Diversification trajectories and evolutionary life-history traits in early sharks and batoids

Jürgen Kriwet^{1,*}, Wolfgang Kiessling² and Stefanie Klug²

¹*Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany*

²*Museum für Naturkunde der Humboldt-Universität zu Berlin, Invalidenstrasse 43, 10115 Berlin, Germany*

Different interpretations on the timing of early diversification and radiation of modern sharks and batoids (Neoselachii) in the Earth's history exist and are related to discrepancies in taxonomic and phylogenetic interpretations favouring a Late Triassic or earliest Jurassic diversification and subsequent radiation event, respectively. Sampling standardization based on pooled taxonomic occurrences made it possible to overcome the problem of a much richer neoselachian record in the Late Jurassic than earlier on. The standardized pattern of genus richness is one of low and fairly constant diversity in the Late Triassic and earliest Jurassic with a steep rise in the Toarcian (*ca* 180 Myr ago), representing the maximum diversification rate in the Jurassic towards a Middle and Late Jurassic plateau. The major Toarcian diversification agrees with the conclusions based on phylogenetic analyses, but is in conflict with older interpretations based on raw data. Early Jurassic expansion of neoselachians was opportunistic in the aftermath of the end-Triassic mass extinction and the reasons for their rapid diversification and radiation probably include small body size, short lifespans and oviparity, enabling faster ecological reorganizations and innovations in body plans for adapting to changing environmental conditions.

Keywords: Early Jurassic; Triassic–Jurassic boundary; opportunistic radiation

1. INTRODUCTION

Living sharks comprise over 498 species (Compagno *et al.* 2005; Ebert & Compagno 2007) and living batoids (rays and skates) account for 574 species (Ebert & Compagno 2007). Until now, historical biodiversity patterns of neoselachians were inferred directly from the fossil record, either (i) by counting genera actually sampled within time intervals (Cuny & Benton 1999) or (ii) by using first and last occurrences of taxa (Underwood 2006). Applying different methods for analysing past neoselachian diversity patterns apparently provides different interpretations. It is obvious from previous studies (e.g. Kriwet & Benton 2004; Underwood 2006; Kriwet & Klug 2008) that neoselachian taxonomic concepts are not very accurate and much taxonomic information is based on the publications from the nineteenth or the beginning of the twentieth century. The preservation of fossil neoselachians is generally poor and the taxonomic concepts are generally based on isolated teeth. Allocation of fossil neoselachian teeth to any of the extant clades is sometimes uncertain and different concepts of supra-specific allocation might exist. Nevertheless, despite these apparent systematic restrictions, the teeth of neoselachians provide important taxonomic features (e.g. Naylor & Marcus 1994; Underwood 2006).

Consequently, the limited datasets and inaccurate faunal descriptions form a serious problem in analysing past diversity patterns of sharks and batoids. Phylogenetic hypotheses could provide better estimates if species are

considered. Recently, phylogenetic hypotheses have been employed to suggest an early radiation and diversification of neoselachians (Maisey *et al.* 2004; Underwood 2006). On the genus or family level, these methods, nevertheless, will also possibly obscure real patterns because they generally include almost exclusively extant groups. The evolutionary history of neoselachians encompasses 300–350 million years based on rare isolated teeth, which are morphologically similar to modern neoselachian teeth, and include a scattering of taxa, which may be closely related to this group (e.g. Turner & Young 1987; Maisey *et al.* 2004; Ivanov 2005).

According to recent research, two different interpretations of the early diversification and radiation of neoselachians are favoured. Cuny & Benton (1999) consider the Late Triassic as the critical period in the early evolution of modern-level neoselachians based on taxonomic considerations, whereas phylogenetic hypotheses indicate the earliest Jurassic, *ca* 10–15 million years later, as the important time interval in the early radiation of neoselachians (Maisey *et al.* 2004). In this paper, we use subsampling methods to analyse and discuss sample-standardized diversity patterns of Triassic–Jurassic neoselachians for a comparison with the existing models and to discuss the mechanisms underlying early neoselachian diversity trends.

2. NEOSELACHIAN SYSTEMATICS AND DEFINITION

Sharks, rays and skates form a monophyletic group, the Neoselachii (Euselachii: Moy-Thomas 1939, Reif 1977 and Schaeffer & Williams 1977; Euselachiformes: Maisey 1975), which is well supported by morphological and molecular data. Even though the monophyly of

* Author for correspondence (kriwet.smns@naturkundemuseum-bw.de).

