.) fossil constraints used to calibrate the timetree were obtained from the literature (7, 8, 10, 34). These include the divergence of Centrophoridae from other Squaliformes (min. 89 Ma); the divergence of Squatinidae and Echinorhinidae (min. 151 Ma); the divergence of Hexanchidae and Chlamydoselachidae (min. 176 Ma); the divergence of Triakidae and Carcharhinidae (min. 89 Ma); the divergence of Scyliorhinidae and other Carcharhiniformes (min. 165 Ma); the divergence of Carchariidae and Lamnidae (min. 100 Ma); the divergence of Parascyllidae and other Orectolobiformes (min. 100 Ma); the divergence of Heterodontidae and other sharks (min. 176 Ma); the divergence of Dasyatidae and Myliobatidae (min. 100 Ma); the divergence of Rajidae and other batoids (min. 176 Ma); the divergence of sharks and batoids (min. 190 Ma); the divergence of elasmobranchs and holocephalans (min. 410 Ma, max. 495 Ma); the divergence of amniotes and amphibians (min. 340 Ma, max. 370 Ma); and the divergence of actinopterygians and sarcopterygians (min. 435 Ma, max. 495 Ma).

Times of divergence obtained from the separate *RAG1* and *12S/16S* analyses differ markedly for most comparisons. Of the nodes shared between these two analyses, only the estimates for nodes within Batoidea and Lamniformes, and among derived carcharhiniform families (Carcharhinidae, Hemigaleidae, Triakidae), show noteworthy temporal concordance. In general the *RAG1*-based estimates are much older than those based on *12S/16S* sequences (Table 1). In some cases, the discrepancy in age estimates is quite large. For example, *RAG1* data result in times more than 100 million years older than *12S* and *16S* data for divergences among the major chondrichthyan groups (chimaeras, batoids, galeomorph sharks, and squalimorph sharks). This may be caused by the large amount of branch length variation in the *RAG1* data set (7), while the *12S* and *16S* data have relatively less variation (18). Time estimates from the combined analysis, discussed later, are generally between values from the individual analyses. Conclusions based on the combined analysis must be tempered by the knowledge that not all genes are present for all taxa (i.e., a large amount of missing data) and the large differences in times of deep branches obtained with *RAG1* as compared to *12S* and *16S* data.

Notwithstanding the discrepancies in age estimates among genes, the timetree (Fig. 2) suggests that holocephalans and elasmobranchs diverged in the Ordovician, 471 (494–434) Ma. Fossil evidence indicates

that these subclasses had diverged by at least 410 Ma (8). The living families of Holocephali apparently diverged in the Mesozoic (251–66 Ma). The divergence of sharks and batoids is inferred to have occurred in the Devonian, 393 (431–354) Ma. This date is more than 100 million years older than the first appearance of neoselachian elasmobranchs in the fossil record, and over 200 million years older than unambiguous evidence of modern orders (10). If these estimates are accurate, one must infer a large ghost range in the fossil record for early divergences within modern elasmobranchs. Times obtained with only *12S* and *16S* data are substantially younger, at 357 (402–319) Ma, but still suggests a large ghost range. Our analyses of the presented molecular data suggest that ordinal divergences were largely completed by the beginning of the Triassic, 251 Ma (whether considering the combined, *RAG1*, or *12S/16S* analyses) and that living families diverged throughout the Mesozoic, but especially during the Cretaceous (146–66 Ma). With the possible exceptions of Ginglymostomatidae (nurse sharks) and Stegostomatidae (zebra shark), all elasmobranch families are estimated to have appeared by the end of the Cretaceous.

