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Interrelationships of Mesozoic hybodont sharks as indicated by dental morphology – preliminary results

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ABSTRACT:

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As many hybodont sharks are known solely from their teeth, this investigation approaches the phylogeny of the group with an emphasis on tooth morphology and dentitional patterns. The preliminary results presented here suggest that at least four different lineages of hybodont sharks occurred in the Mesozoic. Dentitional characters imply a close relationship within the Lonchidiidae (*Lonchidion*, *Vectiselachos*, *Parvodus*, and tentatively *Hylaeobatis*), within the Hybodontinae (*Hybodus* and *Egertonodus*) and in another, unnamed subfamily of the Hybodontidae, including *Planohybodus*, *Secarodus* and *Priohybodus*. There is also weak support for a grouping of *Acrodus*, *Asteracanthus* and *Palaeobates* in the Acrodontinae, while *Lissodus* is left without family designation due to a rather unique dentition and cephalic spine morphology. "*Polyacrodus*" is considered a *nomen dubium* as there are no characters to diagnose the genus based on the type species.

Key words: Hybodont sharks, Tooth morphology, Dentition, Mesozoic, Phylogeny.

INTRODUCTION

Hybodont sharks represent one of the most successful chondrichthyan lineages of all time, first occurring in the Devonian and becoming extinct in the Late Cretaceous. Their remains are frequently found in many different Mesozoic strata and numerous species have been identified. There are still fundamental gaps in our knowledge of their interrelationships, however, particularly between those taxa that are exclusively known from teeth. Mesozoic hybodonts, together with some Palaeozoic relatives, form the Hybodontoidea that is united by quite a few skeletal characters and the presence of cephalic spines (MAISEY 1989; MAISEY & *al.* 2004). Previous attempts to resolve the interrelationships within the Mesozoic members of the group using teeth have either relied on rough dental morphology (e.g. crushing or piercing dentitions), tooth structure (orthodont or osteodont teeth), or a combination of the two. It is clear that far more detailed studies of tooth morphology and dentitional pattern must be taken into account when assessing phylogenetic relationships based on dentitions. It is difficult to diagnose hybodont genera based on teeth with discrete characters and most often the entire (reconstructed) dentition is needed. Many genera and species will still be diagnosed by a combination of characters, an approach that seems to give a reasonably fair assessment of hybodont diversity (e.g. REES & UNDERWOOD 2008). Tooth histology does not appear to be a relevant character in tracing phylogenetic relationships as orthodont teeth are likely to be plesiomorphic in hybodonts (MAISEY 1989), and both orthodont and osteodont teeth can be found in a single species (BŁAŻEJOWSKI 2004). This study is an attempt to decipher the phylogenetic relationships within the Hybodontoidea using detailed dental morphology and, to

a lesser extent, fin spine and cephalic spine characters, in combination with previous results concerning skeletal and cranial anatomy (e.g. MAISEY 1987, 1989).

CAPPETTA (1987) recognised three major families among well-known Mesozoic hybodonts; Hybodontidae OWEN, 1846, Acrodontidae CASIER, 1959 and Polyacrodontidae GLIKMAN, 1964. He excluded *Acrodus* AGASSIZ, 1837 from the Hybodontidae, following CASIER (1959), but included *Pororhiza* CASIER, 1969, a poorly known genus with very peculiar teeth, in addition to *Hybodus* AGASSIZ, 1837 and *Priohybodus* D'ERASMO, 1960. In the Acrodontidae, CAPPETTA (1987) tentatively placed three genera with crushing dentitions (*Acrodus*, *Asteracanthus* AGASSIZ, 1837 and *Bdellodus* QUENSTEDT, 1882), although he cautiously commented that the family needed further investigation. The histological grounds on which the Polyacrodontidae was originally based (GLIKMAN 1964)