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Figure 1. Phylogenetic relationships of living neoselachian clades combined with stratigraphic information based on (a) morphological characters (de Carvalho 1996) and (b) molecular data (Maisey *et al.* 2004; Winchell *et al.* 2004). Batoids are considered to be derived sharks based on (a) morphological features, whereas batoids represent the basal sister group to sharks in the hypothesis based on (b) molecular data, which reduces the length of ghost lineages considerably. Thick bars correspond to confirmed stratigraphic distribution of taxa and thin bars represent ghost lineages (gaps in fossil records). First occurrences of taxa are used to infer minimum ages of cladogenetic events. Ages are from Gradstein *et al.* (2004).

Neoselachii is beyond dispute, the diagnosis of this group varies (Compagno 1973, 1977; Reif 1977; Maisey 1984, 1986; Thies & Reif 1985; Gaudin 1991; de Carvalho 1996; Shirai 1996; Maisey *et al.* 2004). If Neoselachii is restricted to living forms, then only those extinct taxa that are phylogenetically nested within modern groups alone would be considered neoselachians. This approach, however, is not favourable when extinct taxa are considered (Klug *et al.* in press). Here, we define Neoselachii to incorporate all living forms and those extinct groups that fall just outside modern groups but are united by derived characters (e.g. triple-layered tooth enameloid, fused but not coalesced left and right coracoids, elongated metapterygium in pelvic fin, well-calcified vertebral centra, segmentally constricted notochorda). Although great progress has been accomplished in recent years with regard to resolving the interrelationships within sharks and batoids, the monophyly and systematic position of several groups (e.g. Hexanchiformes, Squaliformes, Batoidea) are still debated (e.g. Shirai 1992, 1996; de Carvalho 1996). Morphological data suggest, for instance, that batoids and sharks are

monophyletic, and that batoids are derived sharks, joined with saw sharks and angel sharks in the clade Hypnosqualea (figure 1a; Shirai 1992; de Carvalho 1996; de Carvalho & Maisey 1996), whereas molecular analyses using larger sets of gene sequences support the interpretation of batoids representing the basal sister of sharks within a monophyletic clade Neoselachii (figure 1b; Douady *et al.* 2003; Winchell *et al.* 2004). This interpretation is also supported by the fact that molecular phylogenies are more congruent with the fossil record (figure 1), whereas phylogenetic hypotheses based on morphological characters (e.g. de Carvalho 1996) require long ghost lineages to be congruent with the fossil record (figure 1). The major issue here is that most neoselachians clades are characterized by high amounts of plesiomorphic morphological characters. Additionally, it is obvious that the systematic position of batoids is not trivial.

3. MATERIAL AND METHODS

The palaeontological record is biased and care must be taken to remove as much bias as possible. Only if biologically meaningful patterns emerge can solid conclusions be drawn.

For the study of ancient diversity patterns, the most severe bias results from the heterogeneous quality of the fossil record. Time intervals with many records (occurrences) of a particular group alternate with times when only a few occurrences are reported. As measured diversity strongly depends on sample size, this heterogeneity needs to be compensated. The relationship between sample size and diversity is nonlinear and thus diversity cannot be assessed by extrapolation. The most widely used approach to sample-standardized diversity is subsampling by simple rarefaction. This method randomly draws the same number of occurrences (quota) from each time interval (bin), where the quota is dictated by the most poorly sampled bin. The random draws (subsampling trials) are repeated several times (100 in our case) and the average number of taxa (genera in our case) drawn represents the estimate of the number of taxa that would have been observed in each bin (sampled in bin, SIB) if the fossil record were uniform.

