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Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous

Charlie J. Underwood

RRH: DIVERSIFICATION OF THE NEOSELACHII

LRH: UNDERWOOD

Abstract. -The Neoselachii are a monophyletic group including all of the extant sharks and rays. They underwent rapid diversification throughout the Jurassic and Cretaceous, going from low-diversity assemblages of members of extinct orders in the Late Triassic to diverse assemblages containing representatives of most extant clades by the end of the Cretaceous. The known fossil record of Mesozoic neoselachians is composed largely of isolated teeth, with articulated skeletal remains being known from a limited number of sites. The small tooth size of a large proportion of neoselachians, including almost all taxa in existence prior to the mid Cretaceous, led to very poor representation in older publications. Their state of knowledge has improved dramatically since 1970 with the increased use of bulk sampling for isolated dental remains. Despite this, the high proportion of Lazarus taxa from some stages suggests that the state of knowledge is still intermittent. Increase in assemblage diversity throughout the Jurassic and Cretaceous suggests that radiation events resulted in real and dramatic increases in diversity, and that the perceived diversification is not an artefact of poor knowledge. Cladogenesis inferred from the fossil record typically compares more favourably with divergence predicted from molecular analysis, where Batoidea form a discrete basal clade, than with divergence predicted from morphological analysis, where Batoidea are considered a derived crown group within the Squalea. The timing of diversification events is discussed in light of the known fossil record, cladistically generated divergence times, and the paleoenvironmental distribution of faunas.

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Introduction

The Neoselachii represent one the most successful and diverse groups of chondrichthyans, encompassing all of the extant sharks and rays, in addition to several extinct clades. Undoubted neoselachians first appeared in the Early Triassic (e.g. Cuny 1998) but remained relatively insignificant until the Jurassic. During the Jurassic and Cretaceous, neoselachians diversified rapidly, resulting in members of most of the extant clades being present by the mid to Late Cretaceous. Although well-preserved skeletal remains of neoselachians are known from several localities (e.g. Cappetta 1987a), most of the fossil record of the group comprises isolated teeth. Despite this apparent restriction on the quality of the fossil record of the group, teeth are typically recognisable to specific level and give an accurate record of the neoselachian record (Cappetta 1987a).

Data

Data for this study were compiled from as many publications as possible figuring or describing Mesozoic neoselachians. Some publications with very poorly constrained stratigraphical framework were discounted. Unfigured species have been included only when the authors have a track record of publishing on neoselachian taxonomy. Generic affinity of taxa within publications was reassessed in light of subsequent work, and some specimens figured in open nomenclature were assigned to genera for this study. Figured specimens that cannot be assigned to described genera were added into lists of generic diversity despite having to be left in open nomenclature. Although there is some subjectivity in using data of this type, the poorly known nature of many Jurassic assemblages makes the inclusion of unnamed specimens necessary.

Perception of the Jurassic and Early Cretaceous Neoselachian Fossil Record

Early studies on Mesozoic fossil neoselachians typically concentrated on larger remains that would have been readily collected in the field. Although this has allowed large numbers of fossil taxa to be documented (e.g. Agassiz1833-1844; Woodward 1889), these were typically limited to taxa collected as skeletal remains or with large isolated teeth. This has given an extremely biased view of the neoselachian fossil record, with taxa bearing larger teeth being well represented (especially lamniforms) and taxa with smaller teeth being largely unrecorded, other than as skeletal remains from a small number of plattenkalks. Most of the specimens recorded before the 20th century were from northern and central Europe, and to a lesser extent, North America.

The concentration on macroscopic Mesozoic neoselachian remains remained relatively unchanged during most of the 20th Century, and by 1970 almost no studies had included sampling for microvertebrate remains, even though this had become common practice amongst Cenozoic vertebrate workers (e.g. White 1931). A notable exception to this, a study on faunas from Maastrichtian phosphorites by Arambourg (1952), still appeared to miss out most of the smallest teeth that have been subsequently recovered from the same rocks (e.g. Noubhani and Cappetta 1997). As a result of this concentration

on larger remains, the record of taxa with larger teeth (some larger Hexanchiformes and Palaeospinaciformes and Late Cretaceous Lamniformes) was relatively good. In contrast, almost the entire record of taxa with smaller teeth was known from the plattenkalks of Cerin (Saint Seine 1949), Solnhofen (e.g. Woodward 1918) and Nuplslinger (e.g. Schweizer 1961) and some Cretaceous sites (e.g. Cappetta 1980) (see Figure 1). Faunas were therefore well known from the Kimmeridgian, Tithonian and some levels within the Upper Cretaceous but not from earlier or intervening levels. The pre-Kimmeridgian record of several orders (Orectolobiformes, Carcharhiniformes, Squatiniformes and Batoides) was mostly unknown. In addition, the very poor Early Cretaceous neoselachian record resulted in the knowledge of these groups being purely based on lazarus ranges, with the record being inferred from earlier and later occurrences.
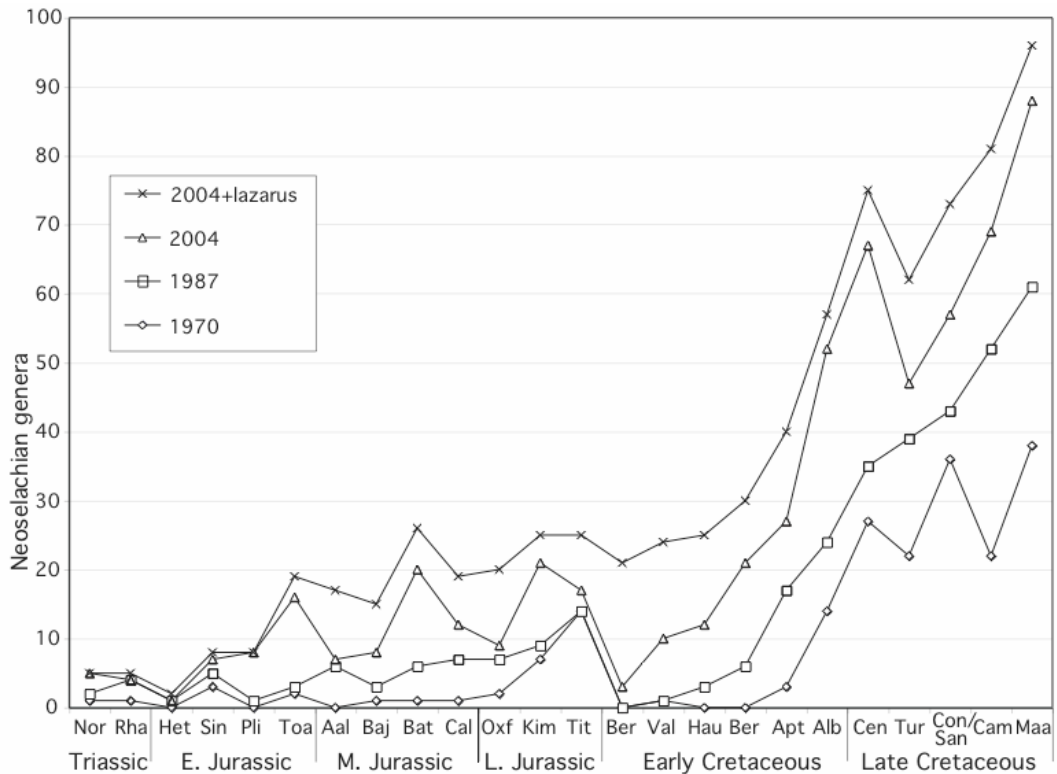

FIGURE 1. Increase in the knowledge of Mesozoic neoselachians, showing the numbers of genera (as currently recognised) figured or recorded from each stage (except for the combined Coniacian-Santonian) from the Norian to Maastrichtian by 1970, 1987 and mid 2004. A total number of known genera plus minimum number of lazarus genera and suprageneric clades is also shown as an indicator of the current state of knowledge. Note the dramatic apparent diversity increases in the late Early Jurassic, relating to the first appearance of extant clades, and the mid to Late Cretaceous, largely relating to diversification within these clades.

In 1987, a review of the neoselachian record known to date (Cappetta 1987a) revealed that the record of Mesozoic neoselachians was still heavily biased towards taxa represented by articulated skeletons or with larger teeth. These records were, however, augmented by material from piecemeal bulk sampling for micro teeth. Although relatively few studies had recorded small teeth from the Jurassic or Early Cretaceous (e.g. Thies

1981, 1983; Thurmond 1971) these had considerably improved the known neoselachian record of this time. The non-systematic nature of the collection of Jurassic and Early Cretaceous selachians resulted in very poor representation of faunas from some stages, with no neoselachians recorded from the Berriasian. This was in marked contrast to the great improvements in the knowledge of Late Cretaceous neoselachian faunas, with a diverse range of small-toothed taxa that had been described from studies of transgressive sediments across Europe (e.g. Herman 1977, 1982) and North America (e.g. Case 1978). The poor knowledge of pre-Late Cretaceous neoselachians in 1987 led to pre-Jurassc taxa being excluded from a study of diversification by Cappetta (1987b), and Berriasian to Barremian taxa being grouped together as a single data point.