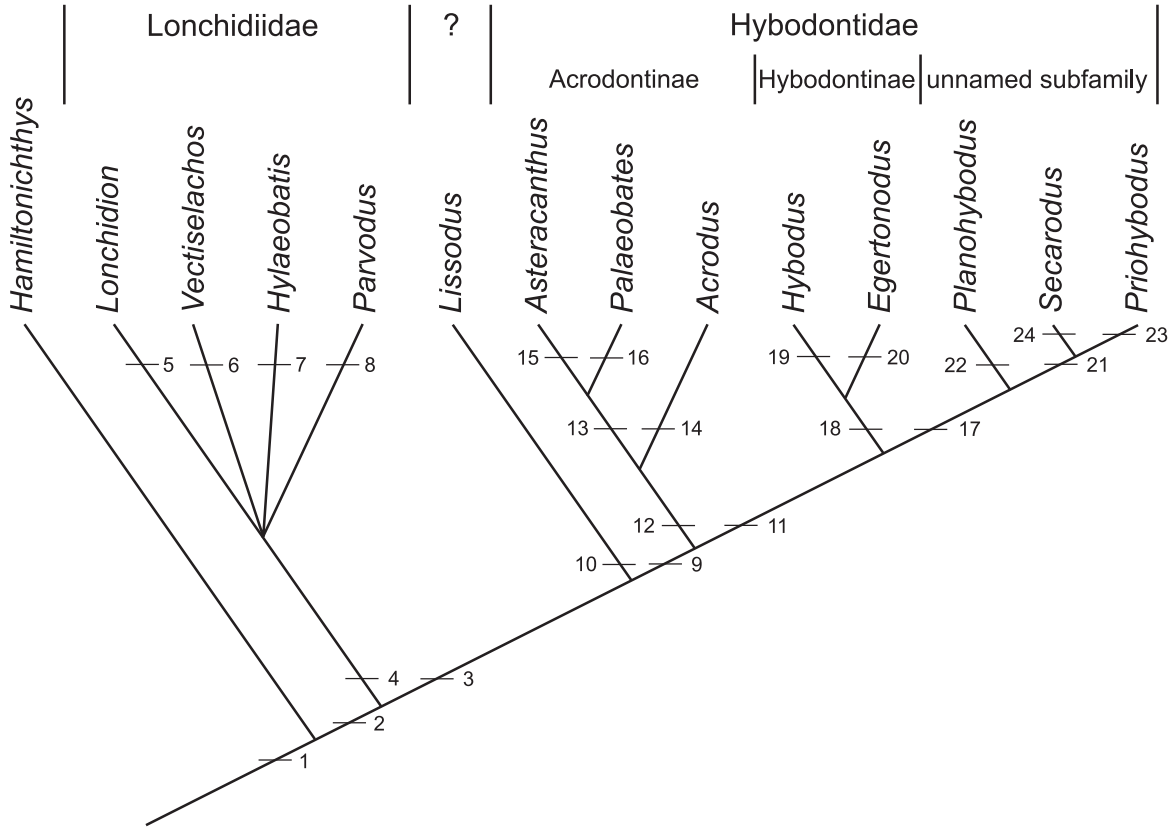

Fig. 1. Hypothesis of phylogenetic relationships among selected Mesozoic hybodonts. Nodes and definitions of terminal taxa are defended by the following characters or combinations of characters (for skeletal characters, see MAISEY 1989): 1, cephalic spines present; 2, cephalic spines without large lateral cusplets; 3, T-shaped basal plate of cephalic spines; 4, low-cusped teeth with labial protuberance, low root with row of small foramina on the upper part, arrow-shaped basal plate of cephalic spines; 5, labio-lingually narrow, gracile teeth without ornamentation, strong and narrow labial protuberance; 6, bulky teeth ornamented with granulae; 7, crushing dentition and complex, partly reticulate ornamentation; 8, moderately high cusp and cusplets, labial protuberance rounded, ornamentation with few folds; 9, T-shaped basal plate of cephalic spines with short and rounded posterior lobe; 10, domed teeth with low cusp and cusplets, wide and triangular labial protuberance, ornamentation with numerous weak folds, posterior lobe of basal plate of cephalic spine long and dorso-ventrally flattened, anterior lobes of basal plate thin and having raised anterior edges; 11, high-crowned teeth with cusplets, no differentiated, small circular foramina on root; 12, crushing dentition with enlarged lateral teeth, complex ornamentation; 13, interlocking teeth with flat crown, asymmetrical lateral teeth, reticulate ornamentation, massive root with well defined foramina; 14, cusps in anterior teeth, symmetrical enlarged lateral teeth, porous root; 15, wide lateral teeth, reduced number of tooth files, fin spines with tubercles on the anterior side; 16, narrow lateral teeth; 17, cutting dentition with wide, flattened cusp, serrated cutting edges; 18, high, narrow and slender or conical cusps with close to circular cross-section, porous root; 19, stout cusplets, strong ornamentation; 20, sigmoidal curvature of the cusp, slender cusplets, weak ornamentation; 21, diverging cusplets, weak or no ornamentation; 22, high and wide symmetrical teeth, strong, rarely serrated cutting edges, simple ornamentation with short folds; 23, strongly diverging cusplets, evenly serrated cutting edges, high and massive root; 24, diverging cusplets in anterior teeth, recurved crown in lateral teeth, poorly serrated cutting edges

