

2. Fossil Record and Origin of Squaliform Sharks

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Abstract.—Squaliform sharks constitute a monophyletic group of predominantly deep-water neoselachians. Their fossil record mainly consists of isolated teeth; complete skeletons or skeletal remains are very rare. The quality of the fossil record of squaliform sharks is analyzed using a phylogenetic hypothesis based on a supertree to establish the timing of cladogenetic events, those related to descent from a common ancestor, and gaps in the fossil record. The supertree is the most inclusive estimate of squaliform interrelationships that has been proposed to date and contains 23 fossil and extant members of all major groups. In addition, the simple completeness metric is used to examine the quality of the fossil record of squaliforms as an independent measure. Although different (48% and 61%, respectively), both measures indicate that the fossil record of squaliforms is very incomplete considering that most living and extinct squaliforms are deep-water sharks and corresponding sediments are very scarce. Gaps in the fossil record range from 5 to 100 million years. The most basal and stratigraphically oldest group within Squaliformes consists of *Squalus* and †*Protosqualus*¹. The phylogenetic hypothesis indicates a gap in the fossil record of *Squalus* spp. of about 25–30 million years. Our results show a postJurassic origination of squaliforms in the shallow waters of the northern Tethyal margin. The hypothetical ancestor of squaliforms is characterized by two dorsal fin spines and absence of dignathic heterodonty (the morphology of upper and lower teeth differs significantly). Lower teeth are characterized by a slightly oblique basal root face and overlapping upper teeth. Although disappearance and appearance of organisms is a fact of life, the very long geologic range and success of *Squalus* highlights the need for very careful management of its current population crisis, which is due to causes that never occurred before in Earth's history—the anthropogenetic impact.

Introduction

Dogfish sharks *Squalus acanthias* (the Squaliformes) are a highly diverse group of neoselachian sharks occurring in coastal and oceanic, cool temperate, and deep tropical waters worldwide (Compagno 1999; Musick et al. 2004; Figure 1). They are common in the deep sea and include the largest predators that thrive in these ecosystems (Gartner et al. 1997). Most species are benthonic but many mesopelagic forms undertake nightly vertical migrations in search for food (Martin and Treberg 2002).

Although great progress has been made in the last few years with regard to resolving the phylogenetic relationships of neoselachian sharks (e.g., Shirai 1992; Carvalho 1996; Carvalho and Maisey 1996; Maisey et al. 2004), the monophyly and interrelationships of Squaliformes are still debated (e.g., Maisey 1980; Shirai 1992, 1996; Carvalho 1996). We follow Carvalho's (1996) arguments and deem squaliform sharks to constitute a monophyletic group, which is supported by four homoplastic characters (those being similar but not derived from a common ancestor): subnasal fenestra present; constrictor hyoideus dorsalis inserting partly on hyomandibula and partly on palatoquadrate; linearly arranged tooth rows with teeth overlapping each other; and dorsal fin

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¹ † = extinct

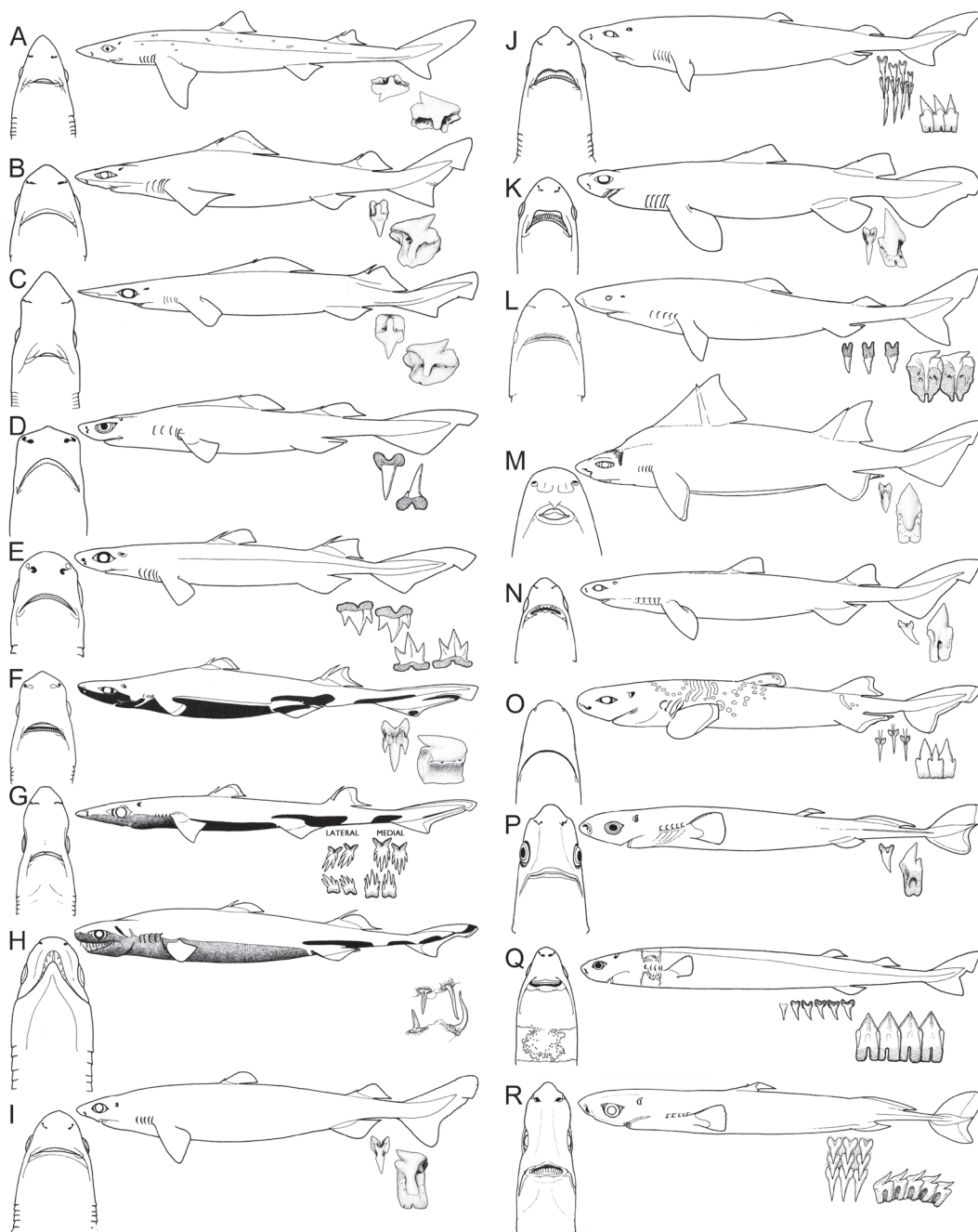


Figure 1.—Representative extant squaliform sharks considered in this study: (A) *Squalus acanthias*, (B) *Centrophorus granulosus*, (C) *Deania calcea*, (D) *Aculeola nigra*, (E) *Centroscyllium fabrici*, (F) *Etmopterus spinax*, (G) *Miroscyllium shekoi*, (H) *Trigonognathus kabeyai*, (I) *Centroscymnus coelelepis*, (J) *Scymnodalatis sherwoodi*, (K) *Scymnodon ringens*, (L) *Somniosus microcephalus*, (M) *Oxynotus centrina*, (N) *Dalatias licha*, (O) *Euprotomicroides zantedeschia*, (P) *Euprotomicrus bispinatus*, (Q) *Isistius labialis*, (R) *Squaliolus laticaudus*. Drawings of teeth in Figures A–C, E, I, K, M–N, and P from Ledoux (1970). Drawings of body outlines modified from Compagno et al. (2005) if not otherwise stated. Figures not to scale.

skeleton composed of basal cartilage and fin spine. Six families (Squalidae, Centrophoridae, Etmopteridae, Somniosidae, Oxynotidae, and Dalatiidae), with 98 extant species, are recognized at present within the order Squaliformes. The monogeneric family Echinorhinidae is excluded from squaliforms based on odontology (Pfeil 1983; Herman et al. 1989), skeletal features (Shirai 1992; Carvalho 1996), and molecular evidence (Bernardi and Powers 1992).