Since 1987, a number of workers have undertaken to systematically sample Jurassic and Early Cretaceous rocks for neoselachian remains. Although these studies have typically focussed on European successions, knowledge of neoselachians from the Early Jurassic (e.g. Rees 1998, 2000), Middle Jurassic (e.g. Underwood and Ward 2004) Upper Jurassic (e.g. Candoni 1995; Underwood 2002) and latter part of the Early Cretaceous (e.g. Biddle 1993; Cappetta and Case 1999; Kriwet 1999; Underwood and Mitchell 1999) have dramatically improved. Neoselachian faunas from some stages remain poorly known, with no extensive faunas having been described from the Bajocian, Oxfordian or Berriasian. This is in part due to the general lack of suitable marine facies for bulk sampling of these horizons across northern Europe; this being especially true of the Berriasian where the three taxa that have been described come from low salinity palaeoenvironments (Rees 2002; Underwood and Rees 2002). In addition, several other neoselachian faunas (from the Toarcian [Delsate 2003], Callovian [Brown and Keen 1991] and Valanginian [Cappetta 1990]) have been mentioned in the literature, but have yet to be fully described.

Completeness of the neoselachian fossil record.

Despite the dramatic increases in knowledge of the early neoselachian fossil record, it remains poor. An overall view of the quality of the generic-level record may be assessed by comparing the number of known genera at any stage with the minimum number of lazarus genera (see Figure 2). Values for the Triassic and earliest Jurassic are difficult to assess due to the low standing diversity and uncertainty of the affinities of many taxa (e.g. Cuny 1998; Cuny and Benton 1999). Within the Early Jurassic, it is only within the Pliensbachian that no lazarus occurrences are predicted. Above this, the only Jurassic and Early Cretaceous stages where the number of lazarus genera represent less than 25per cent of the entire fauna are within the Toarcian, Bathonian and Kimmeridgian in the Jurassic and the Albian in the Early Cretaceous. Within the Berriasian, 17 of 20 genera known to have been extant are only known as lazarus "occurrences". A general idea of the degree of study of any stage may be indicated by the variety of facies sampled. Although many of the key taxonomic papers describing neoselachian faunas contain little or no account of the sedimentological and stratigraphical context, it has been possible to document the general facies groups from which neoselachian fossils have been recovered. In post Early Jurassic assemblages, low degrees of study, as indicated by low numbers of different facies recorded as yielding neoselachian material, relate to high proportions of lazarus taxa (see Figure 2). This is especially pronounced within the earliest Cretaceous, but is also the case in the Oxfordian and Turonian.

The high level of discovery of new species and genera also demonstrates the current poor knowledge of Jurassic and Early Cretaceous neoselachians. Most bulk sampling based studies of Jurassic and Early Cretaceous selachian faunas produce previously undescribed taxa, which commonly dominate. As an example, in one study of neoselachians from the Bathonian (Underwood and Ward 2004) only one of about 26 species recognised had previously been named, and about five others figured in open nomenclature. In addition to biases caused by poor sampling of many stratigraphic levels, recorded neoselachian faunas from the Triassic to Early Cretaceous are extremely biased geographically. Most Jurassic and earliest Cretaceous neoselachian faunas are known from Europe, with European and North American sites dominating studies of Triassic and mid Cretaceous neoselachians; the bulk of palaeogeographical regions remaining unstudied. There is frequently also a palaoenvironmental bias, with many of the studies of Triassic sharks being concentrated on shallow to marginal marine bone beds, and the bulk of Jurassic shark studies concentrating on faunas from neritic mudstones. The extent of this bias is suggested by a study carried out within the British Bathonian (Underwood and Ward 2004), where no single palaeoenvironment produced more that 15 of 26 taxa recovered during the study, despite the common presence of very large sample sizes.
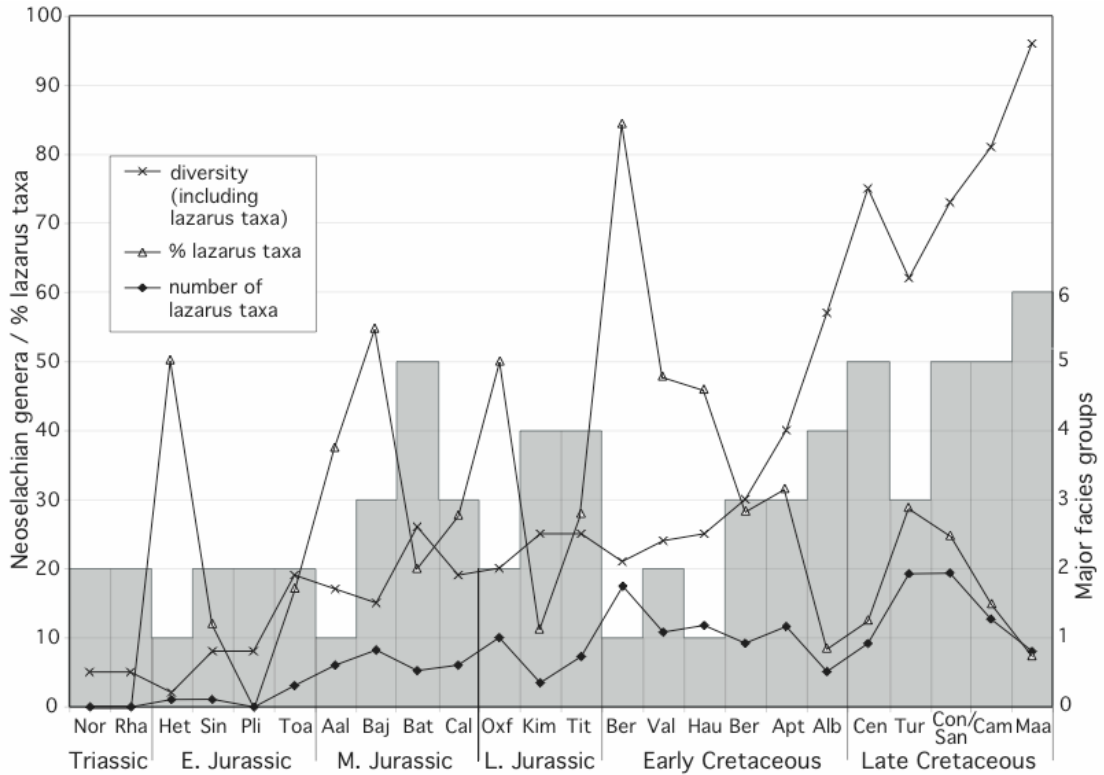

FIGURE 2. Completeness of the neoselachian fossil record as shown by number and percentage of lazarus taxa compared with total diversity as currently known. Histogram shows number of major facies groups that have been studied for neoselachian remains. Strong inverse relationships between high numbers of lazarus taxa and small numbers of facies studied are seen on the Oxfordian, Early Cretaceous and Turonian. Facies groups used are: anoxic neritic mudstone, aerobic neritic mudstone, coccolith mudstones (chalk), shelf siltstones and sandstones, shelf carbonates (including plattenkalks), phosphorites, shoal oolites, marginal bone bed and related facies, lagoonal facies, estuarine and deltaic facies.

Changes in assemblage structure

Strict interpretation of a plot of generic diversity of neoselachians through the Mesozoic appears to show a general low diversity within the late Triassic. There is evidence for a significant neoselachian diversification in the Early Jurassic and possibly Middle Jurassic, resulting in the first appearance of many new orders, and a second, larger phase of diversification through the mid to Late Cretaceous. As mentioned above, however, diversity curves are prone to a number of major biases, with variations in sample sizes, sampling intensity, palaeogeographical coverage and palaeoenvironmental specificity at different points in time. The general changes in diversity within assemblages may be clearly demonstrated by looking at the diversity of neoselachian taxa present within individual assemblages over time (Figure 3). The maximum assemblage diversity shows a dramatic increase in diversity over time, even when probable allochthonous and mixed assemblages (such as the two highest diversity faunas from the Maastrichtian phosphorites of Morocco) are not considered.
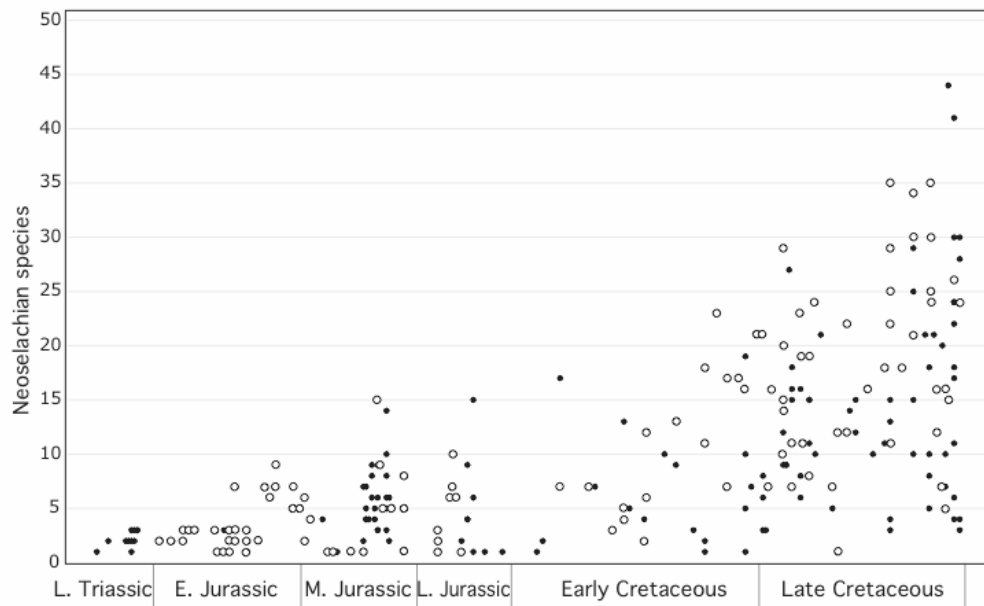
FIGURE 3. Numbers of neoselachian species recorded within published assemblages where taxa with very small teeth were included in the study. Open circles represent faunas from northern and central European muddy neritic sediments (siliciclastic and coccolith mudstones). Filled circles represent other assemblages.