were doubted by CAPPETTA (1987), but he still included two genera, *Lissodus* BROUGH, 1935 and *Polyacrodus* JAEKEL, 1889, as these were considered morphologically similar. He tentatively also attributed *Palaeobates* VON MEYER, 1849 to this family.

MAISEY (e.g. 1983, 1987, 1989) studied the skeletal and cranial morphology of most of the better known Mesozoic hybodonts and provided a phylogeny based on results from these investigations and gross dental morphology. He included two subfamilies in the Hybodontidae, Hybodontinae OWEN, 1846 (including *Hybodus* and *Egertonodus* MAISEY, 1987) and Acrodontinae CASIER, 1959 (including *Acrodus* and *Asteracanthus*). In the "Polyacrodontidae", MAISEY (1989) tentatively placed *Lissodus* and *Polyacrodus* on the basis of a single character ("convict-arrow" shaped cephalic spines) that is unknown in the type species of *Polyacrodus*.

Comments on "*Polyacrodus*" JAEKEL, 1889

This genus was originally based on tooth histology and teeth of the type species, *P. polycyphus* (AGASSIZ, 1837), have an orthodont structure. Unfortunately, the holotype of this species is apparently lost (KRIWET 2004) and the teeth figured by JAEKEL (1889) do not show any characters that can separate them on a generic level from those of *Hybodus*, neither on morphology nor dentitional pattern (REES & UNDERWOOD 2002). Other species that are skeletally similar to *Hybodus reticulatus* AGASSIZ, 1837, the type species of *Hybodus*, have teeth with a morphology approaching that of *P. polycyphus* (see MAISEY 1987; REES & UNDERWOOD 2008) in being robust and possessing nodes on the lower part of the crown. Consequently, as *Polyacrodus* cannot be diagnosed on dental morphology and as tooth structure is no longer regarded a useful character, it is here suggested that this genus is considered a *nomen dubium* and all species currently identified are referred to *Hybodus*, awaiting a revision of the latter genus. Many species currently included in *Polyacrodus* will probably be referred to other or new genera in the light of future research. The use of Polyacrodontidae should also be terminated as the family unites a number of genera based on a single plesiomorphic character (see MAISEY 1989), the orthodont tooth structure.

Comments on *Hybodus* AGASSIZ, 1837

This genus contains numerous nominal species as most hybodont teeth with a well defined cusp and lateral cusplets have been referred to *Hybodus* over the years. Many species have teeth that are far from similar to the type species, *H. reticulatus*, and the genus must be thoroughly revised before the generic diversity can be assessed. It is likely that the dental morphology of *Hybodus* will be considerably more constrained after such a revision. In this investigation, only the dentitions of the type species and *H. hauffianus* will be taken into account as these two species are skeletally similar (see MAISEY 1987).