Because of these apparent ancient divergences, oceanic habits of chondrichthyans, and large differences in time estimates depending upon analysis used, it is difficult to infer the biogeographic history of the living families. Most chondrichthyan families today are cosmopolitan in distribution, or found in widely divergent (i.e., separate ocean basins) areas of suitable habitat. For the many families with pelagic or deep-sea distributions, it may be impossible to infer biogeographic history due to the worldwide nature of their habitats. Extensive plate tectonic activity has contributed to substantial changes in ocean basins since the divergence of most families of Chondrichthyes. Although all ocean floor is geologically young (Mesozoic and Cenozoic), oceans differ in age when considered as bodies of water (aquatic habitat). For example, the Atlantic is relatively young (~150 Ma) compared with the Pacific (35, 36), which may explain why no living families are restricted to the Atlantic. Other families may have their origins in basins that no longer exist. For example, many inshore, benthic families, such as batoids, diverged in the Cretaceous (based on the results of the presented analyses, as well as fossil data) when the sea level was much higher and shallow continental seaways covered large portions of North America and Asia. At the same time, the now-gone Tethys Sea existed between the northern and southern continents (35, 36). These water bodies may have

been the early sites of diversification within batoids and inshore sharks. The timetree (Fig. 2) is compatible with previous interpretations of shark evolution based on the fossil record, including a major radiation of neoselachian sharks in the Jurassic and Cretaceous (200–66 Ma), possibly related to a parallel radiation of prey, actinopterygian fishes (37). In order to better understand the factors leading to diversification in Chondrichthyes, additional fossil (especially skeletal) and paleogeographic data will be needed to complement the emerging molecular phylogenetic data. In addition, more comprehensive molecular data, including nuclear gene loci that exhibit more uniform rates of evolution among lineages, are needed to resolve poorly known parts of the chondrichthyan tree and to estimate better-constrained times of divergence.

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## References

1. L. J. V. Compagno, D. A. Didier, G. H. Burgess, in *Sharks, Rays, and Chimaeras, the Status of the Chondrichthyan Fishes*, S. L. Fowler *et al.*, Eds. (IUCN/SSC Shark Specialist Group, Gland, 2005), pp. 4–11.
2. D. A. Didier, in *Biology of Sharks and their Relatives*, J. C. Carrier, J. A. Musick, M. R. Heithaus, Eds. (CRC Press, Boca Raton, 2004), pp. 115–138.
3. S. Shirai, in *Interrelationships of Fishes*, M. L. J. Stiassny, L. R. Parenti, G. D. Johnson, Eds. (Academic Press, San Diego, 1996), pp. 9–34.
4. M. R. de Carvalho, in *Interrelationships of Fishes*, M. L. J. Stiassny, L. R. Parenti, G. D. Johnson, Eds. (Academic Press, San Diego, 1996), pp. 35–62.
5. J. D. McEachran, K. A. Dunn, T. Miyake, in *Interrelationships of Fishes*, M. L. J. Stiassny, L. R. Parenti, G. D. Johnson, Eds. (Academic Press, San Diego, 1996), pp. 63–84.
6. J. G. Maisey, *Zool. J. Linn. Soc.* **82**, 33 (1984).
7. J. G. Maisey, G. J. P. Naylor, D. J. Ward, in *Mesozoic Fishes 3—Systematics, Paleoenvironments and Biodiversity*, G. Arriata, A. Tintori, Eds. (Verlag Dr. Friedrich Pfeil, München, 2004), pp. 17–56.
8. M. I. Coates, S. E. Sequeira, in *Major Events in Early Vertebrate Evolution: Paleontology, Phylogeny, Genetics and Development*, P. E. Ahlberg, Ed. (Taylor & Francis, London, 2001), pp. 241–262.