The increase in neoselachian diversity within individual assemblages suggests that there is a general trend towards greater numbers of coexisting taxa, presumably due to

increasing degrees of niche partitioning through time. This is especially evident within fine grained neritic facies, where a dramatic increase in diversity is seen through the Jurassic and Cretaceous (see Figure 3). It is therefore evident that the increase in neoselachian diversity indicated by raw plots of occurrence data is empirically supported and not an artefact of greater numbers of studies of Late Cretaceous assemblages.

Although there is an increase in the number of neoselachian clades through the Mesozoic, not all of the increase in assemblage diversity is due to the addition of members of additional clades. This is especially well demonstrated by the Squaliformes, which are diverse within some of the high diversity later Cretaceous assemblages but are absent in others.

Timing of cladogenesis

Family ranges.-Familial level appearances of Mesozoic neoselachians roughly parallel the increases in total diversity seen at generic level. Although some degree of uncertainty of the familial affinities exists within some groups (especially the orectolobiforms and the batoids), the first and last known occurrences of many families are well constrained (see Figure 4). Comparison of these ranges with the different phylogenetic models allows the relationships between the known fossil record and predicted origination times to be assessed.

FIGURE 4. (Page 8) Range chart of Late Triassic to Cretaceous neoselachian families. Note that some groups used (stem group neoselachians, Dalatiiformes, Sclerorhynchoidei) probably contain several related families of uncertain relationship, whilst the Rajiformes inc. fam. contains a number of poorly known taxa that may not form a monophyletic group. Full details of the data used are in the appendix. Some ranges presented here (such as the Carcharhinidae) are based on unpublished material and are not included in other analyses.

Classification of the Neoselachii.-The classification of the Neoselachii has recently been in a state of flux (Maisey et al. 2004). Cladistic analyses (using morphological characters) of extant (e.g. Carvalho 1996; McEachran et al. 1996; Shirai 1996) and well preserved fossil (e.g. Carvalho and Maisey 1996) neoselachians have shown a relatively high level of consensus in the general patterns of neoselachian cladogenesis (Figure 5). These show the presence of two major clades, the Galea and the Squalea (also recognised in earlier works such as Maisey 1984), but with the third main suborder of Maisey (1984), the Batomorphii, being a derived group within the Squalea. Subsequent studies of the phylogeny of extant selachians using molecular data (e.g. Douady et al. 2003; Maisey al. 2004; Winchell et al. 2004) have produced a rather different suite of possible phylogenies. These molecularly derived phylogenies differ from those generated from morphological data chiefly in having the Batoidea as a clade originating from stem neoselachians and having no close relationship to the Squalea. This sister group relationship between the Batoidea and the sharks is supported by recent work on the former by McEachran and Aschliman (2004).

The presence of phylogenetic trees, albeit of two rather different morphologies, allows the known fossil record of the Neoselachii to be compared with the minimum predicted appearance time as inferred from divergence of sister taxa. Most previous studies of the possible divergence times of neoselachian groups (e.g. Thies 1983; Shirai 1996; Underwood et al. 1999) have been hindered by the lack of an extensive study of the Mesozoic neoselachian fossil record and pre-dated the publication of molecularly derived phylogenetic schemes. A more recent study by Maisey et al. (2004), however, concluded that the known neoselachian fossil record bore more relationship to the predicted clade origination times of a molecularly derived phylogenetic scheme than to morphologically derived phylogenies.

FIGURE 5. (Page 10) Summaries of the main neoselachian phylogenies discussed here showing the different positions of the batoids. In all trees, the galeids are shown to the left and the batoids to the right for consistency. 1 and 2 are based on morphological characters, 3, 4 and 5 on molecular data. 1, After Shirai 1996. 2, After Carvalho 1996, with Protospinax added in the position indicated in Carvalho and Maisey 1996. 3, After Douady et al. 2003. 4, After Winchell et al. 2004, with Pristis added in the position indicated by cytochrome *b* analysis in the same publication. 5, After Maisey et al. 2004. All trees shown without reanalysis. The temporal significance of the predicted divergence points is discussed below.

Diversification of the Neoselachii
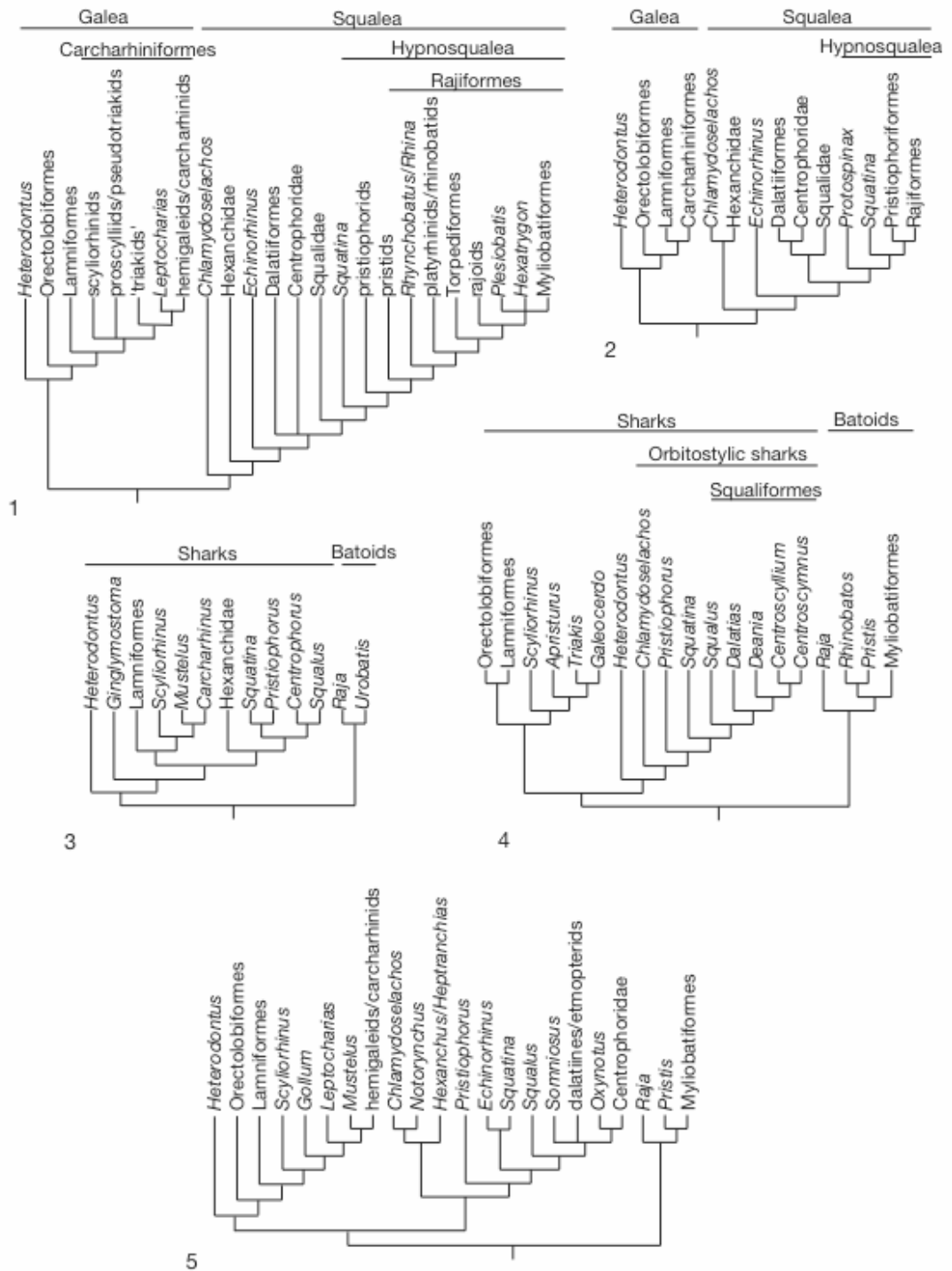
The divergence of neoselachian phylogenetic trees obtained by different methods has necessitated the consideration of both in this study. Many extinct groups have never been included into extensive cladistic analysis, with their phylogenetic position being poorly known. As this lack of inclusion is generally due to the lack or poor quality of non-dental remains, and it was considered that the lack of morphological data would prevent meaningful re-analysis for this study. The phylogenetic position of some groups is even more tentative within the molecularly derived trees, with some extant groups, such as the Torpedinoidea and Rhynchobatidae, having not been included in analyses. The relative merits of the positions within phylogenies occupied by fossil and problematic taxa are discussed below.