HIGHER TAXA

In this review, the following hybodont genera have been included as they have either been studied first hand by the author or have been well illustrated by other authors, and are represented by at least several complete teeth, derived from different tooth positions: *Acrodus*, *Asteracanthus*, *Egertonodus*, *Hybodus*, *Hylaeobatis* WOODWARD, 1916, *Lissodus*, *Lonchidion* ESTES, 1964, *Palaeobates*, *Parvodus* REES & UNDERWOOD, 2002, *Planohybodus* REES & UNDERWOOD, 2008, *Priohybodus*, *Secarodus* REES & UNDERWOOD, 2008, and *Vectiselachos* REES & UNDERWOOD, 2002 (Text-fig. 1). The most complete Palaeozoic hybodont, *Hamiltonichthys mapesi* MAISEY, 1989 has been used as the outgroup, since it is considered to be a cladistically primitive hybodontoid (MAISEY 1989). It was not possible however, to find any dental characters to confirm this view.

Lonchidiidae HERMAN, 1977 *sensu* REES & UNDERWOOD, 2002

INCLUDED GENERA: *Lonchidion*, *Parvodus*, *Vectiselachos* and tentatively *Hylaeobatis*.

This family was recently revised by REES & UNDERWOOD (2002), who included five genera: *Lonchidion*, *Lissodus*, *Parvodus*, *Vectiselachos* and *Hylaeobatis*. These are all small-sized sharks with either delicate, thin teeth or wide and low crushing teeth. There seems to be a close relationship between *Lonchidion*, *Parvodus* and *Vectiselachos* based on the morphology of weakly ornamented, low and rather thin teeth (although swollen in *Vectiselachos*), and a root with a single row of small, circular foramina close to the crown-root junction. The morphology of the basal plate of the cephalic spine is similar in *Lonchidion* and *Parvodus* (possibly also in *Vectiselachos*), and is arrow-shaped in dorsal view. Including *Hylaeobatis* in the family is tentative as the dentitional pattern of the genus is somewhat similar not only to that of *Vectiselachos*, but also to members of the Acrodontinae, particularly *Acrodus*. *Lissodus* is removed from the family (see below).

Lissodus Brough, 1935

Teeth of *Lissodus* are really rather different from those of other hybodonts and share characters with both those of the Lonchidiidae and those of the Acrodontinae. The heterodonty pattern is more similar to that of *Acrodus* than to any other genus and many species actually possess enlarged lateral teeth. The domed, often ornamented, crown with clearly demarcated cusps and cusplets in anterior teeth is also similar to teeth of some species of *Acrodus*, while the presence of a labial protuberance, albeit wide and triangular, is a character that occurs in some Lonchidiidae, in particular *Vectiselachos*. As *Lissodus* has few other characters in common with this family, it is left without family assignment for the time being. The basal plate of the cephalic spine (at least in *L. cassangensis*, see Antunes & *al.* 1990) is also quite unique in having a long and dorsoventrally flattened posterior lobe and anterior lobes that are thin and have a raised anterior edge.

Acrodontinae Casier, 1959 *sensu* Maisey, 1989

INCLUDED GENERA: *Acrodus* and tentatively *Asteracanthus* and *Palaeobates*.

The crushing dentitions of the three included genera may be a valid character that unite these taxa, in combination with enlarged lateral teeth (although this character also occurs in *Lissodus*). Based on dental morphology, it appears that *Asteracanthus* and *Palaeobates* are more closely related to each other than to *Acrodus*, but the anterior ornamentation of the fin spines of these two taxa is completely different. The more common longitudinal ribs in *Palaeobates* and most other hybodonts are replaced by tubercles in *Asteracanthus*. It is however unlikely that ornamentation with tubercles is unique to the latter genus as this type of fin spines occur in the Purbeck of southern England where no teeth of *Asteracanthus* have been found, despite extensive collecting (Underwood & Rees 2002). The relationships between the three genera need further investigation and it is likely that the suggested composition of the Acrodontinae will be re-evaluated in the future.

Hybodontinae Owen, 1846 *sensu* Maisey, 1989

INCLUDED GENERA: *Hybodus* and *Egertonodus*.