9. E. D. Grogan, R. Lund, in *Biology of Sharks and their Relatives*, J. C. Carrier, J. A. Musick, M. R. Heithaus, Eds. (CRC Press, Boca Raton, 2004), pp. 3–32.
10. C. J. Underwood, *Paleobiology* **32**, 215 (2006).
11. J. G. Maisey, *Cladistics* **2**, 201 (1986).
12. D. A. Didier, *Am. Mus. Nov.* **3119**, 1 (1995).
13. H. W. Bigelow, W. C. Schroeder, in *Fishes of the Western North Atlantic, Part I*, J. Tee-Van *et al.*, Eds. (Yale University Press, New Haven, 1948), pp. 59–576.
14. H. W. Bigelow, W. C. Schroeder, in *Fishes of the Western North Atlantic, Part II*, J. Tee-Van *et al.*, Eds. (Yale University Press, New Haven, 1953), pp. 1–514.
15. S. Shirai, *Squalean Phylogeny: A New Framework of “Squaloid” Sharks and Related Taxa* (Hokkaido University Press, Sapporo, 1992), pp. 151.
16. U. Arnason, A. Gullberg, A. Janke, *Zool. Scripta* **30**, 249 (2001).
17. J. Mallatt, C. J. Winchell, *Mol. Phylogenet. Evol.* **43**, 1005 (2007).
18. C. J. Douady, M. Dosay, M. S. Shivji, M. J. Stanhope, *Mol. Phylogenet. Evol.* **26**, 215 (2003).
19. G. Bernardi, G. A. Powers, *Mol. Phylogenet. Evol.* **1**, 161 (1992).
20. K. A. Dunn, J. F. Morrissey, *Copeia* **1995**, 526 (1995).
21. T. Kitamura *et al.*, *Fish. Sci.* **62**, 340 (1996).
22. C. J. Winchell, A. P. Martin, J. Mallatt, *Mol. Phylogenet. Evol.* **31**, 214 (2004).
23. G. J. P. Naylor, J. A. Rayburn, O. Fedrigo, A. Lopez, in *Reproductive Biology and Phylogeny of Chondrichthyes: Sharks, Batoids, and Chimaeras*, W. C. Hamlett, Ed. (Science Publishers, Enfield, 2005), pp. 1–25.
24. K. A. Dunn, J. A. McEachran, R. L. Honeycutt, *Mol. Phylogenet. Evol.* **27**, 259 (2003).
25. B. A. Human, E. P. Owen, L. J. V. Compagno, E. H. Harley, *Mol. Phylogenet. Evol.* **39**, 384 (2006).
26. S. P. Iglesias, G. Lecointre, D. Y. Sellos, *Mol. Phylogenet. Evol.* **34**, 569 (2005).
27. J. A. Lopez, J. A. Ryburn, O. Fedrigo, G. J. P. Naylor, *Mol. Phylogenet. Evol.* **40**, 50 (2006).
28. A. P. Martin, A. T. Pardini, L. R. Noble, C. S. Jones, *Mol. Phylogenet. Evol.* **23**, 205 (2002).
29. A. P. Martin, G. J. P. Naylor, S. R. Palumbi, *Nature* **357**, 153 (1992).
30. N. R. Lovejoy, E. Bermingham, A. P. Martin, *Nature* **396**, 421 (1998).
31. E. Valsecchi *et al.*, *J. Evol. Biol.* **18**, 436 (2005).
32. R. Lawson *et al.*, *J. Zool. Lond.* **237**, 101 (1995).
33. M. P. Heinicke, W. E. Duellman, S. B. Hedges, *Proc. Nat. Acad. Sci. U.S.A.* **104**, 10092 (2007).
34. J. E. Blair, S. B. Hedges, *Mol. Biol. Evol.* **22**, 2275 (2005).
35. A. G. Smith, D. G. Smith, B. M. Funnell, *Atlas of Mesozoic and Cenozoic Coastlines* (Cambridge University Press, Cambridge, 1994), pp. 99.
36. F. M. Gradstein, J. G. Ogg, A. G. Smith, Eds., *A Geologic Time Scale 2004* (Cambridge University Press, Cambridge, 2004), pp. 610.
37. M. J. Benton, *Vertebrate Paleontology* (Blackwell Science, Oxford, 2000), pp. 452.