BIROn - Birkbeck Institutional Research Online

Underwood, Charlie J. and Ward, D.J. and Guinot, G. (2015) Development of understanding of the Mesozoic and Cenozoic chondrichthyan fossil record. Geological Society, London, Special Publications 430 , ISSN 0305-8719.

Downloaded from: https://eprints.bbk.ac.uk/id/eprint/13178/

Usage Guidelines:
Please refer to usage guidelines at https://eprints.bbk.ac.uk/policies.html or alternatively contact lib-eprints@bbk.ac.uk.

Development of understanding of the Mesozoic and Cenozoic chondrichthyan fossil record.

Charlie Underwood[1*], David Ward[2], Guillaume Guinot[3]

[1]*Department of Earth and Planetary Science, Birkbeck College, Malet Street, London WC1E 7HX, UK.*

[2]*Crofton Court, 81 Crofton Lane, Orpington, Kent BR5 1HB, UK.*

[3]*Département de Géologie et Paléontologie, Muséum d'Histoire Naturelle, 1, Rte de Malagnou, CP 6434, CH-1211 Geneva 6, Switzerland*

**Corresponding author (e-mail: c.underwood@bbk.ac.uk)*

Abstract: Fossils of post-Palaeozoic sharks and rays are common and well known, and have been extensively studied. Early studies, especially the monographic works of Agassiz and Woodward, described species based on macroscopic remains of isolated teeth, fin spines and rostral 'teeth' as well as rare specimens of articulated skeletons and skulls. This material was obtained from a range of sources but especially from commercial collectors in Britain and mainland Europe. Additional research over subsequent decades also concentrated on large specimens, giving a very biased perception of the chondrichthyan record. The use of large scale bulk sampling in the latter part of the 20th Century revealed a previously unknown wealth of small fossils, especially teeth, and vastly improved knowledge of ancient sharks and rays. Widening use of these techniques to obtain small specimens has let to a dramatic increase in the fossil taxa known. In addition, re-assessment of previously known taxa has allowed has allowed generic diversity of some clades to be appreciated. Detailed work on

skeletal anatomy, in part aided by new non-destructive methods, continues to improve knowledge of shark and ray diversity, phylogeny and radiation.

The fossils of sharks and rays have been well known and recorded in numerous publications since the early part of the nineteenth Century. Primarily represented as isolated teeth, shark and ray fossils have been extensively collected, and remain some of the most iconic of fossils. Key publications by Agassiz (1833-1844) and Woodward (1889) provide an accurate summary of the knowledge of fossil sharks and rays at the times of publication. The knowledge of the fossil record of post-Palaeozoic chondrichthyans has improved dramatically since the publication of these early works. Monographic studies of the fish, including sharks, of the British Purbeck (mostly Berriasian; Woodward 1916-1918) and Chalk (Cenomanian to Campanian; Woodward 1902-1912), updated the earlier studies but added relatively little, with a greater emphasis placed on actinopterygian fish preserved as complete or partial skeletons. In the subsequent century, improvements in knowledge of the diversity of fossil species, their taxonomic affinity and their palaeobiological context has dramatically changed our understanding of fossil chondrichthyan faunas (e.g. Underwood 2006, Guinot *et al.* 2013). Whilst this improvement in knowledge is a global phenomenon, it is especially striking when the shark and ray faunas of Britain, which formed the basis for most of Woodward's work and provided a lot of Agassiz's type specimens are considered.

Sampling methods

Field collecting

Different parts of the skeleton of a chondrichthyan have very different preservation potentials. The endoskeleton is comprised of cartilage, with different skeletal elements having varying degrees of secondary mineralization by apatite tesserae. Whilst some elements of the skeleton, such as the jaw cartilages and vertebral centra, may be heavily mineralized, the tesserae readily disarticulate during decomposition of interstitial organic matter. As a result, well-preserved skeletal remains are far less common than is the case with osteichthyans and tetrapods where the skeleton is composed of bone. In contrast, the teeth, as well as placoid scales, rostral 'teeth' of sawfishes and similar groups, tail spines of stingrays and dorsal fin spines are formed of robust and strongly mineralized dentine and enameloid. Shark and ray teeth, as well as these other dermal elements, therefore have a very good preservation potential. In addition, the dentition of sharks and rays is deciduous and teeth are shed regularly thoughout life and each individual can produce large numbers of potential fossils in its lifetime. Larger shark and ray teeth are therefore frequently common and conspicuous fossils in the field. It is therefore not surprising that a large diversity of these teeth was recorded by early workers. Material collected from Britain featured disproportionately in these early studies, in part due to the long history of "gentleman collectors" on that country.