The fossil record of squaliforms consists predominantly of isolated teeth and dates back to the Barremian (Early Cretaceous), ca. 125 million years ago (Cappetta 1987). Articulated fossil skeletons are only known from Late Cretaceous limestone deposits of Lebanon (e.g., Cappetta 1980; Figure 2). Fossil selachian taxonomy based on teeth is useful for reconstructing the fossil record of past diversity, but is rarely utilized to infer phylogenetic relationships, mainly due to the fact that convergences in tooth structures are common. Moreover, the character sets from teeth that can be coded in cladistic analyses are generally limited. In this respect, squaliforms are exceptional, because their dentition typically displays high morphological variation and specialization (Figures 1 and 3). Adnet and Cappetta (2001) were the first to use these differences to propose a phylogenetic hypothesis of fossil and extant squaliform sharks based on odontological characters and cladistic principles, and also the first to discuss the length of ghost-lineages (lineages inferred by gaps in the fossil record) for the clades. Although their work certainly represents the most comprehensive phylogenetic analysis based exclusively on dental characters for any neoselachian group including fossil and extant members, there are major problems with coding based on outgroup composition. The outgroup we used was considered monophyletic and includes some taxa with *Pristiophorus* as the root of the cladogram (conversely to Adnet and Cappetta 2001, who used a basal polytomy). Consequently, all its character states were changed to the plesiomorphic condition [0]. This procedure required the re-coding of ten characters of Adnet and Cappetta (9, 10, 14, 15, 18, 19, 23, 26, 27, 29). The hypothetical background of supertree analyses is explained in Baum and Ragan (2004). The resulting supertree, which is based on several partial phylogenetic hypotheses, is the most inclusive hypothesis combining fossil and extant taxa to date, and so is employed to establish the quality of the fossil record of squaliform sharks. The purpose of this paper is twofold: to examine

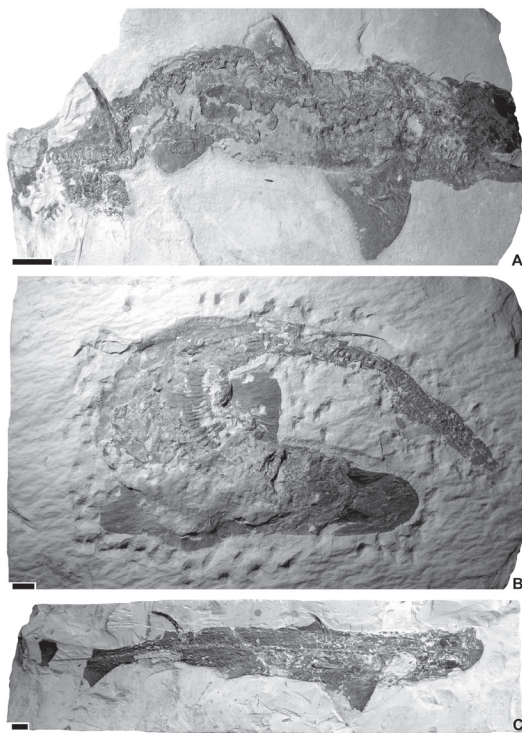


Figure 2.—Articulated fossils of squaliform †*Centrosqualus primaevus* from Santonian (Upper Cretaceous) of Sahel Alma, Lebanon: (A) Specimen BMNH P. 9469. (B) Specimen BMNH P. 4859. (C) Specimen BMNH P. 4779. All scale bars equal 1.0 cm.

the quality of the fossil record of squaliform sharks and to discuss the fossil record and origin of the Squaliformes and the genus *Squalus*, which is the most plesiomorphic member of this order.

Methods and Data

The quality of the fossil record of squaliform sharks is tested by applying the simple completeness metric (SCM) of Benton (1987) and using the supertree of squaliform interrelationships. This approach is advantageous because it disregards cladogenetic events but considers Lazarus taxa that must have been present in a certain stage (based on older and younger occurrences of this taxon) but have not yet been recorded from the fossil record. The SCM is assumed to be a measure that considers several factors contributing to the completeness of the fossil record, including sediment volume deposited during

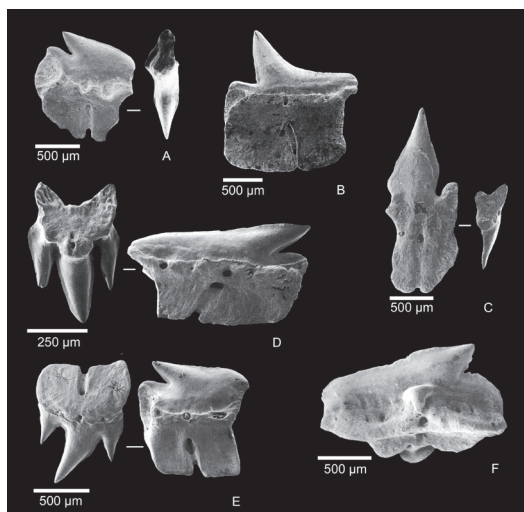


Figure 3.—Representative teeth of fossil squaliforms. (A) Lower and upper tooth of †*Cretascymnus westfalicus*. Modified from Thies and Müller (1993, fig. 14b) and Müller (1989, pl. 23, fig. 3b). (B) Lower tooth of †*Eoetmopterus supracretaceus*. Modified from Thies and Müller (1993, fig. 6b). (C) Lower and upper tooth of †*Paraphorosoides ursulae*. Modified from Thies and Müller (1993, figs. 10b, 8b). (D) Upper and lower tooth of †*Microetmopterus wardi*. Modified from Siverson (1993, pl. 3 figs. 3, 11). (E) Upper and lower tooth of †*Proetmopterus hemmooriensis*. Modified from Siverson (1993, pl. 4, figs. 2, 6). (F) Lower tooth of †*Protosqualus* cf. *P. sigei*. Modified from Müller and Diedrich (1991, pl. 15, fig. 6a).

a given stage, area of exposure, and intensity of palaeontological research (Benton 1987, 1998; Fara and Benton 2000). For calculating the quality of the fossil record, all known fossil occurrences are summed up and then divided by the sum of all known plus all Lazarus occurrences.

For the supertree, we combined the topologies of eleven phylogenetic hypotheses using three types of data sets: odontological characters (Adnet and Cappetta 2001; unpublished data from the authors), morphological features (Carvalho 1996; Carvalho and Maisey 1996; Shirai 1996), molecular data (Douady et al. 2003; Maisey et al. 2004; Winchell et al. 2004; unpublished data from the authors), and combined morphological–molecular data (Maisey et al. 2004). The supertree was constructed using the MPR approach (Baum and Ragan 2004) at genus level, including 23 ingroup taxa, six of which are known only from the fossil record (†*Cretascymnus*,

†*Eoetmopterus*, †*Microetmopterus*, †*Paraphorosoides*, †*Proetmopterus*, and †*Protosqualus*). *Echinorhinus* or a combined outgroup was used to root the source trees.

In this analysis, each node (branching point between two taxa) is treated as a character. For the exact procedure see Baum and Ragan (2004). Currently, the supertree approach provides the best prospect to combine information regarding fossil organisms, which are known only from isolated skeletal parts, with that of extant taxa for which many anatomical and molecular data are available. Here, the supertree is used to assume that each node represents a cladogenetic event and that sister groups with the same ancestor, characterized by a dichotomy, must have originated at the same time. The oldest representatives of both sister taxa should occur in the same sediment layer if the fossil record is complete. To quantify the fossil record, we summed up the actual stratigraphic range of all lineages and the minimal time of the evolutionary lines based on the ghost-lineages. Both values are added and then divided by the sum of actual occurrences. The result indicates the completeness of the fossil record as a percentage.

Results

Phylogenetic hypothesis

The supertree resulting from combining published partial phylogenetic hypotheses (Figure 4) represents the most inclusive estimate of squaliform interrelationships to date, showing 23 out of about 35 known fossil and extant genera. The results presented here are in general agreement with most published phylogenetic hypotheses and differ only slightly from others. According to our hypothesis, Squaliformes is composed of six monophyletic groupings of family rank; Squalidae (*Squalus* and †*Protosqualus*) is separated at the deepest branching level from all other squaliforms according to this reconstruction. The arrangement of Squalidae and Centrophoridae in our supertree differs from that of previously published phylogenetic trees but the basal position of Squalidae and Centrophoridae in our study is congruent with Carvalho (1996) and Carvalho and Maisey (1996).

Our study shows a sister group relationship between Oxynotidae and Somniosidae, which is also found by Carvalho and Maisey (1996) and Shirai (1996). However, Somniosidae sensu Shirai (1996) is not monophyletic, according to our hypothesis.