Pre-Jurassic Neoselachii.-All pre-Jurassic neoselachians are known from isolated teeth, and affinities have usually been deduced by study of enameloid microstructure (see Cuny and Benton 1999). Several taxa of Palaeozoic selachians have been suggested to have neoselachian affinities (e.g Duffin and Ward 1983a). Despite taxa having teeth that are morphologically similar to those of some neoselachians, they have a microstructure suggesting that morphological similarities are likely to be due to convergence (Cuny 1998).

The first definite neoselachians are known from the Triassic, being represented by teeth of Mucrovenator Cuny et al. 2001 and similar taxa (such as "Hybodus" minor Agassiz 1839 and Rhomphaiodon Duffin 1993). These share a very similar general tooth morphology with post-Triassic members of the Synechodontiformes, and may probably be included into it (Cuny and Benton 1999). Definite Synechododontiformes, in the form of several species of Synechodus Woodward 1888, are also present in Triassic assemblages. The same gross tooth morphology as present in the Synechodontiformes, comprising a low, bulky root with irregularly distributed foramina and a single or multiple erect cusps, is shared by other Triassic taxa such as Grozonodon Cuny et al. 1998 and Pseudocetorhinus Duffin 1998a. Although there are some differences in microstructure (e.g. Cuny and Benton 1999), these Triassic taxa may be closely related. Hueneichthyes Reif 1977, although poorly known, is also considered a to be a probable synechodontiform by Cuny and Benton (1999). The Late Triassic genus Reifia Duffin 1980, has a tooth morphology rather different from that of other Triassic neoselachians, with a flattened crown overhanging a gracile root with few foramina. The presence of this morphologically distinct form suggests that after the origination of the Neoselachii in the Early Triassic, cladogenesis within the Middle or early Late Triassic resulted in both a radiation within the Synechodontiformes and the generation of at least one other ordinal level group, presumably from within the paraphyletic Synechodontiformes. Other taxa (Vallisia Duffin 1982 and Pseudodalatias Reif 1978) with teeth morphologically similar to those of certain neoselachians, lack characteristic neoselachian microstructure (e.g. Reif 1977; Cuny and Benton 1999), but their affinities are otherwise poorly understood.

Post-Triassic Synechodontiformes and Hexanchiformes.-The systematic position of Synechodus and other palaeospinacids have been considered problematic (e.g. Maisey 1985, Maisey et al. 2004, Cappetta 1987a), and it has been suggested that they do not

form a monophyletic group (e.g. Maisey et al. 2004). The Synechodontiformes appear to lack any derived characters (Maisey et al. 2004), a state not unexpected within a basal group that is likely to be paraphyletic. They possess a dentition that shares many features with that of members of the Hexanchiformes (anaulacorhize root with grooves on the labial face, multiple cusplets in anterior/anterolateral files, symmetrical lower symphysial teeth, specialised crushing posterolateral/commissural teeth), with the dentitions of Welcommia Cappetta 1990 and Pseudonotidanus Underwood and Ward 2004 being morphologically intermediate between the two groups. Despite this similarity, all Synechodontiformes have asterospondylic vertebrae (e.g. Underwood and Ward 2004), unlike the cyclospondylic vertebrae of the Hexanchiformes. Although the presence of different vertebral types may suggest a distant relationship, asterosondylic vertebrae are present in Pseudonotidanus, and longitudinal 'lamellae' on the vertebrae of some Mesozoic Hexanchiformes (see Cappetta 1980) may suggest an intermediate stage in vertebral ossification and that the cyclospondylic state is a derived character within later Hexanchiformes.

All analyses of neoselachian phylogeny have placed the Hexanchiformes, and hence if closely related, the Synechodontiformes, close to the origin of the Squalea / orbitostylic sharks (see Figure 5). Dental characters appear to suggest a close, presumably paraphyletic, relationship between the Hexanchidae s.l., Pseudonotidanidae (Underwood and Ward 2004) and Palaeospinacidae (Duffin and Ward 1993). The presence of hexanchids in Early Jurassic rocks suggests that this radiation event must have occurred during the earliest Jurassic or possibly Late Triassic.

Sphenodus Agassiz 1843 has been placed within a number of neoselachian groups (Maisey et al. 2004), but the similarities of a number of skeletal (Böttcher and Duffin 2000) and dental (Duffin and Ward 1993) characters suggest that it is most likely to be closely related to Synechodus. The absence of a pseudopolyaulacorhize tooth root characteristic of the Palaeospinacidae may suggest a Mucrovenator-like, and hence probable Triassic, ancestor. Alternatively, it is possible that Sphenodus was derived from within the early Hexanchiformes, where pseudopolyaulacorhizy was already lost. The elongate teeth of Sphenodus are superficially similar to those of lamniforms, differing in the form of the root and the possession of Synechodontiforme/Hexanchiforme-type commissural teeth. The possession of upper 'intermediate' teeth is a typically lamniform character, relating to the separation of lateral and anterior dental hollows where the jaw is at its point of maximum curvature. This state is correlated with prevention of the elongate teeth from impinging on each other during rotation into their functional position, being far less evident within smaller-toothed Lamniformes (such as Alopias pelagicus and planktivorous taxa). If this is the case, it is likely that the similar character in Sphenodus is a function of the same developmental constraints, and is of little taxonomic value.

The relationship of Chlamydoselachus Garman 1884 to the Hexanchidae is not well resolved. RAG-1 analysis by Maisey et al. (2004), suggest that it is a sister group to Notorynchus within the Hexanchidae. Other studies position Chlamydoselachus outside the Hexanchidae, with it being considered a sister group to the Hexanchidae by Carvalho (1996), but a sister group to all other Squalea, including the Hexanchidae, by Shirai (1996). The basal position of Chlamydoselachus (Winchell et al. 2004) and Hexanchiformes (Douady et al. 2003) relative to other orbitostylic sharks (Pristiophorus,

Squatina and Squaliformes) is also suggested by genetic studies. Whatever the true relationships of the Chlamydoselachidea, an earliest Jurassic or Late Triassic origin is inferred, far pre-dating the first appearance in the fossil record of the clade. This poor fossil record is to be expected if early members of the family shared the deep marine habitats of the extant species, as there has been an almost complete lack of studies into selachian remains from pre-Campanian deep marine rocks.

Ostenoselache.-The Early Jurassic genus Ostenoselache Duffin 1998b possesses a number of unique characters, including an elongated neurocranium and lack of dorsal fins. There are few derived, non-autapomorphic characters (Duffin 1998b), and as such there is little indication of systematic position. The poorly preserved teeth have a morphology that, despite having a single cusp, is similar to that of Chlamydoselachus, but also bear some resemblance to teeth of some Triassic Synechodontiformes. In either case, an earliest Jurassic or Late Triassic origin is likely.

"Stem Group" Squalea / other orbitostylic sharks.-The relative position of orders within this (paraphyletic or monophyletic) group is somewhat disputed, as the presence or absence of batoids as a derived clade influences the positions of other taxa within the phyolgeny. Studies based on morphology place the batoidea as a highly derived group, with Pristiophorus and Squatina, as well as the fossil Protospinax, as moderately derived, the Squaliformes being least derived. Molecular analyses (which obviously do not include Protospinax) place the Squaliformes as the most derived group and the Pristiophoriformes and Squatiniformes / Echinorhiniformes as either progressively more derived stem groups (Winchell et al. 2004; Maisey et al. 2004) or as sister groups (Douady et al. 2003).

Only a single molecular study (Maisey et al 2004) has included Echinorhinus, and this has it as a sister taxon to Squatina. Several other studies, based on both dental and whole-body morphology, have suggested that Echinorhinus is a basal squalean, sharing a number of characters with the Hexanchidae (e.g. Carvalho 1996; Shirai 1996; Adnet and Cappetta 2001). Although the earliest fossils of the Echinorhinidae are known from the 'mid' Cretaceous, it is predicted that the origination time of the clade was during the Early Jurassic. The poor fossil record of echinorhinids is probably a function of their deep water habits.

Although many of the taxa within the remainder of the orbitostylic sharks have a relatively poor Mesozoic fossil record, the minimum timing of cladogenesis is well constrained by the first appearance of the derived squalean Protospinax and batoids in the later Early Jurassic, at least within the phylogeny of Carvalho and Maisey (1996).

The Squaliformes are considered to be a paraphyletic group by Shirai (1996), although analyses by Carvalho (1996) and Adnet and Cappetta (2001) and molecular studies suggest that they form a monophyletic group, the latter interpretation agreeing far better with the known fossil record of the group. Morphological analyses give a predicted origination time of the Squaliformes within the Early Jurassic, even though they are unknown in the fossil record prior to the Early Cretaceous. It is possible that any Jurassic Squaliformes were largely restricted to boreal regions, as they were in the Cretaceous

(Jurassic boreal successions having yet to be systematically studied for selachians). The lack of Jurassic squaliform fossils, however, agrees better with the position as the most derived clade within the orbitostylic sharks as suggested by molecular studies, which do not require an origination prior to that of the Squatiniformes or Pristiophoriformes. Although the Dalatioidea (of Carvalho 1996) are considered to be a sister group to the Squalidae (sensu Carvalho 1996) by Adnet and Cappetta (2001) and Carvalho (1996), it is possible that they evolved within a paraphyletic Squalidae by increasing heterodonty. It is therefore possible that the latest origination time for the Dalatioidea was either during the Early Cretaceous (if there is a sister group relationship) or during the earliest Late Cretaceous (when they first appear in the fossil record; see Adnet and Cappetta 2001).