Within the British Mesozoic and Cenozoic, early finds of shark and ray remains were collected by a number of methods. Some of the richest fossil shark and ray sites in Britain are actively eroding coastal exposures of soft mudstone, with many of the hard and dense vertebrate remains being collected loose on the beach. This is especially

true of the Isle of Sheppey, the source of many holotypes of sharks and rays (e.g. Agassiz 1845), where very few fossils are seen *in situ* and the vast majority of fossils recorded have been collected from beach concentrations (e.g. Clouter *et al.* 2000). Many other specimens were recovered from active quarries. It is probable that many of the early finds from quarries were collected by quarry workers for sale as a means of supplementing their income, much as is the case in the phosphorite quarries of northern Morocco today. As a result, there is a significant overrepresentation of large and robust teeth in museum collections, as they represent the most conspicuous and durable specimens for beach collection, and would have represented the most obvious and valuable specimens exposed during quarrying. In addition, unusual and rare specimens are likely to have been more valuable for commercial trade, and are likely to have been more sought after than smaller and commoner material. An example of these biases is seen in the teeth of the enigmatic chondrichthyan *Ptychodus*. Whilst present throughout the Late Cretaceous Chalk facies of northern Europe, teeth are almost always rare in the British Chalk, even in the most fossiliferous levels (e.g. Guinot *et al*. 2013). In contrast, large numbers of teeth, as well as partial articulated and associated dentitions, are present in museum collections of British Chalk fossils. This extreme bias is almost certainly the result of extensive commercial collecting by quarry workers, with the large, shiny and dark coloured teeth being very conspicuous in white Chalk matrix, and the large and impressive articulated dentitions being especially sought after for sale. Similar bias toward large but rare remains due to quarry-based commercial collecting is manifested by the partial skeletons of a number of shark species from the Chalk of the Lews area, SE England, and the teeth, dentitions and skeletons of hybodont sharks from the Early Jurassic Lias of Lyme Regis, southern England (e.g. Dineley and Metcalf 1999). Outside Britain, active

quarrying remained the source of a large proportion of shark and ray fossils entering collections. This is especially true of the laminated late Jurassic limestones of Solnhofen and Nusplingen in Germany and Cretaceous laminated limestones of Lebanon, where rare but excellently preserved skeletons of and many other vertebrates were, and still are, traded after being excavated within working quarries (e.g. Davis 1887, Kriwet and Klug 2004). This collection of large and conspicuous remains resulted in large numbers of specimens of sharks and rays being acquired for private collections, many of which were later passed to museums.

In 19th Century collections from Britain, Jurassic sharks are largely represented by hybodont teeth and fin spines from Lyme Regis (Hettangian and Sinemurian) and Stonesfield (Bathonian) and to a lesser extent Peterborough (Callovian) and Weymouth (Kimmeridgian). Cretaceous non-marine hybodonts are well represented from Swanage (Berriasian) as well as some Wealden sites (Valangianian to Barremian). In the Upper Cretaceous Chalk, lamniforms and *Ptychodus* are well represented, along with rarer *Heterodontus* and *Synechodus*, but few other taxa seen. Paleogene sharks and rays are likewise dominated by teeth of lamniform sharks as well as dentitions of myliobatid rays. Whilst material from many parts of the world was known during the latter part of the nineteenth Century, British specimens are disproportionally represented in the monographic work of Agassiz (1833-1844), and formed much of the museum collection catalogued by Woodward (1889). As a result, the early published record of sharks and rays had a strong bias towards material from a relatively small number of localities in Europe in general and southern England in particular.

Monographic works from the earlier parts of the 20th Century (e.g. Woodward 1916-1919;1902-1912), largely relied on *ex-situ* material from other collectors, and this led to a continuation of these older biases. Site specific studies (e.g. White 1931) based on the collection largely or exclusively by the author removes some of the biases that had been present in older works, but still only focused on macroscopic material. Throughout much of the remainder of the 20th Century, studies focusing on British material provided only small numbers of new taxa, although increasing amounts of work elsewhere was adding to the number of species known globally. Additional species represented by large teeth are still being recorded in Tethyan regions of Europe (e.g. Vullo *et al.* 2007) as well as further afield.

Bulk sampling

In addition to a geographical bias, the earlier work on sharks and rays was strongly biased towards larger specimens, typically representing larger taxa. Skeletal remains of a number of Jurassic and Cretaceous sharks and rays were recorded by Agassiz (1833-1844) and Woodward (1889) demonstrated that many species present within the Mesozoic were small and possessed small to minute teeth. The lack of small-toothed taxa within the assemblages of isolated teeth was not mentioned by Woodward or contemporary workers and it is uncertain whether this bias was recognized as such.

A very large proportion of modern sharks and the majority of modern batoids have teeth that are four millimetres or less in maximum dimension. The size and taxonomic

affinities of the majority of shark and ray skeletons known from Jurassic sites such as Solnhofen (Münster 1842) and Cretaceous sites such as those in Lebanon (Davis 1887) suggested from the early days of chondrichthyan palaeontology that the same situation was likely to have been the case in the past. It is therefore surprising, with the hindsight of modern knowledge at least, that there was no systematic attempt to study isolated small teeth until the latter part of the 20th Century.