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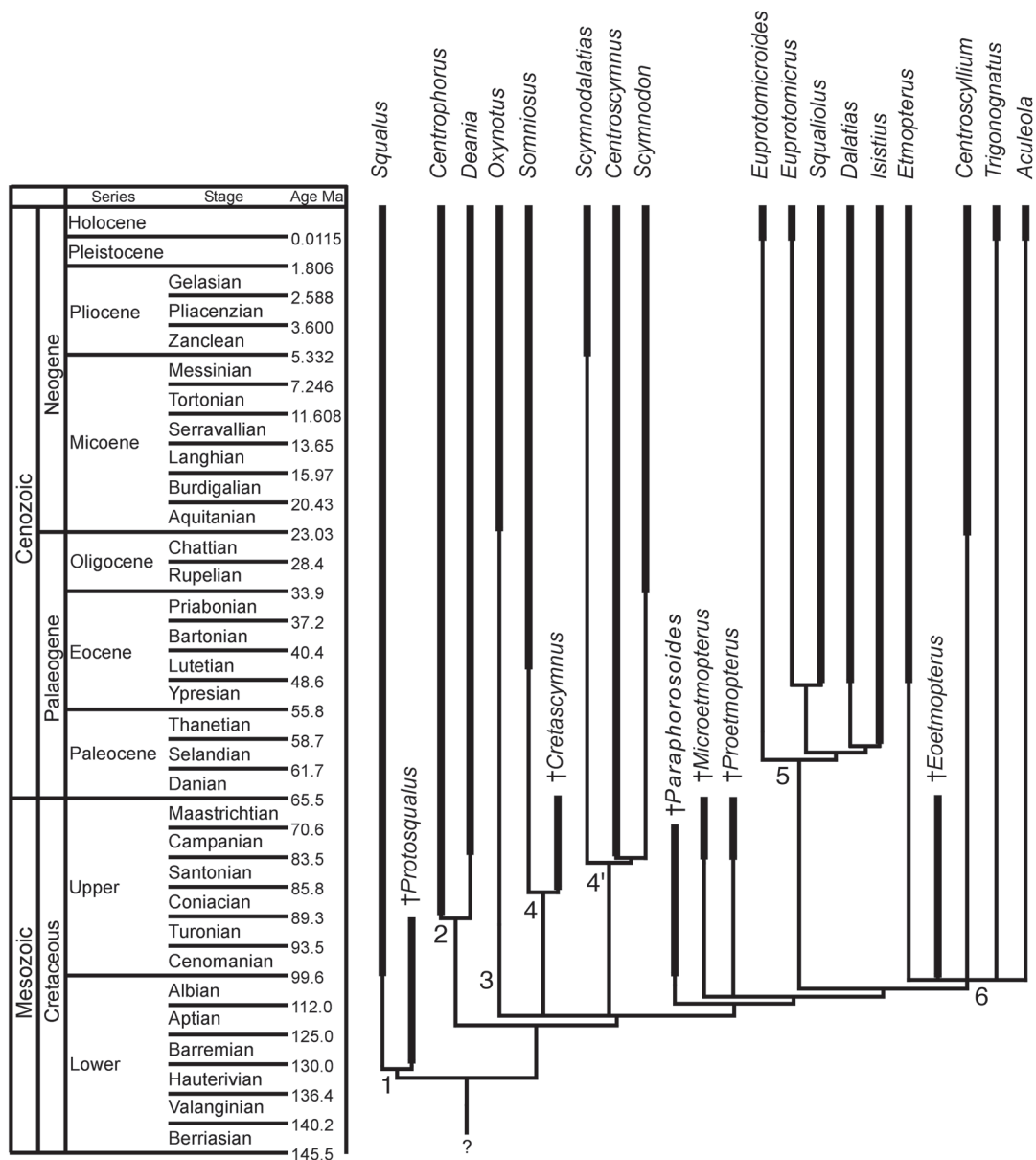


Figure 4.—Phylogenetic supertree resulting from combination of published partial phylogenetic hypotheses and stratigraphic information. Thick bars correspond to confirmed stratigraphic distribution of taxa, thin bars represent ghost-lineages (gaps in fossil records). First occurrences of taxa are used to infer minimum ages of cladogenetic events. Stratigraphic ages are from Gradstein et al. (2004). Tree length is 110 steps. The consistency index (CI) of each MPPT is 0.73, the retention index (RI) is 0.86. Numbers indicate monophyletic groups. 1 = Squalidae, 2 = Centrophoridae, 3 = Oxynotidae, 4 + 4' = Somniosidae (sensu Shirai 1996, Adnet and Cappetta 2001), 5 = Dalatiidae, 6 = Etmopteridae. Note the unresolved relationships of †*Microetmopterus* and †*Proetmopterus* and within Etmopteridae. Squalidae is the sister group to a clade containing all other squaliforms.

The interrelationships of Etmopteridae (Figure 4) are unresolved in this phylogenetic tree, but the composition resembles that seen in previous analyses. The assignment of †*Eoetmopterus* to Etmopteridae (Müller and Schöllmann 1989) is based on odontological evidence alone and indicates that this group originated in the Early Cretaceous, some 110 million years ago. Cladogenesis between Dalatiidae and Etmopteridae must have occurred some 95 million years ago, although the fossil record of Dalatiidae extends back only to the Paleocene. The stratigraphic age of †*Eoetmopterus* also supports a similar time of origination for Dalatoidei (Figure 4). The phylogenetic hypothesis presented here indicates a postJurassic origin of Squaliformes.

Fossil record

Stratigraphic occurrences of squaliforms were extracted from a vast literature record (e.g., Cappetta 1987; Cappetta et al. 1993; Underwood and Mitchell 1999, 2004; Adnet and Cappetta 2001 and references therein; Cappetta and Adnet 2001; and Kriwet and Benton 2004). The data are summarized in Appendix 1. Calibration of taxon ranges based on the supertree of squaliforms with the fossil record (Figure 4) produces approximately 800 million years of known fossil ranges of the order and 873 million years of evolutionary lines based on ghost-lineages, indicating a significant Lazarus effect (Jablonski 1986).

The calculated relative completeness of the fossil record of squaliform genera is accordingly 47.81%, which suggests a very incomplete fossil record for this group. Ghost lineages, representing gaps in the fossil record, range from some 5.5 to nearly 100 million years. This contradicts the interpretation of Adnet and Cappetta (2001) that stratigraphic gaps in the fossil record of squaliforms do not exceed 20 million years.

For calculating the SCM of squaliform sharks, we generated a matrix of 223 squaliform records at genus level, ranging from the Barremian to the Pleistocene. We excluded extant occurrences to minimize “the pull of the Recent” (e.g., Smith 2001). Of these records, 137 were known fossil distributions; the remaining 86 records represent Lazarus occurrences. A SCM for the entire fossil record of squaliforms is $137/223 = 61.43\%$. This value is considerably better than that achieved from the phylogenetic approach. However, it also testifies to the rather incomplete fossil record of squaliforms with large gaps in the

stratigraphic distribution. The SCMs for all stages analyzed are shown in Table 1. The Coniacian and Santonian were combined because of very poor information and data on Coniacian occurrences.

Fossil record and origin of *Squalus* species

The most basal group within Squaliformes is Squalidae. This group is characterized by a dignathic homodonty, which is considered here to represent the plesiomorphic condition within Squaliformes. Other squalid taxa show very weak or lack of dignathic heterodonties, including *Centrophoroides* and *Centrosqualus*, indicating that this feature is homoplastic. Currently, eight extant species of *Squalus* are recognized (Compagno et al. 2005) with six additional unnamed species. The occurrences of most extant species are quite restricted. Spiny dogfish, shortnosed dogfish *S. megalops*, and shortspined dogfish *S. mitsukurii* are the only extant members of this group with almost world-wide distributions. Spiny dogfish, the most common modern *Squalus*

Table 1.—Simple completeness metric (SCM) values of squaliform fossil record per stratigraphic unit. Barremian and Aptian stages are excluded because of the presence of a single taxon and single Lazarus occurrence respectively. For occurrences and references see Appendix 1.

Stage	SCM
Pleistocene	5.88%
Pliocene	57.73%
Miocene	69.72%
Oligocene	37.73%
Eocene	88.90%
Palaeocene	45.54%
Maastrichtian	91.67%
Campanian	85.71%
Coniacian-Santonian	37.50%
Turonian	50.00%
Cenomanian	100.00%
Albian	100.00%
Aptian	0.00%
Barremian	100.00%

representative, occurs in boreal to warm-temperate oceans from the intertidal zone down to at least 900 m (probably down to 1,446 m) of the upper continental and insular slopes. It is an epipelagic shark in cold waters, usually found near the bottom, and it may enter bays and estuaries (Compagno et al. 2005; see Hauser 2009, this volume, for a genetically based, contemporary perspective on distribution).

The general dental morphology of *Squalus* spp. has not changed since their first appearance in the fossil record, making identification of fossil species very difficult. Siverson (1993) argued that important ontogenetic and sexual variations in tooth morphologies hamper the identification of nominal fossil species. However, the extent of dental variations through ontogeny, between sexes, and within and between different populations has not yet been analyzed or tested. The only available study on dental variations within Squaliformes is that of Straube (2006), who analyzed tooth sets of extant Etmopterus species.

Teeth of *Squalus* spp. are generally characterized by low crowns with well-developed labial aprons, lingual uvulae, and low roots, generally with an infundibulum (Cappetta 1987; Herman et al. 1989; Cappetta and Adnet 2001). However, there might be a thin bridge present separating two axial foramina in different tooth positions of extant and fossil *Squalus* spp. Consequently, presence or absence of a root infundibulum is not a sufficient feature for taxonomic purposes.

We found the most useful character for identifying fossil *Squalus* spp. represented by teeth alone to be the morphology of the root, which is usually very generalized within Squaliformes but differs between species. The form and angle of the basal face might represent one of the most useful characters for separating fossil taxa (Siverson 1993). Using these features, it is possible to assign fossil species within the genus *Squalus*.