The Protospinacidae are an extinct family of squaleans (Carvalho and Maisey 1996) first known from rocks of Early Jurassic age. Shared (if not unique) characters within the Protospinacidae and Squatinidae (Carvalho and Maisey 1996) suggest that the latter should share an Early Jurassic predicted origination time. Although fossils of the Squatinidae are not known from rocks older the Late Jurassic, teeth of Jurassic species differ from those of post-Jurassic species (Underwood 2002) and are likely to be very difficult to distinguish from teeth of some Orectolobiformes.

The Pristiophoridae are considered relatively underived in all molecular studies, with a predicted origination time similar to, or earlier than, that of the Squatinidae. Assuming a close squatinid-protospinacid relationship, this would give an early Jurassic origination for the order. Although considered more derived in morphological studies, the early Jurassic appearance of rays would likewise suggest an origination of the Pristiophoridae in the early Jurassic. The fossil record of the Pristiophoridae is quite poor, with the earliest known fossils being from Late Cretaceous rocks, considerably post-dating their predicted divergence time in the Early Jurassic. It is possible that the small, relatively undiagnostic, oral teeth of this group could be overlooked, with the distinctive oral teeth being a derived character only appearing within the clade in the Cretaceous.

Batoidea/ Rajiformes.-In addition to the great discrepancy as to the position of the Batoidea within the Neoselachii (see Figure 5), there is little consensus on the pattern of phylogeny of the rays, with very different trees being proposed by different workers (e.g. McEachran et al. 1996; McEachran and Aschliman 2004; Shirai 1996). Different phylogenetic schemes vary considerably in the relative position of different groups, with molecular studies having included relatively few batoid taxa. Examples of this uncertainty include whether the Pristidae or Torpedinoidea are the least derived batoids (see Shirai 1996 and McEachran and Aschliman 2004 respectively), or the possibility that the Pristidae are a sister group to the Rhinobatidae (Wincell et al. 2004). In addition, there is disagreement in the degree of paraphyly recognised within the rhinobatids s.l. (two clades according to Shirai 1996, and at least five in McEachran et al. 1996). More recent work has suggested that whilst the rhynchobatids, rhinobatids and rajids form a monophyletic group, the platyrhinids form a sister group to the Myliobatoidea. This would suggest that the 'rhinobatid' body plan (elongate with a muscular caudal region) is primitive and the highly expanded pectoral fins and reduced caudal region of the Rajidae and the Myliobatoidea is independently derived. There is even less agreement on the phylogeny of the 'rhinobatids s.l. when extinct forms are added to the analyses (e.g. Brito

and Seret 1996). The highly specialised nature of the batoids leaves assessment of homology of characters very open to interpretation, and it is likely that this is the main reason for the lack of consensus of batoid phylogenies.

Molecular analyses consistently show the Batoidea as a monophyletic clade forming a sister group to all other extant neoselachians. This would suggest an origination time preceding the first appearance of any extant shark groups, and would hence indicate an origin within the basal Jurassic or Late Triassic. In this case, the batoids would probably have arisen from within the paraphyletic complex of Triassic neoselachians. If the batoids are considered to be derived squaleans, their first appearance in the latter parts of the Early Jurassic would match their expected origination time, close to that of Protospinax. In the latter model, an earlier origination time would also indicate earlier origination for all other Squalea, for which there is no evidence (e.g. Maisey et al. 2004).

Presumed batoid teeth from the Early Jurassic have a general morphology characteristic of that of rhinobatids and other less derived batoids, but at least two genera, Jurobatos Thies 1983 and Doliobatis Delsate and Candoni 2001, have a multilayered enameloid microstructure present in neoselachian sharks but absent in all other rays. If, as the microstructure of Triassic neoselachians would seem to suggest, multilayered enameloid is a primitive feature of the Neoselachii, the apparently simpler enameloid of the Batoidea would be a derived character (a similar state occurs within the molariform lateral teeth of Heterodontus). It is therefore likely that these, and possibly other poorly defined genera of similar tooth morphology (Delsate and Candoni 2001), mark a stage in batoid evolution where the characteristic tooth design has appeared but enameloid structure has not. As no remains other than isolated teeth are known, it is unclear whether these taxa should be regarded as true batoids or not.

The relative position within batoids of Spathobatis Thiolliere 1854 and Belemnobatis Thiolliere 1854 is poorly known. This clade is considered more derived than the Pristidae and Rhynchobatidae by Brito and Seret (1996), although in their analysis fin spines were regarded as a derived character (although they are more likely to represent a primitive feature [J. Maisey personal communication 2003]) and did not include the poorly developed synarcual within this clade as a character. Due to these probably primitive characteristics, it is here considered that the "Spathobatidae", which first appear in the fossil record in the latest Early Jurassic, are likely to be at, or close to, the base of the Rajiformes.

It is likely that all extant batoid groups, with the possible exception of the Torpedinoidea are derived from within the paraphyletic "Spathobatidae". The fossil record of any proposed 'near basal' batoid (Pristidae, Torpedinoidea and Rhynchobatidae) is poor, with only the Rhynchobatidae having any known Mesozoic representatives (it is not here considered that Peyeria Weiler 1935 is a pristid). This may be due to a result of a poor knowledge of marine microvertebrates in general, possibly in combination with the late origin of distinctive characters (rostral teeth in the Pristidae and distinctive tooth morphology in the Torpedinoidea) within the history of the clade. Despite the basal position of the Pristidae in morphological analyses, molecular studies have included Pristis as more derived than Raja (Maisey et al. 2004) and as sister taxon to Rhinobatos (Winchell et al 2004). It is possible that the basal position of the Pristidae (and therefore possibly other families) obtained from morphological cladistic studies is an artifact of

convergence with derived orbitostylic sharks. This is presumably as a result of use of the caudal fin for propulsion and hence development of a "shark-like" body plan. A derived position, and hence later divergence, of the Pristidae (and Torpedinidae) agrees better with the fossil record.

The fossil record of the more derived batoid clades appears to be rather better than that of the stem group batoids, with fossils indicative of the Rhinobatidae, Myliobatoidea and probably other groups (e.g. Kriwet, 1997) all known from Late Jurassic or Early Cretaceous rocks. The first fossil appearance of these groups ties in well with an origination time during the latter part of the Jurassic. The systematic position of extinct groups such as the Hypsobatidae is uncertain. The systematic position and origins of the Sclerorhynchoidea, which first appears in the Barremian (Kriwet 1999), are poorly known, but overall morphological features may suggest a relationship to the Rhinobatiodae or Pristidae. Several genera of supposed sclerorhynchoid affinity (such as Celtipristis Kriwet 1999, Kiestus Cappetta and Case 1999 and Ptychotrygon Jaekel 1894) are known from oral teeth only, and do not appear to have possessed rostral teeth. The relationships between these and 'true' sclerorhynchoids are poorly understood, and it is possible that these taxa represent additional, separately evolving, clades.

Galea.-The earliest recorded member of the Galea is the enigmatic Early Jurassic genus Agaleus. Agaleus is only known from isolated teeth, which show a combination of characters similar to those of the Heterodontiformes and Orectolobiformes (Duffin and Ward 1983b), but also some autapomorphic characters (Duffin and Ward 1983b, Rees 2000), suggesting that it is likely to represent a sister group to other galeids. A sister group relationship between the Agaleidae and other Galea implies an initial radiation during the earliest Jurassic. The origin of the Galea is poorly understood. The (especially anterior) teeth of Agaleus are morphologically very similar to teeth of genus Vallisia (Underwood and Ward 2004), but the microstructure of Vallisia suggests that it is not a neoselachian (e.g. Cuny and Benton 1999). Resemblances must therefore be superficial unless the Neoselachii are a polyphyletic group. As the monophyly of the Neoselachii is well supported (e.g. Maisey et al. 2004), a relationship between Vallisia and Agaleus can be discarded.

Almost all phylogenetic analyses have the Heterodontiformes as sister group to all other extant Galea, although there is some (statistically insignificant) suggestion from molecular studies that they represent a group of basal neoselachians (Winchell et al. 2004). The presence of teeth of both heterodontids and orectolobids in rocks of later Early Jurassic age (e.g. Thies 1983) suggest an Early Jurassic divergence time within the Galea. Although most of the oldest known fossil orectolobids have a tooth morphology similar to that of modern hemiscylliids (e.g. Underwood and Ward 2004), analyses of Shirai (1996), Compagno (1988) and Maisey et al. (2004) suggest that the Parascylliidae are a sister group to all other Orectolobiformes. Although the earliest known fossils positively attributable to the Parascylliidae are mid Cretaceous in age, it is possible that Jurassic representatives of the clade are represented by teeth of uncertain affinity such as Annea Thies 1983, which have an elongate main cusp and compact, high root similar to that of known parascylliids. The affinities of many other Jurassic and Cretaceous Orectolobiformes are likewise very poorly known, and radiations within the order are

therefore poorly constrained, although several distinct tooth morphotypes are known from the Middle Jurassic, suggesting a later Early Jurassic to Middle Jurassic radiation event.