Probably the earliest record of large scale and systematic processing of Mesozoic rocks for vertebrate remains was the study by Moore (1860) of Triassic fissure fill deposits in the quest for mammal remains. It is recorded that this study collected 70,000 fish remains in addition to tetrapod fossils, including 45,000 perfect teeth of *Acrodus* (now *Lissodus*) *minimus* (Macfadyen, 1970, Moore 1860). Later study of the same and other sites by Kühne (1946 and later publications) also processed very large samples and collected large numbers of fish remains.

Whilst large numbers of small shark teeth had been collected as a byproduct of bulk sampling for mammal remains, the method was not used in any systematic manner for over a century after the work of Moore as a technique specifically for collecting small shark and ray teeth. There are a number of published studies that contain teeth of a size that suggest that bulk sieving was carried out, but there is no discussion of the methodology. Arambourg (1952) monographed material from the Cretaceous and Paleogene of the phosphorites of Morocco and clearly used some form of sieving to concentrate small specimens. The size range and diversity of the species figured suggests that a mesh size of approximately two millimetres was used. Whilst this allowed the collection of many small species, the mesh was not fine enough to catch

many of the smallest species, many of which were monographed subsequently by Noubhani and Cappetta (199), with the disparity between the species recorded in the two works clearly showing the importance of collecting small specimens.

Sieving for small specimens was first used extensively in site-specific studies of the European Cenozoic (e.g. Cappetta 1970), but few of these earlier studies gave an account of the methodology. The first monographic work to include bulk collected Mesozoic material was a study of Late Cretaceous and Paleocene of northern Europe by Herman (1977). Faunas from some of the localities covered include some very small teeth, which would have necessitated the use of a fine sieve mesh, but the methods were not described, and some of the other faunas appear to only comprise macroscopic material.

The first detailed accounts of bulk collecting methods (e.g. Ward 1981) was closely followed by the first publications based on the extensive use of bulk sieving of Jurassic rocks for sharks and rays by Thies (1983). The use of sieving techniques occurred alongside the first extensive use of acids to collect microvertebrates from post-Palaeozoic rocks. These were used both to remove shelly material from bulk sieve residues, greatly aiding the study of very large samples, and to break down more lithified carbonate rocks or clastic rocks with a carbonate cement (e.g. Sykes 1971). Additional extensive studies of faunas from a number of British Jurassic, Cretaceous and Paleogene were carried out but not published (see provisional species lists by Ward in Dineley and Metcalf 1999). The use of large scale sieving became standard practice for studies of chondrichthyan faunas during the latest part of the 20th Century, with the application of this methodology being fundamental to the dramatic

rise in the number of figured species (Fig. 1). It is notable that many of the most significant contributions to chondrichthyan taxonomy at this time were non-professional workers, both in Europe and North America.

The use of large scale sieving as a method of obtaining small teeth has made a very significant impact on the known diversity of sharks and rays. Most Mesozoic and Cenozoic fossil chondrichthyan assemblages are prove to be dominated by species with very small teeth, and it is now generally recognized that sampling for very small material is essential to achieve a realistic assessment of the fauna (e.g. Guinot *et al.* 2013).

It is therefore evident that collection of macroscopic specimens of isolated teeth alone is not likely to yield a meaningful census of the chondrichthyan fauna present. Whilst there are obviously constraints on the practicality of bulk sampling for small specimens, bulk sampling should be regarded as the standard method for collecting shark and ray teeth, with surface collecting only used when this not possible or to supplement the collected assemblage with larger, rare, specimens. As assemblages recovered are also strongly biased by the sieve mesh size used, recording mesh sizes used should be regarded as an essential part of specimen collection. Samples from Mesozoic rocks (e.g. Underwood and Ward 2004, Guinot *et al*. 2013) have yielded teeth absent in coarser samples in mesh sizes of 355µm. In these studies, finer mesh sizes only produced additional teeth of species present in coarser fractions. It is therefore evident that any assemblage from a sample which cannot be readily sorted to 355µm (typically due to the abundance of other grains) may be missing some of the species present and this should be acknowledged when the fauna is described.

Improving study methods

Taxonomy and phylogeny

It was recognized at a very early stage that Palaeozoic chondrichthyan remains could not readily be accommodated within living groups Agassiz (1833-1844). Whilst some post-Palaeozoic forms (such as hybodonts and *Ptychodus*) were also clearly unrelated to any living taxa and have never been considered as closely related to them, there are similarities between many other fossil forms and extant species. As a result many fossil species, especially of lamniform sharks, were placed within extant genera. This assignment of lamniform, and to a lesser extent other sharks and rays, into extant genera continued until a large number of new genera were erected by Glickman (1957). Although these new genera were often poorly diagnosed and figured, a number of Cretaceous genera were accepted by Herman (1977) giving the first idea of the true diversity of lamniform sharks in the European Cretaceous. The general conservatism towards fossil genera has led to misconceptions such as that a close relationship existed between *Carcharocles megalodon* and *Carcharodon carcharias* and the converse close relationships between *Otodus* and *Carcharocles* and between *Cosmopolitodus* and *Carcharodon* (e.g. in Applegate and Espinosa-Arrubarrena 1996).