To date, 14 fossil *Squalus* species have been described. In addition, *S. acanthias* and a species very close to *S. megalops* occur in the Miocene (ca. 13–15 Ma) of central Europe (Ledoux 1972). The oldest teeth of *Squalus* spp. were, however, reported from Cenomanian strata (ca. 94 Ma) of England (Underwood and Mitchell 1999). These teeth display very similar morphologies to teeth of the modern *Squalus acanthias*. Additional Late Cretaceous records are from the Campanian (ca. 75–72 Ma) of western Germany (†*S. vundermarcki*, Müller and Schöllmann 1989), Wyoming (†*S. worlandensis*, Case 1987),

and Texas (*Squalus* sp., Welton and Farish 1993); Campanian-Maastrichtian (ca. 70 Ma) of Angola (†*S. aff. S. vundermarcki*, Antunes and Cappetta 2002); and Maastrichtian (ca. 68 Ma) of Sweden (†*S. ballingsloevensis*, †*S. balsvikensis*, †*S. gabrielsoni*, Siverson 1993) and Texas (†*S. huntensis*, Case and Cappetta 1997).

In the Palaeogene (65–23 Ma), *Squalus* spp. are widespread but mainly known from Europe, USA, and Morocco (Appendix 1). Most remains are assigned to †*S. minor*, †*S. crenatidens*, or †*S. alsaticus*. The oldest remains of *S. acanthias* and *S. megalops*, or closely related species, are from the Miocene (13–15 Ma) of central and northern Europe (Scandinavia, Germany, Netherlands, France). *Squalus* remains also are quite common in Miocene deposits of the USA: †*S. occidentalis* occurs in Pacific coast deposits whereas †*S. cubensis* is known from Florida and the Caribbean. The oldest records of a species closely related to *S. acanthias* in northern America are from the Eocene (ca. 50 Ma) of the eastern coastal plains (Müller 1999) and lower Pliocene (5 Ma) of the Lee Creek mine, North Carolina. In the Pleistocene, undisputable teeth of *S. acanthias* occur in Pleistocene sediments in Orange County, California (J. Kriwet, personal observation, San Diego Natural History Museum collection).

The genus *Squalus* is closely related to †*Protosqualus* based on the presence of a slightly oblique basal root face in lower teeth and overlapping of upper teeth. Together they form a monophyletic grouping, the Squalidae (e.g., Adnet and Cappetta 2001: note that the genera *Cirrhigaleus* and *Megasqualus* are considered here to represent junior synonyms of *Squalus*). Because the oldest record of †*Protosqualus* is from the Barremian of Germany some 125 million years ago, the origin of Squalidae must have been at least in the Early Cretaceous. This indicates that there is a gap in the fossil record of *Squalus* resulting in a ghost-lineage of about 25–30 million years.

The basal sister taxon of Squaliformes is supposed to be †*Protospinax* from the Middle to Late Jurassic of Europe; †*Protospinax*, however, is not a member of Squalimorphii (Carvalho and Maisey 1996). Consequently, this taxon cannot be considered to be the ancestor of Squaliformes (Adnet and Cappetta 2001; Kriwet and Klug 2004). In our analyses, we used extant neoselachians (e.g., *Pristiophorus*) as outgroup because of the possibility of attaining molecular sequences for character polarization.

Discussion and Conclusions

Most extant and fossil squaliforms possess a rather high degree of dental variation (Figures 1 and 2). These differences permit the recognition of a suite of characters that can be analyzed with phylogenetic methods and used to infer their fossil record and evolutionary patterns or processes. However, the odontological features of several extant taxa remain incompletely documented, and many fossil taxa are still too poorly known to provide useful data. Phylogenetic studies such as that of Adnet and Cappetta (2001) and that of the present study (Figure 4) can highlight the importance of dental characters in resolving squaliform interrelationships.

The quality of the general fossil record of organisms has been debated considerably in recent decades. Whereas many analyses have been carried out to assess the quality of the fossil record of tetrapods (e.g., Fara and Benton 2000; Fountaine et al. 2005), assumptions on the completeness of the fossil record of neoselachians are scarce and generally ambiguous. Shirai (1996) assumed the fossil record of neoselachians to be incomplete; whereas Maisey et al. (2004) concluded that the fossil record of neoselachians might not be too poor when molecular phylogenies are tested against the stratigraphic distribution of taxa, although morphology-based phylogenies conversely indicate relatively large gaps in the fossil record, as is also exemplified for squaliforms by Adnet and Cappetta (2001) and in this study. Kriwet and Benton (2004) conducted SCM to infer the quality of the fossil record of neoselachians and concluded that their fossil record across the K/T boundary (Maastrichtian = 94% and Danian = 85%) is undeniably good.

Our phylogenetic hypothesis based on the supertree provides information not only on squaliform interrelationships but also on the timing of cladogenetic events. In addition, the quality of the fossil record of squaliforms can be deduced from the supertree. We assume a postJurassic origination of squaliform sharks in the shallow waters of the Tethyal margin. Two dorsal fin spines and absence of a dignathic dental heterodonty characterize the hypothetical ancestor of Squaliformes. This is independently supported by the provenance of †*Protosqualus* in the Barremian. To date, no compelling older fossil of any squaliform has been reported and, considering that †*Protospinax* is not a squaliform (Kriwet and Klug 2004), the order Squaliformes

seems to have evolved in the earliest Cretaceous. The similarities between squaliform sharks and the Triassic genus †*Pseudodalatias* in dental morphology are considered to be convergent (Cuny and Benton 1999). However, with regard to the discussion of the quality of the fossil record of squaliforms, which is quite incomplete, it is important to note that this interpretation might change in the future when more work has been carried out on small-toothed selachian assemblages from various environmental settings of Early Cretaceous and Late Jurassic age.

Most fossil and living squaliform sharks are typical deep-water sharks, although many may have been able to thrive in shallow coastal waters. The long gaps in the fossil history as indicated by our analyses can be explained by the scarcity of deep-water deposits yielding micro-teeth of sharks.

The rather poor quality of the squaliform fossil record expressed by the supertree is not supported by the SCM, although this measure might not give an appropriate measure of the relative incompleteness of the fossil record (Benton 1987). The relatively high amount of Lazarus occurrences (86) indicates that the fossil record for several stages is probably less complete than the SCM of about 61% might indicate (e.g., in the Danian [SCM = 25%], latest Eocene [SCM = 40%], Oligocene [SCM = 38%], and Pleistocene [SCM = 6%]) (Table 1). It is noteworthy that the quality of the squaliform fossil record is much better for the Cretaceous (SCM = 71% on average) than for the Cenozoic (SCM = 57% on average) despite the fact that there is more Cenozoic rock volume and preserved area that might yield material. However, the rocks available for exploration were predominantly deposited in shallow marine settings rather than in the deep sea; some question whether the lithologic record is in fact sufficient enough to accept observed oscillations as reflecting the actual pattern (e.g., Gregor 1985; Wilkinson and Walker 1989; Wold and Hay 1990; Signor 1990; Peters and Foote 2001). Consequently, small-toothed squaliforms, which are assumed to have primarily occurred in bathyal environments, are comparably rare elements in most selachian assemblages. Nevertheless, the fossil record of squaliforms is also very good in several Cenozoic stages (e.g., middle Eocene [SCM = 90%], Miocene [SCM = 70% on average], and early Pliocene [SCM = 84%]). The very complete fossil record of squaliforms during these stages certainly corresponds to more extensive research conducted in those strata (e.g., Adnet 2006). The rather good fossil

record of squaliforms in the Cenomanian, Campanian, and Maastrichtian seems to correlate with the occasionally high abundance in relatively shallow water marine environments (Siverson 1993; Siverson and Cappetta 2001; personal observation) and we assume a considerable shift of ecological adaptation from shallow waters into deep-sea environments at the K/T boundary.

In conclusion, it is important to note that, although the quality of the fossil record of squaliforms for particular stages seems to be exceptionally good, the overall record of the order must be regarded as more or less incomplete. A taxonomic count of squaliform genera reveals that the diversity of squaliforms compared to that of other neoselachian groups is low (Kriwet and Benton 2004). The low diversity and the gaps in the fossil record expressed by the ghost-lineages might be a result of the absence of suitable sediments containing remains of squaliforms; it may also indicate that more palaeontological research into small-toothed selachian assemblages is required to gain better insights into the changes in diversity over time and evolutionary patterns and processes of squaliforms. Finally, we stress that *Squalus* has a very long geologic range, and many species have appeared and disappeared in the past. Disappearance is a fact of life, but the long evolutionary history and success of this taxon also highlights the need for careful management of its current population crisis due to causes that never occurred before in earth's history—the anthropogenetic impact (see Hauser 2009).

Recently, Adnet et al. (2008a) published a revision of Albian and Cenomanian squaliform sharks from Lithuania, introducing a new genus, *Protocentrophorus*, for *Centrophorus balticus* Dalinkevicius 1935. This taxonomic change, however, does not alter our analyses or results. In an additional paper, Adnet et al. (2008b) provided a phylogenetic tree of extant squaliforms calibrated with their stratigraphic occurrences. They concluded that the origin of these deep-water sharks must have occurred in the Early Cretaceous (similar to our analysis). However, the interrelationships of most groups within Squaliformes are not resolved and differ significantly from our analysis presented here. This is mainly related to the exclusion of extinct taxa.