A monophyly of the extant Orectolobiformes is suggested by most analyses. There is, however, disagreement whether the Orectolobiformes are sister group to a clade containing the Lamniformes and Carcharhiniformes (as suggested by morphological analyses and Maisey et al. 2004) or whether the Carcharhiniformes are a sister group to the Orectolobiformes + Lamniformes (Winchell et al. 2004). Palaeocarcharias Beaumont 1960 shows many orectolobiform characters, but with teeth far more similar to those of Carcharhiniformes and Lamniformes, and has been considered as a form intermediate between the Orectolobiformes and Lamniformes (Duffin 1988). An intermediate morphology of Palaeocarcharias would therefore suggest an origin of the Lamniformes (and possibly Carcharhiniformes) within the paraphyletic Orectolobiformes. This paraphyly is further suggested by the presence of a tripodal rostrum, a character generally considered an autapomorphy of the Carcharhiniformes + Lamniformes, in the orectolobiform Acanthoscyllium Cappetta 1980 (see Maisey 1984).

Teeth attributable to the Scyliorhinidae and possibly Proscylliidae are known from the Middle Jurassic (e.g. Underwood and Ward 2004, Early Jurassic records being erroneous (Delsate et al. 2002)). The earliest remains of the Triakidae are from the Early Cretaceous, and although these (forming a clade with other "advanced" carcharhiniforms) were placed in an unresolved trichotomy with the Scyliorhinidae and Proscylliidae / Pseudotriakidae by Shirai (1996), they are considered by Maisey (1984) to have emerged from within the paraphyletic "scyliorhinids"; similar relationships were suggested by Winchell et al. (2004). Despite the proposed sister group relationship between the Carcharhiniformes and Lamniformes, fossils attributable to the latter are unknown prior to the early Cretaceous. Although this may be due to the poor knowledge of the fossil record, it is possible that Jurassic lamniform teeth have been misidentified as teeth of scyliorhinids; indeed lamniform teeth from the earlier Early Cretaceous are uniformly small and look rather similar to teeth of scyliorhinids. It is possible that the lack of a pulp cavity, a character commonly used to differentiate teeth of Lamniformes from those of Carcharhiniformes, is a derived character appearing later within the Lamniforme clade, and not possessed by its earlier members. Further radiation of the Lamniformes is poorly understood, although there is a dramatic increase in generic and familial (e.g. Siverson 1996) diversity in the mid Cretaceous.

Phylogenetic interpretation and the neoselachian fossil record

Despite the relatively poor, but rapidly improving, knowledge of the Jurassic and Cretaceous neoselachian fossil record, it is possible to use the fossil record as an independent test for the likely reliability of the different proposed neoselachian phylogenetic schemes (see Maisey et al. 2004). As discussed above, the known fossil record (typically occurring as isolated teeth) agrees better with the phylogenies developed from molecular studies than those generated from whole-body morphological data. In particular, the presence of batoids as a separate clade rather than a derived group within the Squalea agrees better with the known fossil record. Although this would necessitate the slightly earlier appearance of the batoids (latest Triassic or basal Jurassic), it would not require the first appearance of several groups of stem group squaleans within the early

Jurassic, many of which are unknown prior to the Cretaceous. In addition, phylogenies suggesting high degrees of paraphyly within the squalids (Shirai 1996) or batiods (McEachran et al 1996) are not well supported by the available fossil data, as they would require the presence of diverse lineages early within the development of the group, for which little or no evidence exists. The relative merits of the different phylogenetic schemes are discussed in detail by Maisey et al (2004).

Neoselachian diversification events

Different methods of analysing Jurassic and Cretaceous neoselachian diversification appear to give rather different interpretations. Plots of generic occurrence appear to show a rather irregular pattern of radiation, with the greatest diversity increases occurring in the late Early to Middle Jurassic and in the mid to Late Cretaceous. Plots of maximum marine diversity show a general increase in assemblage diversity throughout the Jurassic and Cretaceous, although the small number of recorded high-diversity assemblages makes interpretations difficult. Diversification patterns predicted from cladogenetic timing indicate rapid diversification during the Early Jurassic, but with lower rates of cladogenesis thereafter. By using all three lines of evidence, however, it is probably possible to gain a far more accurate view of the diversification of this group than would be possible from one method alone.

Extensive sampling for Triassic selachians, in both open marine and lagoonal settings, has consistently produced low diversity neoselachian assemblages, with Synechodus representing the only genus present that is also known from post-Triassic faunas. It is therefore likely that any significant cladogenesis resulting in the evolution of diverse, extant orders occurred after the Triassic. The presence of teeth of Sphenodus and hexanchids in Sinemurian rocks demonstrates that diversification within the Synechodontiformes had occurred during the latest Triassic or earliest Jurassic. Sinemurian fossils of Agaleus indicate the presence of at least one clade of galeids by this time, but it in unclear whether this is the result of a Triassic or earliest Jurassic radiation event. If Agaleus is a true galeid, it would suggest that, if the phyologenies derived from molecular evidence are correct, batoids must have already differentiated by this point. The presence of a batoid-like tooth from the Sinemurian-Pliensbachian (Curtis and Padian, 1999) is highly significant if phylogenies derived from morphological analysis are to be believed, as it indicates a major radiation within the Squalea, with the origination not only of the batoids but also of all of the groups of stem-group Squalea. With the exception of this batoid tooth, extensive studies of Pliensbachian selachian faunas (e.g. Ward 1999; Rees1998, 2000; Delsate 2001), have yielded only Synechodontiformes, Hexanchiformes and Agaleus. It is possible that the failure of these studies to find squalean remains is due to their sampling on neritic rocks from a small palaeogeographical area within the boreal realm.

Studies of Toarcian assemblages (e.g. Thies 1983; Delsate and Lepage 1990; Delsate and Godefroit 1995) suggest a rapid period of Early Jurassic cladogenesis, with the first fossils of Orectolobiformes, Heterodontiformes, Rajiformes and Protospinax occurring within relatively low diversity assemblages. Despite the presence of a number of orders, there is still a noticeable lack of fossils of stem group squaleans. As with studies of Pliensbachian assemblages, all known Toarcian neoselachians have been collected from

open marine sediments representing a single faunal realm (sub-boreal). It is therefore unlikely that a full census of the selachians present at the time is available.

Very few studies of selachian fossils have been carried out on rocks from the earlier Middle Jurassic, although piecemeal studies (e.g. Young 1982; Thies 1983; Delsate 1993) appear to indicate further radiation within the Orectolobiformes; other elements of the fauna remaining very similar to those from the Toarcian. Studies of selachians from the Bathonian have been more extensive (Underwood and Ward 2004), with fossils from a number of palaeoenvironments being collected, although all of the studies were still within a limited palaeogeographical area, (probably within the sub-boreal province). Higher diversity neoselachian faunas were recorded compared with older rocks, with diversities being higher in neritic palaeoenvironments than in shallow marine or lagoonal settings (Underwood 2004a). Most of the clades recorded in earlier Jurassic assemblages were present, with the earliest known examples of members of the Scyliorhinidae and possibly Proscylliidae indicating a further radiation event within the Galea. If monophyly of the Carcharhiniformes as a sister group to the Lamniformes is assumed (e.g. Carvalho 1996; Shirai 1996), it would suggest that that Lamniformes would also have appeared by this time. It is possible that teeth of early Lamniformes could be very difficult to recognise if the clade only developed larger body size and pelagic habits during its subsequent development, with early Lamniformes being very 'scyliorhinid-like'. The existence of 'scyliorhinid-like' early Lamniformes may be evidenced by Pteroscyllium Cappetta 1980, which possesses an apparent mosaic of 'lamnid' and 'scyliorhinid' characters (Maisey 1984, Underwood 2004a). Despite the large sample sizes, the only non-hexanchiform orbitostylic shark recorded was Protospinax. These Bathonian assemblages offer the earliest indication of palaeoenvironmental specificity amongst the neoselachians, with most species and many genera being restricted to either neritic, shallow marine or lagoonal settings.

Callovian and Oxfordian neoselachian faunas have been described on a number of occasions (e.g. Thies 1983; Martill 1991; Kriwet 2003; Popov et al. 2004), although they still remain fairly poorly known. They do, however, appear very similar to those from the Bathonian. Although teeth referred to Squatina by Thies (1983) are present, it is here considered more likely that they belong to an orectolobiforme similar to, or congeneric with, Cretorectolobus (see Underwood 2002).

The Kimmeridgian and Tithonian represent the earliest time period from which both boreal (e.g. Candoni 1993; Underwood 2002) and Tethyan (e.g. Saint Seine 1949; Thies 1981; Candoni 1995) neoselachians are well known. Most of the neoselachians recorded belong to clades recorded from older rocks, although there are a few additional forms. *Squatina* is known from complete skeletons, although the teeth from these (Leidner and Thies 1999) indicate a dentition more closely resembling that of hemiscylliid Orectolobiformes than extant Squatina. It is therefore possible isolated teeth of Squatina are known from rock older than Kimmeridgian, but have yet to be recognised as such (Underwood 2002). Corysodon Saint-Seine 1949 is known from both skeletons and isolated teeth. Although placed in a unique family within the Carcharhiniformes by Thies and Candoni (1998), it is here considered to belong within the Orectolobiformes (the body shape and fin positions are very similar to Nebrius, whilst the teeth are not unlike those of the Ginglymostomatidae, differing largely in the presence of a longitudinal ridge).