Whilst most taxonomic study of fossil shark and ray teeth has focused on gross morphology, tooth microstructure and ultrastructure has been invaluable in understanding higher level taxonomic relationships. Agassiz (1833-1844) figured sections through teeth of several shark and ray species and showed that major

differences were present in the microstructure. Glickman (1964) used differences in tooth histology to divide sharks and rays into high level taxonomic groups. Whilst this proved to be of limited use due to repeated convergence, it has some utility at familial and ordinal level. Study of the microstructure of chondrichthyan enameloid, however, proved invaluable in ascertaining the affinities of many of the more poorly understood taxa of the Upper Palaeozoic and Triassic. Reif (1973) recognized that different chondrichthyans possessed different microstructures, and subsequent work (e.g. Cuny and Benton 1999 and refs. therein) allowed the separation of neoselachians from other groups, and of the batoids from neoselachian sharks. Continued application of this method shows there is still potential in using this method to study interrelationships within the neoselachian sharks (e.g. Guinot and Cappetta 2011).

Detailed study of skeletal material

Whilst the skeletons of sharks and rays are rare in the fossil record, they are critical to the understanding of the palaeobiology and phylogeny of many groups. Well preserved skeletons representing a number of species were well known from the Upper Jurassic of southern Germany during the 19th Century (e.g. Agassiz 1833-1844, Münster 1842, Wagner 1862) but for the most part the descriptions of these concentrated more on overall morphology than skeletal anatomy. The exceptional overall preservation of shark and ray skeletons from some sites (such as Solnhofen in Germany, sites in Lebanon and Monte Bolca in Italy) belies the lack of detail that is often present (e.g. Kriwet and Klug 2004). The skeletons are typically crushed and elements such as the skull difficult to interpret. In addition, the dermal covering of denticles, and sometimes preserved soft tissue, often obscures the endoskeleton. Teeth

are often concealed below other skeletal elements and may be crushed and broken. As a result, whilst the overall body form is readily studied, anatomical details are often obscure and only accessible through study of a number of specimens of the same taxon showing different preservational styles (e.g. Carvalho and Maisey 1996, Carvalho *et al*. 2008). The difficulty in studying the some aspects of the skeletal anatomy of these compressed skeletal fossils has led to a general lack of systematic restudy of species with a generalized or conservative body outline, such as the diverse suite of Lebanese Cretaceous batoids referred to the extant genus *Rhinobatos* by Cappetta (1980), and poor understanding of the batoids in the Eocene rocks of Monte Bolca, Italy (Jaekel 1894).

Three dimensional skeletal material of sharks and rays is even less common than compression fossils. These fossils are also commonly in well indurated rocks that render preparation and study difficult. Three dimensionally preserved skulls of the Cretaceous hybodont *Egertonodus* and neoselachian *Synechodus* were described by Woodward (1889), but the anatomical detail present in these specimens only became apparent when the material was re-analysed by Maisey (1983, 1985).

Non-destructive penetration of specimens

As with other fossils, study of many of the more complete shark and ray specimens has always been limited by the preparation work that has been possible to expose parts of the skeleton from the enclosing matrix. The general fragility of the chondrichthyan skeleton makes preparation of the specimen difficult, with prismatic mineralised cartilage commonly partly disarticulating during decay, and being partly

broken within the rock. In addition, the lack of a solid bone surface renders acid preparation very difficult, with individual tesserae often being liberated during the preparation process, damaging the surface of the skeletal elements. For specimens preserved flattened in laminated rocks, preparation of the specimens is only capable of exposing one surface, and the detail visible is highly dependent on the orientation of the skeleton relative to the bedding surface. Transfer preparation, where the exposed surface of the specimen is coated in supportive resin before preparation of the other side of the specimen, requires considerable time to be invested and has not been used on chondrichthyan fossils to reveal their anatomy.