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Appendix 1.—Occurrences of fossil squaliform taxa used in this study. Data from Antunes and Jonet (1970); Antunes et al. (1999); Arambourg (1952); Balbino (1995); Baut and Genault (1995); Bigelow (1994); Bruggen (1992); Case and Cappetta (1997); Case et al. (1996); Cappetta (1970, 1977, 1980, 1987); Cappetta and Adnet (2001); Cappetta et al. (1967, 1993); Cigala Fulgosi (1986, 1988, 1996); Dalinkevicius (1935); Dutheil (1991); Dutheil et al. (2002); Freeß (1991); Gurr (1962); Herman (1977); Kemp (1982); Keyes (1984); Kruckow (1965); Leriche (1905, 1927); Lewy and Cappetta (1989); Mañé et al. (1996); Mendiola and Martinez (2003); Merle et al. (2002); Müller (1983, 1990, 1999); Müller and Diedrich (1991); Müller and Schöllmann (1989); Naruse et al. (1994); Pfeil (1984); Purdy (1998); Reinecke and Engelhard (1997); Reinecke et al. (2001, 2005); Siverson (1993a, 1993b); Smith (1999); Takakuwa et al. (2003); Thies and Müller (1993); Underwood and Mitchell (1999); Ward and Bonavia (2001); Ward and Wiest (1990); Welton (1981); Welton and Farish (1993); Yabumoto and Uyeno (1994); and references cited in the text.

Genus	Species	Period	Stage	Occurrence
<i>Centropterus</i>	<i>lividus</i>	Early Cretaceous	Aptian	Naples, Italy
<i>Protosqualus</i>	<i>albertsi</i>	Early Cretaceous	Barremian	Braunschweig, Germany
<i>Protosqualus</i>	<i>pachyrhiza</i>	Early Cretaceous	Albian	England
<i>Protosqualus</i>	<i>sigei</i>	Early Cretaceous	Albian	Kent, UK
<i>Protosqualus</i>	<i>sigei</i>	Early Cretaceous	Albian	Haute-Marne, France
<i>Protosqualus</i>	<i>sigei</i>	Early Cretaceous	Albian	Wissant, Boullonnais, France
Somniosinae	indet.	Late Cretaceous	Cenomanian	Germany
<i>Squalus</i>	sp.	Late Cretaceous	Cenomanian	England
<i>Squalus</i>	sp.	Late Cretaceous	Cenomanian	England
<i>Protosqualus</i>	<i>cf. siegei</i>	Late Cretaceous	Cenomanian	Germany
<i>Protosqualus</i>	<i>glickmani</i>	Late Cretaceous	Cenomanian	Saratov Prov., Russia
<i>Protosqualus</i>	sp.	Late Cretaceous	Cenomanian-Turonian	Lithuania
<i>cf. Squaliolus</i>	sp.	Late Cretaceous	Turonian	Lithuania
<i>Centrophorus?</i>	<i>balticus</i>	Late Cretaceous	Turonian	Lithuania
<i>Centrophoroides</i>	sp.	Late Cretaceous	Con-Santon	Western Australia
<i>Protosqualus?</i>	sp.	Late Cretaceous	Con-Santon	Western Australia
<i>Centrophoroides</i>	<i>latidens</i>	Late Cretaceous	Santonian	Lebanon
<i>Centrosqualus</i>	<i>primaevus</i>	Late Cretaceous	Santonian	Lebanon
<i>Cretascymnus</i>	<i>adonis</i>	Late Cretaceous	Santonian	Lebanon
<i>aff. Centrosymnus</i>	sp.	Late Cretaceous	Campanian	Israel
<i>aff. Deania</i>	sp.	Late Cretaceous	Campanian	Germany
<i>Centrophoroides</i>	<i>appendiculatus</i>	Late Cretaceous	Campanian	Germany
<i>Centrophoroides</i>	<i>appendiculatus</i>	Late Cretaceous	Campanian	Germany
<i>Centrophoroides</i>	<i>appendiculatus</i>	Late Cretaceous	Campanian	Lithuania
<i>Centrophoroides</i>	<i>cf. latidens</i>	Late Cretaceous	Campanian	Japan
<i>Centrophoroides</i>	sp.	Late Cretaceous	Campanian	Angola
<i>Centrophoroides</i>	sp.	Late Cretaceous	Campanian	Canada
<i>Centrosymnus</i>	<i>praecursor</i>	Late Cretaceous	Campanian	Canada
<i>Centrosymnus</i>	<i>praecursor</i>	Late Cretaceous	Campanian	Germany
<i>Centrosymnus</i>	<i>praecursor</i>	Late Cretaceous	Campanian	Germany
<i>Centrosqualus</i>	sp.	Late Cretaceous	Campanian	Israel
<i>Cretascymnus</i>	<i>quimbalaensis</i>	Late Cretaceous	Campanian	Angola
<i>Cretascymnus</i>	sp.	Late Cretaceous	Campanian	Canada
<i>Cretascymnus</i>	sp.	Late Cretaceous	Campanian	Israel
<i>Cretascymnus</i>	<i>westfalicus</i>	Late Cretaceous	Campanian	Germany
<i>Cretascymnus</i>	<i>westfalicus</i>	Late Cretaceous	Campanian	Germany
<i>Deania?</i>	sp.	Late Cretaceous	Campanian	Germany
<i>Eoetmopterus</i>	sp. nov.	Late Cretaceous	Campanian	Texas, USA

Appendix Table 1—continued

Genus	Species	Period	Stage	Occurrence
<i>Eoetmopterus</i>	<i>supracretaceus</i>	Late Cretaceous	Campanian	Germany
<i>Eoetmopterus</i>	<i>supracretaceus</i>	Late Cretaceous	Campanian	Germany
<i>Oxynotus</i>	sp.	Late Cretaceous	Campanian	Canada
<i>Paraphorosoides</i>	<i>ursulae</i>	Late Cretaceous	Campanian	Germany
<i>Proetmopterus</i>	<i>hemooriensis</i>	Late Cretaceous	Campanian	Germany
<i>Protoxynotus</i>	<i>misburgensis</i>	Late Cretaceous	Campanian	Germany
<i>Somniosinae</i>	indet.	Late Cretaceous	Campanian	Germany
<i>Squalus</i>	<i>aff. vundermarcki</i>	Late Cretaceous	Campanian	Angola
<i>Squalus</i>	sp.	Late Cretaceous	Campanian	Israel
<i>Squalus</i>	<i>vundermarcki</i>	Late Cretaceous	Campanian	Germany
<i>Squalus</i>	<i>worlandensis</i>	Late Cretaceous	Campanian	Wyoming, USA
<i>Squalus</i>	sp.	Late Cretaceous	Campanian	Belgium
<i>Squalus?</i>	<i>vundermarcki</i>	Late Cretaceous	Campanian	Germany
<i>Centrophoroides</i>	<i>appendiculatus</i>	Late Cretaceous	Maastrichtian	Belgium
<i>Centrophoroides</i>	<i>appendiculatus</i>	Late Cretaceous	Maastrichtian	Germany
<i>Centrophoroides</i>	<i>appendiculatus</i>	Late Cretaceous	Maastrichtian	Holland
<i>Centrophoroides</i>	<i>appendiculatus</i>	Late Cretaceous	Maastrichtian	Holland
<i>Centrophoroides</i>	sp.	Late Cretaceous	Maastrichtian	Angola
<i>Centrophorus</i>	<i>squamosus</i>	Late Cretaceous	Maastrichtian	New Zealand
<i>Centroscymnus</i>	<i>schmidi</i>	Late Cretaceous	Maastrichtian	Germany
<i>Centroscymnus</i>	<i>schmidi</i>	Late Cretaceous	Maastrichtian	Germany
<i>Centroscymnus</i>	<i>schmidi</i>	Late Cretaceous	Maastrichtian	Sweden
<i>Cretascymnus</i>	<i>quimbalaensis</i>	Late Cretaceous	Maastrichtian	Angola
<i>Dalatias</i>	sp.	Late Cretaceous	Maastrichtian	Germany
<i>Eoetmopterus</i>	<i>cf. supracretaceus</i>	Late Cretaceous	Maastrichtian	Sweden
<i>Eoetmopterus</i>	<i>supracretaceus</i>	Late Cretaceous	Maastrichtian	Germany
<i>Microetmopterus</i>	<i>wardi</i>	Late Cretaceous	Maastrichtian	Sweden
<i>Proetmopterus</i>	<i>hemooriensis</i>	Late Cretaceous	Maastrichtian	Germany
<i>Proetmopterus</i>	<i>hemooriensis</i>	Late Cretaceous	Maastrichtian	Sweden
<i>Proetmopterus</i>	<i>hemooriensis</i>	Late Cretaceous	Maastrichtian	Sweden
<i>Squalus</i>	<i>aff. vundermarcki</i>	Late Cretaceous	Maastrichtian	Angola
<i>Squalus</i>	<i>ballingsloevensis</i>	Late Cretaceous	Maastrichtian	Sweden
<i>Squalus</i>	<i>balsvikensis</i>	Late Cretaceous	Maastrichtian	Sweden
<i>Squalus</i>	<i>gabrielsoni</i>	Late Cretaceous	Maastrichtian	Sweden
<i>Squalus</i>	<i>hassei?</i>	Late Cretaceous	Maastrichtian	Texas, USA
<i>Squalus</i>	<i>huntensis</i>	Late Cretaceous	Maastrichtian	Texas, USA
<i>Centrophoroides</i>	<i>volgensis</i>	Palaeogene	early Palaeocene	Russia
<i>Centrophorus</i>	<i>squamosus</i>	Palaeogene	early Palaeocene	New Zealand
<i>Dalatias</i>	<i>crenulatus</i>	Palaeogene	early Palaeocene	Greenland
<i>Megasqualus</i>	<i>aff. orpiensis</i>	Palaeogene	early Palaeocene	Greenland
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	early Palaeocene	Belgium
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	early Palaeocene	Belgium
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	early Palaeocene	Eastern USA
<i>Squalus</i>	<i>crenatidens</i>	Palaeogene	early Palaeocene	Morocco
<i>Squalus</i>	<i>minor</i>	Palaeogene	early Palaeocene	Belgium
<i>Squalus</i>	<i>minor</i>	Palaeogene	early Palaeocene	Greenland
<i>Squalus</i>	<i>minor</i>	Palaeogene	early Palaeocene	Eastern USA
<i>Squalus</i>	<i>minor</i>	Palaeogene	early Palaeocene	New Jersey, USA