Although the batoids known from northern and central Europe are all members of the "Spathobatidae", fossils from elsewhere suggests that there was a significant pre-Kimmeridgian radiation within the batoids. An indeterminate batoid from the Tithonian of Argentina (Cione 1999) has a 'rhinobatid' body plan and a well-developed synarcual, suggesting the presence of either the Rhinobatidae or Rhynchobatidae. Morphologically generalted phylogenies would therefore also suggest the presence of at least two clades of paraphyletic 'rhinobatids', the Pristidae and the Torpedinoidea (Carvalho 1996), by the Kimmeridgian. Teeth of other, enigmatic, genera (Kriwet 1997, 2003; Arratia et al. 2002) suggest further batoid diversification. The lack of derived batoids within well-studied European deposits demonstrates that at least some Jurassic neoselachian groups had restricted biogeographical ranges.

Although neoselachian faunas from the pre-Albian Early Cretaceous are no better known than those of the Jurassic, faunas are known from a greater diversity of palaeogeographical regions, and the strong geographical control on neoselachian occurrence is clearly evident. Neoselachians are as yet very poorly known from the earliest Cretaceous, with studies of selachians from marine facies being extremely limited; indeed all three of the neoselachians known from the Berriasian were recovered from restricted salinity facies (Rees 2002; Underwood and Rees 2002). Selachian faunas from the Valanginian and Hauterivian appear to differ with faunal province, but give the earliest indication of several clades. Whilst an undescribed fauna from France (Tethyan realm) contained no clades unknown in the Jurassic (Cappetta 1990), a fauna from Poland (Boreal or sub-boreal) contained the earliest teeth assignable to a lamniform (Rees in press). An additional assemblage from England, from the strongly Boreal North SeacBasin, lacked lamniformes, but contained teeth of a batoid assignable to the Dasyatidae and a probable triakid (Underwood et al. 1999). There is therefore evidence that cladogenesis had occurred within both the batoids and advanced Galea during, or immediately prior to, the earliest Cretaceous. Although, assuming Carcharhiniform + lamniform monophyly, Lamniformes would have first appeared during the Jurassic, and the other new taxa are likely to represent post-Jurassic radiation events. If the batoid phylogeny of McEachran et al. (1996) were true, the first appearance of <u>Dasyatis</u> would indicate very considerable batoid radiation, with the appearance of a number of clades. Although not requiring as extreme a radiation event, the batoid phylogeny of McEachran and Aschliman (2004) would also suggest the appearance of a number of clades by this time. There is further evidence of the appearance of new clades in assemblages from the Barremian. Tethyan and sub-boreal faunas contain a number of additional batoid groups (Kriwet 1999; Biddle and Landemaine 1988), including the earliest Sclerorhynchoidea, whilst the earliest fossils of the Squalidae are known from more boreal regions (Thies 1981, Underwood 2004b). In addition, diversification within the Lamniformes had resulted in several genera being present in some assemblages (Kriwet 1999). Aptian neoselachian assemblages (e.g Cappetta 1975; Batchelor and Ward 1990; Underwood 2004b) typically contain a higher diversity of lamniform taxa than in older rocks, including the earliest examples of the Anacoracidae (Underwood 2004b) and Mitsukurinidae (Cappetta 1975). Aptian lamniform diversity included several families, with the first evidence for moderately large lamnids.

The Albian represents the earliest time period to have been extensively studied for neoselachian remains, with assemblages having been recorded from a range of marine and

marginal marine facies from several continents. There is evidence for considerable variations in taxonomic composition of assemblages from different palaeogeographical regions and facies (e.g. compare Biddle 1993; Welton and Farrish 1993; Underwood and Mitchell 1999). Some assemblages from the Albian give the first indication of a major increase in marine neoselachian ecological diversity since the Bathonian (e.g. Biddle 1993; Underwood and Mitchell 1999; Ward in press). Much of this overall increase is due to an increase in the diversity of the Lamniformes, with the appearance of a number of genera, as well as an increase in diversity of batoids and Squaliformes. Despite the relatively high degree of knowledge of Albian neoselachian faunas, the only major clade with a first occurrence in the Albian is the Echinorhinidae (see Kemp 1991, described as an anacoracid; Siverson, 1996), with a continued lack of a number of phylogenetically predicted clades (Chlamydoselachidae, Dalatioidei, Pristiophoridae, Pristidae and Torpedinoidea). The lack of a number of predicted clades from Albian assemblages may be due to poor knowledge of faunas from some palaeoenvironments (especially tropical carbonate shelves and deep marine settings, sediments from which have not been studied). It is also possible that some of these 'missing groups' have not been recorded due to misidentification of dental remains of basal members of the clades. Alternatively, the lack of some clades, especially those where many representatives inhabit shallow water (Pristiophoridae, Pristidae and Torpedinoidea), may be taken as evidence against phylogenetic models that predict their presence.

Knowledge of Late Cretaceous neoselachians is far better than that of faunas from the Jurassic and Early Cretaceous. There is a general increase in diversity within assemblages, with high diversities of Lamniformes, batoids and sometimes Squaliformes being present, especially within neritic settings. Despite the generally very good record of Late Cretaceous neoselachians, there is no good evidence for Pristidae and Torpedinoidea until the Palaeocene.

Palaeoenvironmental controls on neoselachian radiations

Despite the poor published record of the geological context of many neoselachian assemblages, it is clear that remains have been recorded from a wide range of palaeoenvironments, from offshore marine to lagoonal and deltaic.

The palaeoenvironmental controls on the distribution of Triassic neoselachians are currently poorly understood, with relatively low numbers of facies having been sampled from many stages (see Figure 2). Whereas some Triassic neoselachian-bearing rocks are clearly open marine (e.g Cuny et al. 2001; Figure 3), many of the best known faunas are from more cryptic "Rhaetic Bone Bed" facies or within cave-fill deposits (e.g. Duffin 1998c). The palaeoenvironmental significance of these deposits is poorly understood (e.g. Martill 1999), but it appears to indicate the presence of neoselachians within lagoonal, coastal and possibly reduced salinity settings as well as within the open sea.

All neoselachians recorded from the Early Jurassic are known from open marine facies, generally neritic mudstones. Although there is no evidence for neoselachians in other palaeoenvironments, by comparison with Late Triassic and Middle Jurassic faunas it is likely that there were other assemblages in lagoonal and other marginal settings at the time. It is possible that the apparent sudden and simultaneous appearance of a number of

neoselachian clades during the Toarcian was due not to a radiation event at that time but to a colonisation event. Members of clades that had already developed within lagoonal settings moved into open marine habitats, possibly as a consequence of the Toarcian transgression. Indirect evidence for the possibility of evolution of many neoselachian clades within marginal marine settings comes from analysis of Bathonian faunas, where members of all families that first appear in open marine facies in the Toarcian to Bathonian interval are also present within lagoonal facies.

Despite the presence of a wide range of neoselachian clades within lagoonal and neritic facies in the Middle Jurassic, several squalean groups are predicted to have been present that are unknown in the fossil record. Although it is possible that several of these (such as the Pristiophoridae) lacked distinctive teeth and may have been found but misidentified, others (such as the Chlamydoselachidae and Echinorhinidae) would probably have had distinctive dental remains and their absence from the fossil record is more likely due to the absence of members of these clades from rocks that have been studied. It is possible that these groups existed in geographical areas away from Europe. Indeed, the Squaliformes, despite being well known and diverse in the Late Cretaceous, are almost entirely restricted to boreal regions. Similar provinciality to that of the Cretaceous Squaliformes within the far less well studied Jurassic could easily account for their lack of a fossil record. An alternative explanation if that several squalean clades were present within deep marine environments, deposits from which have not been studied. This would be consistent with the modern, generally deep water, distribution of the Chlamydoselachidae, Echinorhinidae and many Squaliformes.

The presence of different neoselachian clades in lagoonal, shelfal and deep marine conditions by the later Early and Middle Jurassic suggests that the taxonomic diversification was most likely associated with an ecological diversification, with a dramatic and possibly near simultaneous colonisation of a range of marine habitats. It is possible that it was the ability to readily modify a basic body plan and tooth morphology to allow the colonisation of a wide range of palaeoenvironments that were the key to the post-Triassic success of the Neoselachii.

Acknowledgements

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Appendix

Known occurrence of families and other suprageneric clades of Jurassic and Cretaceous neoselachians. Sources referenced where ranges differ from those given in Cappetta (1987) and Cappetta et al. (1993).

Synechodontiformes.-

Synechodontiformes inc. fam. Several taxa of uncertain affinity are known from the Norian and Rhaetian and probably constitute members of unnamed families.

Palaeospinacidae. Scythian to Paleocene.

Orthacodontidae. Sinemurian to Paleocene.