To translate this SIB diversity into estimates of diversity dynamics (extinction, origination and diversification rates), the data need to be ranged through; that is, a taxon that is first reported in bin x and last reported in bin $x+n$ is assumed to have existed in all bins between bin x and bin $x+n$, irrespective of actual records in the subsampled dataset (Lazarus taxa). This method is plagued by edge effects, because the likelihood of inferred (but not observed) presence is maximal in the middle of the time series and minimal towards the edges. In addition, rates cannot be calculated for the first and last bins. New methods are currently being developed, which allow for an estimate of diversity dynamics without edge effects (Alroy *et al.* 2008), but these methods require far larger datasets than available for our study and an estimate of taxonomic evenness. We thus report both SIB and range-through diversity and qualitatively address the edge effects. There are two basic methods to count the diversity of through-ranging taxa: one counts either all taxa in a bin or taxa that jointly cross bin boundaries (boundary crossers). The latter counting method has the advantages that only taxa which have actually coexisted in time are counted, and that origination and extinction rates are more clearly separated (Bambach *et al.* 2004; Kiessling *et al.* 2007). We therefore apply the boundary-crosser metric herein, which has the additional advantage of inherently excluding short-lived singleton taxa. The dataset used here was compiled from a vast literature on fossil neoselachians, and considerable generic and species revision was carried out (see table S1 in the electronic supplementary material). This resulted in rearrangements of taxa or changes in taxonomic compositions. A total of 507 European occurrences from 154 localities were compiled. This list comprises 69 distinct genera and 131 named species. The stratigraphic resolution of the analyses is geological stages (figure 1; electronic supplementary material, table S2). Non-European records were excluded because there are only a few predominantly Late Jurassic neoselachian occurrences outside Europe: Argentina (Cione 1999); Ethiopia (Goodwin *et al.* 1999); Somalia (D'Erasmus 1960); and Tanzania (Arratia *et al.* 2002).

4. RESULTS

(a) Occurrence data and raw diversity

There is a general trend towards more occurrences in younger time intervals (figure 2). This roughly exponential trend is interrupted by sampling peaks in the latest

Figure 2. Data inventory of Triassic and Jurassic neoselachian sharks. The curves depict the counts of geographically distinct taxonomic occurrences (thick solid line), and named genera (squares) and species (circles) by geological stages. Note the general trend of better sampling in younger strata. For abbreviations see fig. S1 in the electronic supplementary material.

Triassic and Toarcian. Recorded genus and species diversity closely match the occurrence pattern. A first peak of raw diversity is ascertainable at the end of the Triassic followed by a pronounced decline in the earliest Jurassic (figure 2). Diversity increased in the Sinemurian (*ca* 190 Myr ago), resulting in a similar species diversity as in the latest Triassic but with a very distinct taxonomic composition. In the Toarcian, a steep increase in taxonomic standing diversity is recognizable, followed by a similarly steep decline. Two additional diversity peaks of different intensities occur in the Bathonian (*ca* 166 Myr ago) and in the Kimmeridgian (*ca* 153 Myr ago).

A similar pattern emerges when the stratigraphic ranges of genera are extended between their first and last occurrences (figure 3a). The curve displays a moderate decrease in diversity across the Triassic–Jurassic boundary with a steep rise towards a Middle Jurassic plateau. Raw data also imply a sudden diversity decrease at the end of the Jurassic (figure 2).

(b) Sampling-standardized diversity trajectories

Because several stages have exceedingly low numbers of taxonomic occurrences (figure 2), we have combined some stages to achieve a reasonable subsampling quota (figure 3b; electronic supplementary material, table S2). This quota is still low (16 occurrences per bin), but is the highest we can use to achieve a complete time series. The sampling-standardized diversity pattern is, again, one of low and fairly constant diversity in the Late Triassic and earliest Jurassic followed by a steep rise in the Toarcian leading to a Middle and Late Jurassic plateau. The comparison of SIB and boundary-crosser diversity (figure 4) indicates that edge effects are substantial only in the first and last bins. As well as the Hettangian–Sinemurian bin (probably due to edge effects), the Toarcian also saw the maximum origination and diversification rates in the Jurassic (figure 5). The plateau of balanced neoselachian diversity during the Middle Jurassic, which extends into the Late Jurassic, is expressed by modest origination and extinction rates of similar magnitude (figure 5a). The extinction rate exceeds the origination rates by a marked magnitude only towards the end of the Jurassic (edge effect).

Although both analyses using raw and sample-standardized data agree in that the Toarcian diversity and diversification rates are significantly elevated, the raw

Figure 3. Raw data on generic diversity when the stratigraphic ranges of taxa are extended between their first and last occurrences. Range-through genera (open squares, plotted midpoint in the intervals) are genera that are sampled in an interval plus those known before and after the interval. Boundary crossers (filled squares, plotted at the base of the intervals) are genera that jointly cross the boundaries between the intervals. (a) Data resolved to individual geological stages. (b) Data with several stages combined to achieve a more even sampling intensity (see table S2 in the electronic supplementary material). For abbreviations see fig. S1 in the electronic supplementary material.

data implied a first diversity peak of neoselachian standing diversity in the Late Triassic and another one in the Middle Jurassic, whereas the subsampling analysis suggests saturated diversities for the Middle and most of the Late Jurassic.