Fossil Record and Origin of Squaliform Sharks

Appendix Table 1—continued

Genus	Species	Period	Stage	Occurrence
<i>Squalus</i>	<i>crenatidens</i>	Palaeogene	early Palaeocene	
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	early Palaeocene	Belgium
<i>Squalus</i>	<i>acanthias</i>	Palaeogene	early Palaeocene	Nova Scotia, Canada
<i>Squalus</i>	<i>minor</i>	Palaeogene	early Palaeocene	Eastern US
<i>Centrophorus</i>	sp.	Palaeogene	late Palaeocene	Germany
<i>Dalatiias?</i>	<i>crenulatus</i>	Palaeogene	late Palaeocene	Morocco
<i>Isitius</i>	<i>tritiratus</i>	Palaeogene	late Palaeocene	England
<i>Isitius</i>	<i>tritiratus</i>	Palaeogene	late Palaeocene	Morocco
<i>Isitius</i>	<i>tritiratus</i>	Palaeogene	late Palaeocene	Russia
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	late Palaeocene	Belgium
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	late Palaeocene	Belgium
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	late Palaeocene	England
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	late Palaeocene	England
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	late Palaeocene	Paris Basin, France
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	late Palaeocene	Paris Basin, France
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	late Palaeocene	Paris Basin, France
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	late Palaeocene	Germany
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	late Palaeocene	Kazakhstan
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	late Palaeocene	Eastern USA
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	late Palaeocene	Eastern USA
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	late Palaeocene	N Dakota, USA
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	late Palaeocene	S Dakota, USA
<i>Squalus</i>	<i>cf. minor</i>	Palaeogene	late Palaeocene	Eastern USA
<i>Squalus</i>	<i>crenatidens</i>	Palaeogene	late Palaeocene	Maret
<i>Squalus</i>	<i>crenatidens</i>	Palaeogene	late Palaeocene	Morocco
<i>Squalus</i>	<i>minor</i>	Palaeogene	late Palaeocene	Denmark
<i>Squalus</i>	<i>minor</i>	Palaeogene	late Palaeocene	England
<i>Squalus</i>	<i>minor</i>	Palaeogene	late Palaeocene	Paris Basin, France
<i>Squalus</i>	<i>minor</i>	Palaeogene	late Palaeocene	Paris Basin, France
<i>Squalus</i>	<i>minor</i>	Palaeogene	late Palaeocene	Germany
<i>Squalus</i>	<i>minor</i>	Palaeogene	late Palaeocene	Maryland & Virginia
<i>Squalus</i>	<i>minor</i>	Palaeogene	late Palaeocene	N Dakota, USA
<i>Squalus</i>	<i>minor</i>	Palaeogene	late Palaeocene	S Dakota, USA
<i>Squalus</i>	<i>minor</i>	Palaeogene	late Palaeocene	Belgium
<i>Squalus</i>	<i>crenatidens</i>	Palaeogene	late Palaeocene	England
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	late Palaeocene	Morocco
<i>Centrophorus</i>	sp.	Palaeogene	early Eocene	Denmark
<i>Dalatiias</i>	<i>crenulatus</i>	Palaeogene	early Eocene	Morocco
<i>Isistius</i>	sp.	Palaeogene	early Eocene	Jordan
<i>Isistius</i>	<i>tritiratus</i>	Palaeogene	early Eocene	Paris Basin, France
<i>Isistius</i>	<i>tritiratus</i>	Palaeogene	early Eocene	Morocco
<i>Isistius</i>	<i>tritiratus</i>	Palaeogene	early Eocene	Virginia, USA
<i>Isitius</i>	<i>tritiratus</i>	Palaeogene	early Eocene	Belgium
<i>Isitius</i>	<i>tritiratus</i>	Palaeogene	early Eocene	England
<i>Isistius</i>	<i>tritiratus</i>	Palaeogene	early Eocene	Belgium
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	early Eocene	Belgium
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	early Eocene	Belgium
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	early Eocene	Belgium

Appendix Table 1—continued

Genus	Species	Period	Stage	Occurrence
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	early Eocene	England
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	early Eocene	Virginia, USA
<i>Megasqualus</i>	<i>orpiensis</i>	Palaeogene	early Eocene	Germany
<i>Squalus</i>	<i>acanthias</i>	Palaeogene	early Eocene	New York, Germany
<i>Squalus</i>	<i>crenatidens</i>	Palaeogene	early Eocene	England
<i>Squalus</i>	<i>crenatidens</i>	Palaeogene	early Eocene	Eastern USA
<i>Squalus</i>	<i>crenatidens</i>	Palaeogene	early Eocene	Morocco
<i>Squalus</i>	<i>minor</i>	Palaeogene	early Eocene	England
<i>Squalus</i>	<i>minor</i>	Palaeogene	early Eocene	Eastern USA
<i>Squalus</i>	<i>smithi</i>	Palaeogene	early Eocene	Belgium
<i>Squalus</i>	sp.	Palaeogene	early Eocene	Russia
<i>Squalus</i>	sp.	Palaeogene	early Eocene	Germany
<i>Acrosqualiolus</i>	<i>mirus</i>	Palaeogene	middle Eocene	SW France (Landes)
<i>Angoumeius</i>	<i>paradoxus</i>	Palaeogene	middle Eocene	SW France (Landes)
<i>Centrophorus</i>	<i>squamosus</i>	Palaeogene	middle Eocene	New Zealand
<i>Centrophorus</i>	<i>cf. granulatus</i>	Palaeogene	Middle Eocene	SW France (Landes)
<i>Centroscymnus</i>	<i>cf. owstoni</i>	Palaeogene	Middle Eocene	SW France (Landes)
<i>Dalatias</i>	<i>aff. crenulatus</i>	Palaeogene	middle Eocene	UK
<i>Dalatias</i>	<i>crenulatus</i>	Palaeogene	middle Eocene	England
<i>Dalatias</i>	<i>licha</i>	Palaeogene	middle Eocene	New Zealand
<i>Dalatias</i>	sp.	Palaeogene	Middle Eocene	SW France (Landes)
<i>Deania</i>	<i>angoumeensis</i>	Palaeogene	Middle Eocene	SW France (Landes)
<i>Eosqualiolus</i>	<i>aturensis</i>	Palaeogene	Middle Eocene	SW France (Landes)
<i>Etmopterus</i>	<i>cabuzaci</i>	Palaeogene	Middle Eocene	SW France (Landes)
<i>?Euprotomicroides</i>	sp.	Palaeogene	Middle Eocene	SW France (Landes)
<i>Isistius</i>	<i>tritiratus</i>	Palaeogene	middle Eocene	Belgium
<i>Isistius</i>	<i>tritiratus</i>	Palaeogene	middle Eocene	Russia
<i>Isistius</i>	<i>tritiratus</i>	Palaeogene	middle Eocene	UK
<i>Isitius</i>	<i>tritiratus</i>	Palaeogene	middle Eocene	Belgium
<i>Isitius</i>	<i>tritiratus</i>	Palaeogene	middle Eocene	Belgium
<i>Isitius</i>	<i>tritiratus</i>	Palaeogene	middle Eocene	England
<i>Isitius</i>	<i>tritiratus</i>	Palaeogene	middle Eocene	England
<i>Isitius</i>	<i>tritiratus</i>	Palaeogene	middle-late Eocene	Russia
<i>Isitius</i>	<i>cf. tritiratus</i>	Palaeogene	Middle Eocene	SW France (Landes)
<i>Isitius</i>	sp.	Palaeogene	middle Eocene	S Germany
<i>Paraetmopterus</i>	<i>nolfi</i>	Palaeogene	Middle Eocene	SW France (Landes)
<i>Scymnodalatias</i>	<i>cigalafulgosi</i>	Palaeogene	Middle Eocene	SW France (Landes)
<i>Squaliodalatias</i>	<i>weltoni</i>	Palaeogene	middle Eocene	SW France (Landes)
<i>Squaliolus</i>	<i>gasconensis</i>	Palaeogene	middle Eocene	SW France (Landes)
<i>Squalus</i>	<i>acanthias</i>	Palaeogene	middle Eocene	Eastern USA
<i>Squalus</i>	<i>minor</i>	Palaeogene	middle Eocene	UK
<i>Squalus</i>	<i>smithi</i>	Palaeogene	middle Eocene	USA
<i>Squalus</i>	sp.	Palaeogene	middle Eocene	Russia
<i>Squalus</i>	<i>minor</i>	Palaeogene	middle Eocene	England
<i>Squalus</i>	<i>minor</i>	Palaeogene	middle Eocene	England
<i>Trigonognathus</i>	<i>virginiae</i>	Palaeogene	middle Eocene	SW France (Landes)
<i>Centrophorus</i>	sp.	Palaeogene	late Eocene	Jordan
<i>Centroscymnus</i>	<i>schaubi</i>	Palaeogene	late Eocene	Barbados