Hexanchiformes (including Chalmydoselachiformes).-

Pseudonotidanidae. Toarcian (Welcommia terencei Delsate and Godefroit 1995 and Pseudonotidanus politus (Thies 1992) to Valanginian (Welcommia bodeuri Cappetta 1990); see Underwood and Ward 2004.

Hexanchidae s. l. These taxa probably constitute several related families sharing a similar tooth design. Sinemurian to Recent.

Chlamydoselachidae. Campanian to Recent. Undescribed specimens have been reporting from the Cenomanian (Ward in Maisey et al. 2004)

Inc.ord.-

Ostenoselachidae. Sinemurian (Ostenoselache stenostoma Duffin 1998b).

Protospinaciformes.-

Protospinacidae. Toarcian (Protospinax sp. Desate and Lepage 1990) to Tithonian or Cenomanian (Pseudospinax pusillus Müller and Diedrich 1991, if Pseudospinax is considered a junior synonym of Protospinax; see Ward in press).

Squatiniformes.-

Squatinidae. Kimmeridgian (Squatina alifera [Münster 1842]; Underwood 2002) to Recent. Pre Kimmeridgian records of Squatina are here considered to be orectolobiforms.

Pristiophoriformes.-

Pristiophoridae. Santonian to Recent.

Echinorhiniformes.-

Echinorhinidae. Albian (Echinorhinus australis [Chapman 1909]) to Recent.

Squaliformes.-

Squalidae. Barremian to Recent.

Centrophoridae. Turonian to Recent.

Dalatiiformes. This group contains several families, but the taxonomy is poorly understood. Cenomanian (unnamed taxon incorrectly identified as Eoetmopterus by Underwood and Mitchell [1999]; see Adnet and Cappetta 2001) to Recent.

Rajiformes.-

?Rajiformes inc. fam. Pliensbachian (unnamed tooth; Curtis and Padian, 1999) to Toarcian (several taxa; see Delsate and Candoni 2001).

"Spathobatidae". Toarcian (<u>Belemnobatis moorbergensis</u> [Thies 1983]); to Aptian (<u>Belemnobatis picteti</u> [Cappetta 1970] or Maastrichtian if <u>Squatirhina</u> belongs within this clade (Underwood et al. 1999).

Rajiformes inc. fam. A number of taxa are known from isolated teeth that cannot be readily accommodated within other families. Examples exist within the Kimmeridgian (<u>Engaibatis schultzei</u> Arratia et al 2002; <u>Leiribatos alienus</u> Kriwet 2004) and throughout the Cretaceous (including such genera as <u>Pseudohypolophus</u> and <u>Turoniabatis</u>).

Rhinobatidae s. l. Tithonian (unidentified skeletal remains, Cione 1999) to Recent.

Rhynchobatidae. Maastrichtian toRecent. Possibly present in the Santonian (pers. obs).

Rajidae. Cenomanian toRecent.

Platyrhinidae. Campanian/Maastrichtian (<u>Tethybatis selachoides</u> Carvalho 2004) to Recent.

Cyclobatidae. Cenomanian.

Hypsobatidae. Campanian to Maastrichtian.

Parapalaeobatidae. Santonian to Maastrichtian.

Dasyatidae. Hauterivian (<u>Dasyatis speetonensis</u> Underwood et al. 1999) to Recent.

Gymnuridae. Cenomanian to Recent.

Myliobatidae. Maastrichtian to Recent.

Rhombodontidae. Maastrichtian.

Sclerorhynchoidei. The taxonomy of this group requires more study, and it is likely that more than one family is present. Barremian (<u>Onchopristis dunklei</u> McNulty and Slaughter 1962; Kriwet 1999) to Maastrichtian.

<u>Inc. ord</u>.--

Agaleidae. Sinemurian to Bathonian (unnamed teeth; Underwood and Ward 2004).

<u>Heterodontiformes</u>.-

Heterodontidae. Toarcian to Recent.

<u>Orectolobiformes</u>.- The affinities of Mesozoic Orectolobiformes are poorly understood (Cappetta 1987, Underwood and Ward 2004), with the majority of taxa being represented by isolated teeth, and the only taxon represented by well preserved skeletons (<u>Phorcynus</u> Thiolliere 1854) showing a mosaic of characters found in several extant families.

Parascylliidae. Albian (<u>Pararhincodon</u> sp. Underwood and Mitchell 1999) to Recent. Toarcian (<u>Annea maubeugei</u> Delsate and Thies 1995) if <u>Annea</u> is included into this family.

Hemiscylliidae. Toarcian (e.g. unnamed material figured in Candoni 1995) to Recent.

Ginglymostomatidae. Albian to Recent.

Inc. fam. 1. Phorcynis and relatives. The body form of Phorcynis may suggest an affinity with the Orectolobidae. Bathonian (Heterophorcynus microdon Underwood and Ward 2004) to Tithonian (Phorcynis catulina Thiolliere1854).

Inc. fam. 2. There are a number of taxa with broadly 'squatinoid' teeth that appear to form a single group. The relationships between these taxa and the Brachaeluridae and Orectolobidae are poorly understood. Toarcian (Palaeobrachaelurus aperizostus Thies 1983) to Maastrichtian (Cretorectolobus sp., Wroblewski 2004).

Inc. fam. 3. Corysodon. Kimmeridgian to Tithonian, with unfigured material from the Barremian (Candoni pers comm.).

   Inc. ord.-

Palaeocarcharidae. Tithonian (Palaeocarcharias stromeri Beaumont 1960); possible Bathonian if poorly preserved teeth can be assigned to this group (see Underwood and Ward 2004).

   Carcharhiniformes.-

Scyliorhinidae. Bathonian (Palaeoscyllium tenuidens Underwood and Ward 2004) to Recent.

?Proscylliidae. Bathonian (Praeproscyllium oxoniensis Underwood and Ward 2004 and Eypea leesi Underwood and Ward 2004) to Recent; if these records are not proscylliids, there is no published pre-Neogene record.

Leptochariidae. No published fossil record; Teeth of "Scyliorhinus" ptychtus Noubhani and Cappetta 1997 could belong to Leptocharias; very similar teeth are present in the Santonian (personal observation).

Triakidae. Hauterivian (?triakid indet., Underwood et al. 1999), otherwise Turonian to Recent.

Carcharhinidae. Paleocene to Recent. Teeth possibly assignable to Rhizopriodon are present in the Santonian (personal observation).

   Lamniformes.-

Cretoxyrhinidae. Valanginian to Eocene.

Odontaspidae. Barremian (? Carcharias sp.; Kriwet 1999) to Recent.

Mitsukurinidae. Aptian to Recent.

Cardabiodontidae. Cenomanian (Cardabiodon ricki Siverson 1999) to Pliocene (Parotodus benedeni (LeHon 1871)).

Anacoracidae. Aptian (unnamed teeth, Underwood 2004) to Maastrichtian.

Latest Triassic Lamniformes (of Duffin 1998a), as indicated by Pseudocetorhinus, are here considered to represent an unrelated taxon.

   Clades unknown from the Jurassic and Cretaceous, but predicted by cladistic models mentioned in this study, allowing for paraphyly of known clades.

Rajiformes.-

Pristidae. Sister group to all other rajiforms (Shirai 1996); sister group to all other rajiforms except the Torpedinoidea (McEachran et al 1996); sister group to the Myliobatiformes (Maisey et al 2004).

Torpedinoidea. Sister group to all other rajiforms (McEachran et al 1996, McEachran and Aschliman 2004); sister group to Rajidae, Myliobatiformes etc (Shirai 1996).

Rhina. Sister group to all other rajiformes except pristids and torpedinoids (McEachran et al 1996); sister group to Rajidae plus rhinobatids (McEachran and Aschliman 2004).

Zanobatus. Sister group to many other rajiforms (McEachran et al 1996); sister group to Myliobatoidea (McEachran and Aschliman 2004).

Hexatrygon. Sister group (with Plesiobatis) to myliobatiforms at unresolved trichotemy (Shirai 1996); sister group to many other rajiforms (McEachran et al 1996; McEachran and Aschliman 2004).

Plesiobatis. Sister group (with Hexatrygon) to myliobatiforms at unresolved trichotemy (Shirai 1996); sister group (with Urolophus; McEachran and Aschliman 2004) to other myliobatiforms (McEachran et al 1996; McEachran and Aschliman 2004).

Urolophus. Sister group to other myliobatiforms (McEachran et al 1996).

Urobatis + Urotrygon. Sister group to most other myliobatiforms (McEachran et al 1996; McEachran and Aschliman 2004).

Several other genera have been considered as sister groups to more derived myliobatiforms (McEachran et al 1996; McEachran and Aschliman 2004).

Orectolobiformes.-

Brachaelurus and Orectolobus. Sister groups to Hemiscylliidae and other orectolobiform families at unresolved trichotemy (Shirai 1996); monophyletic sister group to Hemiscylliidae and more derived orectolobiforms (Goto 2001). It is possible that at least one of the Mesozoic orectolobiform groups belongs within this clade.

Carcharhiniformes.-

Pseudotriakidae. Grouped with Proscylliidae by Shirai (1996).

Lamniformes.-

Alopiidae. It is not considered here that Paranomotodon is an alopiid. Predicted sister group to all other Lamniformes (Douady et al 2003) and Mitsukurina (Winchell et al 2004).