5. DISCUSSION

(a) Early Jurassic radiation

A first major radiation and subsequent diversification event of neoselachians was assumed to be related to the Rhaetian transgression that produced extensive shallow epicontinental seas over most of Western Europe (Cuny & Benton 1999). However, phylogenetic hypotheses and direct analyses of the fossil record suggest that no living neoselachian lineages were present in the Late Triassic (with the exception of the extinct *Synechodontiformes*) and that the origin of modern sharks and batoids occurred in the Early Jurassic (Maisey *et al.* 2004; Kriwet & Klug 2008). This indicates that no radiation of modern neoselachians occurred prior to the Early Jurassic (Maisey *et al.* 2004; Kriwet & Klug 2008), and that there was no significant increase in the number of lineages before this time. Most pre-Jurassic taxa assigned to Neoselachii (e.g. Cuny & Benton 1999) were short-living offshoots of neoselachian-related taxa with very restricted stratigraphic distributions. *Synechodontiform* sharks, an extinct neoselachian group as defined above and by Klug *et al.*

Figure 4. Subsampled generic diversity in the Jurassic (combination of stages as in table S2 in the electronic supplementary material and figure 3b). The graphs represent the mean of 100 subsampling trials using a quota of 16 occurrences from each interval. (a) Number of genera sampled in bins (SIBs) plotted in the middle of the bins. (b) Number of boundary-crossing genera plotted at the base of the bins. For abbreviations see fig. S1 in the electronic supplementary material.

(in press), are the only neoselachian group crossing the Triassic–Jurassic boundary (Ivanov 2005; Klug & Kriwet 2008).

Based on sampling standardization (figure 5), our best estimate of the Toarcian origination and diversification rates of neoselachians is approximately 45 per cent and 37 per cent, respectively, leading to a steep increase in raw diversity from the lowermost Jurassic to the end of the Early Jurassic (figure 4), which agrees with the hypotheses of Maisey *et al.* (2004) and Kriwet & Klug (2008). In the Jurassic, most modern groups originated: Hexanchiformes; Heterodontiformes; Squatiniformes; Orectolobiformes; Carcharhiniformes; Batoidea, with the exception of Squaliformes; Lamniformes; and Pristiophoriformes; e.g. Kriwet & Klug 2004, 2008; Musick *et al.* 2004) figure 1). The extinction rate is considerably low and even decreases towards the Middle Jurassic.

(b) Middle and Late Jurassic diversity stasis

From the Toarcian onwards, neoselachians seem to have been better adapted to their environments, as suggested by a four to five times higher number of boundary crossers. The diversity plateau during the Middle Jurassic and at least during the Oxfordian and Kimmeridgian indicates some sort of stasis as expressed by balanced and low origination, and extinction rates and reduced diversification rates. These background originations and extinctions are probably related to small-scale events acting on the local and regional rather than global scales, such as migrations of taxa among regions or community shifts due to climatic changes (Kriwet & Klug 2008). The balanced diversity after the Early Jurassic could also be linked to the

Figure 5. Underlying diversity dynamics of Jurassic subsampled generic diversity. (a) Origination (open squares) and extinction (filled squares) rates and (b) diversification rates. Note the strong decline in diversification during the Jurassic. For abbreviations see fig. S1 in the electronic supplementary material.

homogenization of two neoselachian biogeographic assemblages (provinces?) to a relatively uniform composition in the Late Jurassic, which might be the result of constant palaeoclimatic conditions and uniform habitats, at least across Europe, with sea-level highstands and no important physical barriers (Kriwet & Klug 2008).

(c) Life-history traits and early neoselachian evolution

Environmental factors (e.g. available energy), properties (e.g. heterogeneous habitat structure) and grade of disturbances (e.g. stressed environment) account for positive or negative diversification rates (Vermeij 1987; Sheldon 1996; Nevo 2001; Kiessling & Aberhan 2007; Peters 2008). However, it is not only extrinsic factors that force extinctions and originations; the risk of extinction (as well as diversification patterns) of neoselachians are certainly associated with life-history traits and adaptability to adapt to new environmental conditions, which is strongly affected by reproduction mode and body size (García *et al.* 2008). Within neoselachians, a wide array of reproduction modes is realized including oviparity (laying eggs) and different forms of viviparity (yolk-sac, histiotrophy, oophagy and placental; Musick & Ellis 2005). Yolk-sac viviparity is the most common reproduction mode of all living neoselachian clades. Oviparity occurs in all Heterodontiformes and Rajiformes, in most Orectolobiformes, and to a lesser degree in Carcharhiniformes. This reproduction mode is considered to be plesiomorphic (Dulvy & Reynolds 1997) and is