Fossil Record and Origin of Squaliform Sharks

Appendix Table 1—continued

Genus	Species	Period	Stage	Occurrence
<i>Squalus</i>	sp.	Palaeogene	late Eocene	Western USA
<i>Squalus</i>	<i>alsaticus</i>	Palaeogene	early Oligocene	Belgium
<i>Squalus</i>	<i>alsaticus</i>	Palaeogene	early Oligocene	Germany
<i>Squalus</i>	<i>alsaticus</i>	Palaeogene	early Oligocene	France
<i>Squalus</i>	<i>alsaticus</i>	Palaeogene	early Oligocene	Paris Basin, France
<i>Squalus</i>	<i>alsaticus</i>	Palaeogene	early Oligocene	Holland
<i>Squalus</i>	<i>alsaticus</i>	Palaeogene	middle Oligocene	Germany
<i>Squalus</i>	<i>stehleni</i>	Palaeogene	middle-late Oligocene	Venezuela
<i>Centrophorus</i>	<i>squamosus</i>	Palaeogene	late Oligocene	New Zealand
<i>Dalatias</i>	<i>licha</i>	Palaeogene	late Oligocene	New Zealand
<i>Dalatias</i>	sp.	Pal-Neogene	late Oligocene	New Zealand
<i>Etmopterus</i>	<i>acutidens</i>	Palaeogene	late Oligocene	Barbados
<i>Scymnodon</i>	sp.	Palaeogene	late Oligocene	Western USA
<i>Megasqualus</i>	<i>aff. orpiensis</i>	Palaeogene	late Oligocene	Germany
<i>Squalus</i>	<i>acanthias</i>	Palaeogene	late Oligocene	Western USA
<i>Squalus</i>	<i>alsaticus</i>	Palaeogene	late Oligocene	Germany
<i>Squalus</i>	<i>alsaticus</i>	Palaeogene	late Oligocene	Eastern USA
<i>Centrophorus</i>	sp.	Palaeogene	early Oligocene	Czechoslovakia
<i>Centrophorus</i>	sp.	Palaeogene	early Oligocene	Western USA
<i>Squalus</i>	<i>alsaticus</i>	Palaeogene	early Oligocene	Poland
<i>Squalus</i>	sp.	Palaeogene	early Oligocene	Czechoslovakia
<i>Squalus</i>	<i>stehleni</i>	Pal-Neogene	early Oligocene	Trinidad
<i>Centrophorus</i>	sp.	Neogene	early Miocene	Spain
<i>Centrophorus</i>	sp.	Neogene	early Miocene	Barbados
<i>Centroscymnus</i>	<i>schaubi</i>	Neogene	early Miocene	Barbados
<i>Centroscymnus</i>	<i>schaubi</i>	Neogene	early Miocene	France
<i>Centroscymnus?</i>	sp.	Neogene	early Miocene	Japan
<i>Dalatias</i>	<i>licha</i>	Neogene	early Miocene	Barbados
<i>Dalatias</i>	<i>licha</i>	Neogene	early Miocene	France
<i>Dalatias</i>	<i>licha</i>	Neogene	early Miocene	S. Sardinia
<i>Etmopterus</i>	<i>acutidens</i>	Neogene	early Miocene	Barbados
<i>Isistius</i>	<i>triangulus</i>	Neogene	early Miocene	France
<i>Isistius</i>	<i>triangulus</i>	Neogene	early Miocene	Switzerland
<i>Isistius</i>	<i>triangulus</i>	Neogene	early Miocene	S. Germany
<i>Oxynotus</i>	<i>crochardi</i>	Neogene	early Miocene	Western USA
<i>Somniosus</i>	sp.	Neogene	early Miocene	Japan
<i>Squalus</i>	<i>cubensis</i>	Neogene	early Miocene	Eastern USA
<i>Squalus</i>	<i>cubensis</i>	Neogene	early Miocene	Caribbean
<i>Squalus</i>	<i>radicans</i>	Neogene	early Miocene	Switzerland
<i>Squalus</i>	sp.	Neogene	early Miocene	Switzerland
<i>Deania</i>	<i>calceus</i>	Neogene	early-middle Miocene	France
<i>Centrophorus</i>	<i>cf. granulosus</i>	Neogene	middle Miocene	Germany
<i>Centrophorus</i>	<i>cf. granulosus</i>	Neogene	middle Miocene	S Germany
<i>Centrophorus</i>	<i>cf. granulosus</i>	Neogene	middle Miocene	S Germany
<i>Centrophorus</i>	<i>granulosus</i>	Neogene	middle Miocene	France
<i>Centroscymnus</i>	sp.	Neogene	middle Miocene	Germany
<i>Centrophorus?</i>	sp.	Neogene	middle Miocene	Japan
<i>Dalatias</i>	<i>licha</i>	Neogene	middle Miocene	Japan

Appendix Table 1—continued

Genus	Species	Period	Stage	Occurrence
<i>Dalatias</i>	<i>licha</i>	Neogene	middle Miocene	S. France
<i>Dalatias</i>	sp.	Neogene	middle Miocene	Japan
<i>Dalatias</i>	<i>licha</i>	Neogene	middle Miocene	Portugal
<i>Etmopterus</i>	sp.	Neogene	middle Miocene	Germany
<i>Isistius</i>	<i>triangulus</i>	Neogene	middle Miocene	Ecuador
<i>Isistius</i>	<i>triangulus</i>	Neogene	middle Miocene	Panama
<i>Isistius</i>	<i>triangulus</i>	Neogene	middle Miocene	Portugal
<i>Isistius</i>	<i>triangulus</i>	Neogene	middle Miocene	Switzerland
<i>Isistius</i>	<i>triangulus</i>	Neogene	middle Miocene	S Germany
<i>Isistius</i>	<i>triangulus</i>	Neogene	middle Miocene	Austria
<i>Isistius</i>	<i>triangulus</i>	Neogene	middle Miocene	S. France
<i>Ististius</i>	<i>triangulus</i>	Neogene	middle Miocene	Germany
<i>Megasqualus</i>	<i>serriculus</i>	Neogene	middle Miocene	Japan
<i>Scymnodon</i>	sp.	Neogene	middle Miocene	Italy
<i>Squaliolus</i>	sp. 1	Neogene	middle Miocene	Germany
<i>Squaliolus</i>	sp. 2	Neogene	middle Miocene	Germany
<i>Squalus</i>	<i>aff. acanthias</i>	Neogene	middle Miocene	off Scandinavia
<i>Squalus</i>	<i>cf. acanthias</i>	Neogene	middle Miocene	Germany
<i>Squalus</i>	sp.	Neogene	middle Miocene	Holland
<i>Squalus</i>	sp.	Neogene	middle Miocene	France
<i>Squalus</i>	<i>cubensis</i>	Neogene	middle Miocene	Caribbean
<i>Squalus</i>	<i>radicans</i>	Neogene	middle Miocene	S Germany
<i>Squalus</i>	sp.	Neogene	middle Miocene	Germany
<i>Squalus</i>	<i>almeidae</i>	Neogene	middle Miocene	Portugal
<i>Squalus</i>	<i>cf. megalops</i>	Neogene	middle Miocene	France
<i>Squalus</i>	sp.	Neogene	middle Miocene	Austria
<i>Squalus</i>	<i>cf. acanthias</i>	Neogene	middle Miocene	Germany
<i>Deania</i>	sp.	Neogene	late Miocene	Italy
<i>Deania</i>	sp.	Neogene	late Miocene	Portugal
<i>Isistius</i>	<i>triangulus</i>	Neogene	late Miocene	Portugal
<i>Isistius</i>	sp.	Neogene	late Miocene	Holland
<i>Isistius</i>	<i>triangulus</i>	Neogene	late Miocene	Ecuador
<i>Isistius</i>	<i>triangulus</i>	Neogene	late Miocene	Mexico
<i>Squalus</i>	<i>almeidae</i>	Neogene	late Miocene	Portugal
<i>Squalus</i>	<i>cubensis</i>	Neogene	late Miocene	S America
<i>Squalus</i>	<i>acanthias</i>	Neogene	late Miocene	Holland
<i>Squalus</i>	<i>occidentalis</i>	Neogene	late Miocene	Eastern USA
<i>Squalus</i>	sp.	Neogene	late Miocene	Germany
<i>Squalus</i>	sp.	Neogene	late Miocene	Holland
<i>Squalus</i>	sp.	Neogene	late Miocene	Portugal
<i>Centrophorus</i>	<i>squamosus</i>	Neogene	Miocene	New Zealand
<i>Centrosyllium?</i>	sp.	Neogene	Miocene	France
<i>Centroscymnus</i>	<i>schaubi</i>	Neogene	Miocene	Jamaica
<i>Centroscymnus</i>	<i>schaubi</i>	Neogene	Miocene	Italy
<i>Centroscymnus</i>	<i>schaubi</i>	Neogene	Miocene	Japan
<i>Centroscymnus</i>	Sp.	Neogene	Miocene	Japan
<i>Dalatias</i>	<i>licha</i>	Neogene	Miocene	Italy
<i>Dalatias</i>	<i>licha</i>	Neogene	Miocene	Japan