The advent of non destructive imaging techniques has allowed features concealed within the matrix to be studied for the first time. X-Rays have been used as a means of studying fossils for some time (e.g. Stürmer 1973), but this has rarely been allied to fossil chondrichthyans. X-ray microtomography (Micro-CT) allows three dimensional images to be generated from X-rays. With this method it is possible to produce a rendered 'virtual fossil' of a specimen, even if it is partly or wholly enclosed in matrix. This technique is most readily applied to uncrushed specimens, and has proven critical to the study of the neurocrania of Palaeozoic chondrichthyans (e.g. Maisey 2001). Whilst application of this method in the study of post-Palaeozoic chondrichthyans is in its infancy, it has allowed the study of specimens that could not be readily prepared from the matrix (e.g. Lane 2010, Claeson *et al.* 2013). Even though the direct application of this method to chondrichthyans may be more limited than in other vertebrate fossil groups, it has vast potential and allows additional information to be extracted from specimens (Fig. 2).

Perception of the post-Palaeozoic chondrichthyan fossil record

The knowledge of the shark and ray fossil record in the 19th Century was heavily biased towards large specimens from a small number of sites, many of them collected commercially. As a result of that, faunas from a small number of formations from central and northern Europe in general, and southern England in particular, dominated the perception of the fossil record. As a result, known faunas from the Triassic and Jurassic comprised almost entirely of medium to large hybodonts, with smaller neoselachian sharks and rays being known primarily from the Tithonian limestones of southern Germany. Early Cretaceous (pre Aptian) faunas comprised almost entirely of non-marine hybodonts from the Purbeck and Wealden facies. Mid to late Cretaceous faunas comprised of largely open marine taxa of lamniform sharks and *Ptychodus*; smaller-toothed forms being largely known from diverse skeletons from Lebanon (Davis 1887) and rare partial skeletons from Chalk facies (Woodward 1912). Paleogene faunas were likewise known largely from lamniforms, as well as myliobatid rays and the rostral "teeth" of pristid sawfish, with larger taxa of carcharhinids also being well known from the Neogene. As in the Jurassic and Cretaceous, rare whole skeletons (e.g. Jaekel 1894) gave the only insight into smaller toothed forms, in particular diverse batoids.

This biased view of chondrichthyan diversity remained relatively unchanged until the 1960s. Although numerous new species were described from both within Europe and elsewhere, virtually all of the new species described conformed to the same general groupings as had been known during the previous century. In addition, little attempt was made to apply a more rigorous analysis to the generic affinities of fossil remains, especially of lamniforms.

Increasing use of bulk sampling and sieving during the 1970's and 1980's, associated with the widespread usage of new genera erected for extinct lamniform sharks, saw the start of a renaissance in fossil selachian study, culminating in the publication of the first review of known genera since the 19th Century (Cappetta 1987). Subsequent studies in both North America (e.g. Case 1987) and Europe (e.g. Müller 1989) established the ubiquity of small shark and ray teeth in Mesozoic rocks. It is notable that some of the richest sources of new species have been rock units that have previously been published without inclusion of small material. One only has to compare the species mentioned from the English Chalk by Woodward (1912) and the recent works of Underwood & Ward (2008) and Guinot *et al*. (2012a,b, 2013) in order to highlight how modern sampling and processing methods have changed our perception of the composition of an elasmobranch assemblage. In the latter studies, the majority of species reported are represented by teeth under five millimetres (Fig. 3), which in some samples constituted over 99% of the specimens recovered. These small teeth include many species of carcharhiniforms, rajiforms and orectolobiforms, all clades previously thought to be of minor significance in the Chalk. It is also evident that rock units that have been studied for larger vertebrate remains over a very long time period, such as the Bathonian of southern England, have recently proved to contain diverse but previously overlooked faunas (Underwood and Ward 2004).

There have been great advances in the understanding of the taxonomy and phylogeny of fossil sharks and rays, and it is now recognized that many of the genera that were in common use until recently were groupings of superficially similar species, sometimes with only very distant relationships. Continued increase in the data

available from preserved skeletal remains, used in parallel with new analyses of the phylogeny of extant forms, is providing an integrated pattern of the development of post-Palaeozoic chondrichthyan faunas.

Future directions

Despite the great improvements in the knowledge of post-Palaeozoic sharks and rays over recent decades, there is still much improvement to be made. Basic taxonomic knowledge is still best regarded as poor. Even within the most intensively studied parts of Europe and North America, most reasonably extensive collections of shark and ray fossils contain species that are unfigured and unnamed. It is not uncommon for unnamed species to be in the majority, at least as far as small-toothed taxa are concerned. Even where taxa have been described and figured, there is commonly a lot of basic taxonomic work remaining to be done. Whilst the generic diversity of lamniform sharks is now relatively well known, the same cannot be said of many other shark and ray groups. Groups urgently requiring detailed reassessment of their generic level taxonomy include hybodont sharks, especially those of the Triassic, Jurassic orectolobiform sharks, Paleogene carcharhinid sharks, Paleogene myliobatid and dasyatid rays, and 'rhinobatid' rays of all ages. Despite the requirement for a detailed primary taxonomic knowledge for almost any applied palaeontological study, one of the main obstacles to publishing the results of studies of this type is the low priority placed on these essential primary taxonomic studies by institutions, funding bodies and journals.