considered an adaptation to increased fecundity, which is at least an order of magnitude higher than that in viviparous forms (Musick *et al.* 2004; Musick & Ellis 2005). Additionally, species with oviparity ensure their evolutionary fitness even with proportionately higher individual and egg predation rates, because the evolutionary fitness of viviparous neoselachians is very low if pregnant females are killed. It has been shown that extinction risk is significantly lower for oviparity than for other reproduction modes (García *et al.* 2008). Within neoselachians, Lamniformes and Squaliformes, which are phylogenetically the youngest clades, were identified to be the most extinction-prone living neoselachian clades (García *et al.* 2008; Kriwet & Klug *in press*; Kriwet *et al.* *in press*).

In the Early Jurassic, neoselachians were generally small and we assume that they were predominantly oviparous, like their closest living relatives, with comparably short lifespans. This is also supported by short stratigraphic ranges as indicated by the high number of stratigraphic singletons (figure 4). Smaller neoselachians, which generally have shorter generation times and oviparous reproduction mode, also have higher substitution and mutation rates resulting in faster modifications (e.g. Martin *et al.* 1992; Martin & Palumbi 1993). However, elevated molecular rates might not always result in higher taxon rates because biotic and physical environmental parameters interact with phenotypic variation (Liow *et al.* 2008). The peak of diversification in the Toarcian coincides with rising sea levels (after regression in the lowermost Jurassic) and humid climatic conditions with fewer warm episodes (Price 1999; Sellwood & Valdes 2007). Rising sea levels resulted in extended shallow marine and epicontinental environments providing numerous habitats for diversification. Similarly, the highest diversity of large predaceous fishes (including sharks) is nowadays found in intermediate latitudes on upper continental slopes, along shores and near prominent topographic features (Worm *et al.* 2003).

Near the end of the Jurassic, the extinction rate is unusually high if compared with the corresponding origination and diversification rates (figure 5), and represents an edge effect related to the absence of suitable marine lowermost Cretaceous sediments for finding small-tooth neoselachians in the aftermath of the Late Jurassic marine regression (Kriwet & Klug 2008). Recent studies of near-coastal Early Cretaceous shark and batoid faunas have indicated that all neoselachian clades were present (Canudo *et al.* 1995; Kriwet 1999; Underwood *et al.* 1999; Rees 2005; Kriwet *et al.* 2008, *in press*), although the complete Early Cretaceous taxonomic diversity of neoselachians remains insufficiently known. A preliminary equalizing of the diversity curves from the Jurassic and Late Cretaceous, such as those provided by Underwood (2006), indicates that the diversity of Early Cretaceous neoselachians must have been much higher and there was probably no significant extinction event at the end of the Jurassic.

6. CONCLUSIONS

Subsampling of pooled taxonomic occurrences was used to obtain a best estimate of the diversity dynamics of neoselachians early in their evolutionary history. Discrepancies between raw data and subsampling analysis are

obvious, indicating sampling bias in the raw data. Sampling standardization suggests a first major diversification peak in the Toarcian, which roughly agrees with the conclusions of Maisey *et al.* (2004) based on phylogenetic analyses (figure 1b). Sample-standardized diversification rates show a plateau of diversity in the Middle and most of the Late Jurassic. The corresponding turnover rates are low at the genus level. The diversity trends of early neoselachians indicate an 'opportunistic' rather than a 'competitive' radiation event. The reasons for the Early Jurassic neoselachian radiation and subsequent rapid increase in their taxonomic diversity are various and include ecological reorganizations in the aftermath of the end-Triassic mass extinction event, probably the addition of evolutionary innovations in body plans not found before, and oviparity (in at least galeomorph sharks) allowing neoselachians to respond better to perturbations and use of habitat resources. The more or less balanced origination and extinction rates and less pronounced diversification in the Late Jurassic were probably related to ecological parameters such as sea-level highstands and the absence of important physical barriers in central and northern Europe (e.g. Rawson & Riley 1982; Haq *et al.* 1988).

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