Fossil Record and Origin of Squaliform Sharks

Appendix Table 1—continued

Genus	Species	Period	Stage	Occurrence
<i>Dalatias</i>	<i>licha</i>	Neogene	Miocene	New Zealand
<i>Dalatias</i>	<i>licha</i>	Neogene	Miocene	West Indies
<i>Deania</i>	<i>radicans</i>	Neogene	Miocene	S. Germany
<i>Deania</i>	sp.	Neogene	Miocene	Jamaica
<i>Deania</i>	sp.	Neogene	Miocene	Japan
<i>Deania</i>	sp.	Neogene	Miocene	Portugal
<i>Deania</i>	sp.	Neogene	Miocene	West Indies
<i>Etmopterus</i>	sp.	Neogene	Miocene	France
<i>Isistius</i>	<i>brasiliensis</i>	Neogene	Miocene	Eastern U.S.A.
<i>Isistius</i>	<i>triangulus</i>	Neogene	Miocene	Barbados
<i>Isistius</i>	<i>triangulus</i>	Neogene	Miocene	France
<i>Isistius</i>	<i>triangulus</i>	Neogene	Miocene	Eastern U.S.A.
<i>Isistius</i>	<i>triangulus</i>	Neogene	Miocene	Eastern U.S.A.
<i>Ististius</i>	<i>triangulus</i>	Neogene	Miocene	Spain
<i>Megasqualus</i>	<i>serriculus</i>	Neogene	Miocene	Western USA
<i>Oxynotus</i>	<i>centrina</i>	Neogene	Miocene	Belgium
<i>Somniosus</i>	sp.	Neogene	Miocene	Japan
<i>Somniosus</i>		Neogene	Miocene	Japan
<i>Squaliolus</i>	sp.	Neogene	Miocene	Jamaica
<i>Squaliolus</i>	sp.	Neogene	Miocene	France
<i>Squalus</i>	<i>almeidae</i>	Neogene	Miocene	France
<i>Squalus</i>	<i>almeidae</i>	Neogene	Miocene	Portugal
<i>Squalus</i>	sp.	Neogene	Miocene	India
<i>Squalus</i>	sp.	Neogene	Miocene	Japan
<i>Centrophorus</i>	sp.	Neogene	Mio-Pliocene	Venezuela
<i>Dalatias</i>	sp.	Neogene	Mio-Pliocene	Venezuela
<i>Etmopterus</i>	sp.	Neogene	Mio-Pliocene	Venezuela
<i>Isistius</i>	<i>aff. triangulus</i>	Neogene	Mio-Pliocene	Venezuela
<i>Squalus</i>	sp.	Neogene	Mio-Pliocene	Venezuela
<i>Centrophorus</i>	<i>aff. granulosus</i>	Neogene	early Pliocene	France
<i>Centrophorus</i>	<i>cf. granulosus</i>	Neogene	early Pliocene	Italy
<i>Centrophorus</i>	<i>squamosus</i>	Neogene	early Pliocene	Italy
<i>Centroscymnus</i>	<i>cf. crepidater</i>	Neogene	early Pliocene	Italy
<i>Dalatias</i>	<i>licha</i>	Neogene	early Pliocene	France
<i>Dalatias</i>	<i>licha</i>	Neogene	early Pliocene	Italy
<i>Dalatias</i>	<i>licha</i>	Neogene	early Pliocene	Italy
<i>Dalatias</i>	<i>licha</i>	Neogene	early Pliocene	Japan
<i>Deania</i>	<i>cf. calcea</i>	Neogene	early Pliocene	Italy
<i>Deania</i>	sp.	Neogene	early Pliocene	France
<i>Deania</i>	sp.	Neogene	early Pliocene	Venezuela
<i>Etmopterus</i>	sp.	Neogene	early Pliocene	Italy
<i>sistius</i>	<i>cf. triangulus</i>	Neogene	early Pliocene	Eastern USA
<i>Isistius</i>	<i>triangulus</i>	Neogene	early Pliocene	Belgium
<i>Isistius</i>	<i>triangulus</i>	Neogene	early Pliocene	Eastern USA
<i>Oxynotus</i>	<i>centrina</i>	Neogene	early Pliocene	Italy
<i>Oxynotus</i>	<i>centrina</i>	Neogene	early Pliocene	Belgium
<i>Scymnodalatias</i>	<i>aff. garricki</i>	Neogene	early Pliocene	Italy
<i>Scymnodon</i>	<i>squamulosus</i>	Neogene	early Pliocene	Italy

Appendix Table 1—continued

Genus	Species	Period	Stage	Occurrence
<i>Iscymnodon</i>	<i>cf. squamulosus</i>	Neogene	early Pliocene	Italy
<i>Scymnodon</i>	<i>ringens</i>	Neogene	early Pliocene	Italy
<i>Somniosus</i>	<i>rostratus</i>	Neogene	early Pliocene	Italy
<i>Somniosus</i>	<i>rostratus</i>	Neogene	early Pliocene	Italy
<i>Somniosus</i>	<i>microcephalus</i>	Neogene	early Pliocene	Belgium
<i>Somniosus</i>	<i>microcephalus</i>	Neogene	early Pliocene	Belgium
<i>Squalus</i>	<i>aff. blainvillei</i>	Neogene	early Pliocene	France
<i>Squalus</i>	<i>cf. acanthias</i>	Neogene	early Pliocene	Eastern USA
<i>Squalus</i>	sp.	Neogene	early Pliocene	Holland
<i>Squalus</i>	<i>acanthias</i>	Neogene	early Pliocene	Holland
<i>Squalus</i>	<i>acanthias</i>	Neogene	early Pliocene	Holland
<i>Trigonognathus</i>	<i>aff. kabeyai</i>	Neogene	early Pliocene	Venezuela
<i>Squalus</i>	sp.	Neogene	middle Pliocene	S. France
<i>Centrophorus</i>	<i>granulosus</i>	Neogene	late Pliocene	Spain
<i>Centrophorus</i>	<i>granulosus</i>	Neogene	late Pliocene	Spain
<i>Dalatias</i>	<i>licha</i>	Neogene	late Pliocene	Japan
<i>Squalus</i>	sp.	Neogene	late Pliocene	Italy
<i>Squalus</i>	<i>acanthias</i>	Neogene	late Pliocene	Belgium
<i>Squalus</i>	<i>minor</i>	Neogene	late Pliocene	Japan
<i>Squalus</i>	sp.	Neogene	late Pliocene	Japan
<i>Squalus</i>	sp.	Neogene	late Pliocene	Spain
<i>Squalus</i>	sp.	Neogene	late Pliocene	Spain
<i>Centrophorus</i>	<i>squamosus</i>	Neogene	Pliocene	New Zealand
<i>Dalatias</i>	<i>licha</i>	Neogene	Pliocene	New Zealand
<i>Scymnodon</i>	sp.	Neogene	late Pleistocene	Western USA
<i>Squalus</i>	<i>acanthias</i>	Neogene	Pleistocene	Western USA
<i>Squalus</i>	sp.	Neogene	Pleistocene	Japan
<i>Squalus</i>	sp.	Neogene	Pleistocene	Western USA