The rare but very significant articulated skeletal remains of Mesozoic chondrichthyans offer vast potential for study, with batoids in particular having undergone very little detailed reassessment. This material is likely to prove invaluable for the construction of phylogenies when combined with phylogenetic data of modern chondrichthyans. There are many aspects of chondrichthyan phylogenetics that remain poorly understood, such as the Triassic and Jurassic radiations of the neoselachians, the Cretaceous diversification of the batoids, squaliforms and lamniforms and the Danian recovery of shark and ray faunas. Integrating data from exceptionally preserved fossils and studies of modern taxa is likely to help improve the understanding of these issues.

Conclusions

Shark and ray fossils typically comprise isolated teeth and other fragmentary remains, but these can be large and conspicuous. Along with rare examples of well preserved skeletal remains, these isolated teeth have been extensively collected and studied. In contrast to the macroscopic remains of sharks and rays, microscopic remains, such as the teeth of the majority of fossil shark and ray species, received very little attention until the latter part of the 20th Century. The advent of widespread use of sieving technology and acid digestion of carbonate rocks allowed the collection and study of teeth and other small remains of a vast range of previously unrecognised species.

Improvements in taxonomy and detailed study of shark and ray skeletal remains have been invaluable in placing fossil taxa within a meaningful taxonomic framework and given a true insight into past diversity. This has been especially true of the lamniform

sharks, which are now recognised as representing an extremely diverse group, of which only a small number of clades survive today. Further insight into the anatomy and hence phylogenetics of fossil sharks and rays is given by non destructive methods of studying the interior of fossil material.

The work of non-professional palaeontologists has been critical to the study of fossil sharks and rays. Much of the investigation and early use of large scale sieving was carried out by non-professionals, and they continue to carry out many important studies. It should also be noted that many key specimens of sharks and rays, including the majority of articulated skeletons, have been the product of commercial fossil collection. Without commercial collection of material from active quarries and rapidly eroding coastlines, a large proportion of the most significant scientific specimens would have been destroyed.

This paper has involved a lot of input from a large number of people, notably Chris Duffin, John Maisey and Dave Martill. Gilles Cuny and Jim Bourdon are thanked for their comments. Paul Siedlecki is thanked for the use of the *Burnhamia* scan data, and the staff at the NHM Image and Analysis Centre for scanning the specimen.

References

Agassiz, J. L. R. 1833-1844. *Recherches sur les poissons fossiles*, 3: 390+32 pp. Imprimerie de Petitpierre, Neuchâtel.

Agassiz, J. L. R. 1845. Report on the fossil fishes of the London Clay. *Report of the*

British Association for the Advancement of Science, 14th meeting, 279-310.

Applegate, S. P. & Espinosa-Arrubarrena, L. 1996. The Fossil History of *Carcharodon* and Its Possible Ancestor, *Cretolamna* A Study in Tooth Identification. *In:* Klimley, A. P. & Ainley, D. (eds) *Great White Sharks. The biology of* Carcharodon carcharias, Academic Press, New York. 19-36.

Arambourg, C. 1952. Les vértebrés fossiles des Gisements de Phosphates (Maroc-Algerie-Tunisie). *Service Géologique Maroc, Notes et Mémoires*, **92**, 1-372.

Cappetta, H. 1970 Les Sélaciens du Miocène de la région de Montpellier. *Palaeovertebrata*, **1970**, 1-139.

Cappetta, H. 1980. Les Sélaciens du Crétacé supérieur du Liban. II. Batoïdes. *Palaeontographica, Abt. A*, **168**, 149-229.

Cappetta, H. 1987. Mesozoic and Cenozoic elasmobranchii. Chondrichthyes II. *In:* Schultze, H. P. (ed) *Handbook of Paleoichthyology*, 3B. Gustav Fischer Verlag, Stuttgart: 193 pp.

Carvalho, M. R. de. & Maisey, J. G. 1996. Phylogenetic relationships of the Late Jurassic shark *Protospinax* Woodward 1919 (Chondrichthyes: Elasmobranchii). *In* Arratia, G & Viohl. G. (eds) *Mesozoic Fishes 1 - Systematics and Paleoecology.* Verlag Friedrich Pfeil, München. 9-49.

Carvalho, M. R. de., Kwiwet, J. & Theis, D. 2008. A systematic and anatomical revision of Late Jurassic angelsharks (Chondrichthyes: Squatinidae). *In:* Arratia, G., Schultze, H-P. & Wilson, M. V. H. (eds) *Mesozoic Fishes 4 - Homology and Phylogeny.* Verlag Friedrich Pfeil, München. 469-502.

Case, G.R. 1987. A new selachian fauna from the Late Campanian of Wyoming (Teapot Sandstone Member, Mesaverde Formation, Big Horn Basin). *Palaeontographica, Abt. A,* **197**, 1-37.

Claeson, K. M., Underwood, C. J. & Ward, D.J. 2013. †*Tingitanius tenuimandibulus,* a new platyrhinid batoid from the Turonian (Cretaceous) of Morocco and the Cretaceous radiation of the Platyrhinidae. *Journal of Vertebrate Paleontology*, **33**, 1019-1036. DOI: 10.1080/02724634.2013.767266

Clouter, F and Medway Lapidary and Mineral Society. 2000. London Clay Fossils from the Isle of Sheppey: A Collector's Guide to the Fossil Animals from the London Clay Between Minster and Warden Point, *Sheppey Paperback.* 100pp.

Cuny, G. & Benton, M.J. 1999. Early radiation of the Neoselachian sharks in Western Europe. *Geobios*, **32**, 193-204. DOI: 10.1016/S0016-6995(99)80032-1

Davis, J.W. 1887. The fossil fishes of the chalk of Mount Lebanon, in Syria. *Scientific Transactions of the Royal Dublin Society*, **2**, 457-636.

Dineley, D.L. & Metcalf, S. J. 1999. *Fossil Fishes of Great Britain*. Joint Nature Conservation Committee. 675pp.

Glickman, L. S. 1957. (On the relationships between the families Lamnidae and Odontaspidae and on new lamnid genera from the Late Cretaceous). «in Russian». *Trudy geol. Muz. «A.P. Karpinskogo» Akad. Nauk S.S.S.R.*, **1**, 110-117.

Glickman, L. S. 1964. Class Chondrichthyes, Subclass Elasmobranchii. «in Russian». *In*: Obruchev, D.V. (Ed.), *Fundamental of Paleontology, Vol. 11. Nauka S.S.S.R., Moscow-Leningra*, 196-237.

Guinot, G. and Cappetta, H. 2011. Enameloid microstructure of some Cretaceous Hexanchiformes and Synechodontiformes (Chondrichthyes, Neoselachii): new structures and systematic implications. *Microscopy Research and Technique*, **74,** 196-205. DOI: 10.1002/jemt.20892

Guinot, G., Underwood, C. J., Cappetta, H. & Ward, D.J. 2012a. Squatiniformes (Chondrichthyes, Neoselachii) from the Late Cretaceous of southern England and northern France with redescription of the holotype of *Squatina cranei* Woodward, 1888. *Palaeontology*, 55, 529-551. DOI: 10.1111/j.1475-4983.2012.01140.x

Guinot, G., Underwood, C. J., Cappetta, H. & Ward, D.J. 2012b. Batoids (Elasmobranchii: Batomorphii) from the British and French Late Cretaceous. *Journal of Systematic Palaeontology*, **10**, 445-474. DOI: 10.1080/14772019.2011.588255

Guinot, G., Underwood, C. J., Cappetta, H. & Ward, D. J. 2013. Sharks (Elasmobranchii: Euselachii) from the Late Cretaceous of France and the UK. *Journal of Systematic Palaeontology*, **11**, 589-671.

Herman, J. 1977. Les Sélachians néocrétacés et paléocénes de Belgique et des contrées limitrophes eléments d'une biostratigraphie intercontinentale. *Mémoires pour server a l'Explication des Cartes Géologiques et Miniéres de la Belgique*, **15**, 1-450.

Jaekel, O. 1894. *Die eocänen Selachier vom Monte Bolca: ein Beitrag zur Morphogenie der Wirbelthiere*. Berlin, J. Springer**.** 176 pp.

Kriwet, J. & Klug, S. 2004. Late Jurassic selachians (Chondrichthyes, Elasmobranchii) from southern Germany: Re-evaluation on taxonomy and diversity. *Zitteliana*, **A44**, 67-95.

Kühne, W.G., 1946. The geology of the fissure-filling “Holwell 2”; the age-determination of the mammalian teeth therein; and a report on the technique employed when collecting the teeth of *Eozostrodon* and Microclepidae. *Proceedings of the Zoological Society, London*, **116**, 729–733.

Lane, J. A. 2010. Morphology of the Braincase in the Cretaceous Hybodont Shark *Tribodus limae* (Chondrichthyes: Elasmobranchii), Based on CT Scanning. *American Museum Novitates*, **3681**, 1-70.

Macfadyen, W. A. 1970. *Geological Highlights of the West Country*. Butterworths, London. 296pp.

Maisey, J. G. 1983. Cranial anatomy of *Hybodus basanus* Egerton from the Lower Cretaceous of England. *American Museum Novitates*, **2758**, 1-64.

Maisey, J. G. 1985. Cranial Morphology of the Fossil Elasmobranch *Synechodus dubrisiensis*. *American Museum Novitates*, **2804**, 1-28.

Maisey, J. G. 2001. CT-scan reveals new cranial features in Devonian chondrichthyan *Cladodus wildungensis*. *Journal of Vertebrate Paleontology*, **21**, 807-810.

Moore, C. 1860. On the contents of three cubic yards of Triassic earth. *The Geologist*, **3**. 315–317.

Müller, A. 1989. Selachier (Pisces: Neoselachii) aus dem höheren Campanium (Oberkreide) Westfalens (Nordrhein-Westfalen, NW-Deutschland). *Geologie und Paläontologie in Westfalen*, **14**, 1-161.

Münster, G. G. 1842. Beitrag zur Kenntniss einiger neuen seltenen Versteinerungen aus den lithographischen Schiefern in Baiern. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, **1842**, 35-46.

Noubhani, A. & Cappetta, H. 1997. Les Orectolobiformes, Carchariniformes, et Myliobatiformes (Elasmobranchii, Neoselachii) des Bassins a phosphate du Maroc (Maastrichtian-Lutétien basal). *Palaeo Ichthyologica*, **8**, 1-327.

Reif, W.E. 1973. Morphologie und Ultrastruktur des Hai–"Schmelzes". *Zoologica Scripta*, **2**, 231-250.

Stürmer, W. & Bergström, J. 1973. New discoveries on trilobites by X-rays. *Paläontologische Zeitschrift*, **47**, 104-141.

Sykes, J. H. 1971. A new dalatiid fish from the Rhaetic Bond Bed at Barnstone, Nottinghamshire. *Mercian Geologist*, **4**, 13-22.

Thies, D 1983. Jurazeitliche Neoselachier aus Deutschland und S-England. *Courier Forschungsinstitut Senckenberg*, 58, 1-117.

Underwood, C. J. 2006. Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous. *Paleobiology*, **32**, 215-235.

Underwood, C. J. & Ward, D. J. 2004. Neoselachian sharks and rays from the British Bathonian (Middle Jurassic). *Palaeontology*, **47**, 447-501.

Underwood, C. J. & Ward, D. J. 2008. Sharks of the Order Carcharhiniformes from the British Coniacian, Santonian and Campanian (Upper Cretaceous). *Palaeontology*, **51**, 509-536. DOI: 10.1111/j.1475-4983.2008.00757.x

Vullo, R., Cappetta, H. & Néraudeau, D. 2007. New sharks and rays from the Cenomanian and Turonian of Charentes, France. *Acta Palaeontologica Polonica*, **52**, 99-116.

Wagner, J. A. 1862. Monographie der fossilen Fische aus den lithographischen Schiefern Bayerns. I. Plakoiden und Pyknodonten. *Abhandlungen der mathematisch-physikalischen Classe der königlich bayerischen Akademie der Wissenschaften*, **9**, 277-352.

Ward, D. J. 1981. A simple machine for bulk processing of clays and silts. *Tertiary Research*, **3**, 121-124.

White, E. I. 1931.*The vertebrate faunas of the English Eocene. I. From the Thanet Sands to the Basement Bed of the London Clay*. British Museum (Natural History), London. 121 pp.

Woodward, A. S. 1889. *Catalogue of the fossil Fishes in the British Museum. Part 1*. British Museum (Natural History), London. 474pp.

Woodward, A. S. 1902. The Fishes of the English Chalk, Part 1. *Monograph of the Palaeontographical Society*, **56**, 1-56.

Woodward, A. S. 1903. The Fishes of the English Chalk, Part 2. *Monograph of the Palaeontographical Society*, **57**, 57-96.

Woodward, A. S. 1912. The fishes of the English Chalk, Part 7. *Monograph of the Palaeontographical Society*, **65**, 225-264.

Woodward, A. S. 1916. The Wealden and Purbeck fishes, Part 1. *Monograph of the Palaeontographical Society*, **69**, 1-48.

Woodward, A. S. 1918. The Wealden and Purbeck fishes, Part 2. *Monograph of the Palaeontographical Society*, **70**, 49-104.

Woodward, A. S. 1919. The Wealden and Purbeck fishes, Part 3. *Monograph of the Palaeontographical Society*, **71**, 105-148.

Figure captions.

Fig. 1. Cumulative number of shark and ray species figured (including under incorrect names) from the UK and total Europe (excluding European Russia) showing the impact of certain publications and increase in known species since the widespread use of sieving for small fossils. Time bins represent 5 years.

Fig. 2. Micro-CT render of the Holotype of the batoid *Burnhamia davisi*, showing details of many teeth of both upper and lower jaw and the form of the jaw cartilages. Compare this with the figure by Woodward (1889) (inset) showing just the exposed part of the lower dentition.

Fig. 3. Maximum tooth dimension of species recorded from the British and French Chalk by Guinot *et al*. 2012a, b, 2013. Records relate to the fist figure of each species encountered. Black crosses indicate isolated dental material; grey crosses indicate skeletal material or associated tooth sets. Note unequal time bins.