The skeletal similarities between these two genera that were recorded by Maisey (1987) are mirrored in their dentitional patterns. It is rather difficult to separate teeth of the two genera but there are a few differences including a sigmoidal curvature of the cusp, higher, more slender cusplets and weaker ornamentation in *Egertonodus* (Rees & Underwood 2008). Male individuals of *Egertonodus* possess only a single pair of cephalic spines (Maisey 1987), a character also recorded in *Tribodus* Brito & Ferreira, 1989. Sharks of the latter genus are equipped with a well developed crushing dentition and probably belong in the Acrodontinae. As the Hybodontinae is limited to *Hybodus* and *Egertonodus*, the group is characterised by teeth with a high and slender or slightly stouter, but never flattened cusp.

Unnamed subfamily

INCLUDED GENERA: *Planohybodus*, *Secarodus* and *Priohybodus*.

This group includes all three hybodont genera that have developed cutting dentitions with strongly flattened and high-cusped teeth. The root morphology of at least *Planohybodus* and *Secarodus* is similar to that of *Hybodus*, apart from being less porous, and this character, together with the *Hybodus*-like morphology of juvenile teeth of *Secarodus*, suggests that the group should be retained in the Hybodontidae.

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REFERENCES

Antunes, M.T., Maisey, J.G., Marques, M.M., Schaeffer, B. & Thomson, K.S. 1990. Triassic fishes from the Cassange Depression (R. P. de Angola). *Ciências da Terra (UNL), Número Especial*, **1990**, 1-64.

Błażejowski, B. 2004. Shark teeth from the Lower Triassic of Spitsbergen and their histology. *Polish Polar Research*, **25**, 153-167.

Cappetta, H. 1987. Chondrichthyes II. *In*: H.-P. Shultze (*Ed.*), Mesozoic and Cenozoic Elasmobranchii, **3B**, 1-193. *Gustav Fischer Verlag*; Stuttgart – New York.

Casier, E. 1959. Contributions à l'étude des Poissons fossiles de la Belgique. XII. Sélaciens et Holocephales sinémuriens de la province de Luxembourg. *Institut Royal des Sciences Naturelles de Belgique Bulletin*, **35**, 1-27.

Glikman, L.S. 1964. Class Chondrichthyes, subclass Elasmobranchii. *In*: D.V. Obruchev (*Ed.*), Fundamentals of paleontology. Akademii Nauk SSSR, Moscow, 292-352. *Akademia Nauk SSSR*; Moscow. [*In Russian*]

JAEKEL, O. 1889. Die Selachier aus dem oberen Muschelkalk Lothringens. *Abhandlungen zur geologischen Specialkarte von Elsass-Lothringen*, **3**, 275-340.

KRIWET, J. 2004. Late Jurassic selachians (Chondrichthyes: Hybodontiformes, Neoselachii) from central Portugal. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **2004**, 233-256.

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

— 1987. Cranial anatomy of the Lower Jurassic shark *Hybodus reticulatus* (Chondrichthyes; Elasmobranchii), with comments on Hybodontid systematics. *American Museum Novitates*, **2878**, 1-39.

— 1989. *Hamiltonichthys mapesi*, g. & sp. nov. (Chondrichthyes; Elasmobranchii), from the Upper Pennsylvanian of Kansas. *American Museum Novitates*, **2931**, 1-42.

MAISEY, J.G., NAYLOR, G.J.P. & WARD, D.J. 2004. Mesozoic elasmobranchs, neoselachian phylogeny and the rise of modern elasmobranch diversity. *In*: G. ARRATIA & A. TINTORI (*Eds*), Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity, pp. 17-56. *Verlag Dr. Friedrich Pfeil*; München.

REES, J. & UNDERWOOD, C.J. 2002. The status of the shark genus *Lissodus* Brough, 1935, and the position of nominal *Lissodus* species within the Hybodontoidea (Selachii). *Journal of Vertebrate Paleontology*, **22**, 471-479.

— & — 2008. Hybodont sharks from the English Bathonian and Callovian (Middle Jurassic). *Palaeontology*, **51**, 117-147.

UNDERWOOD, C.J. & REES, J. 2002. Selachian faunas from the lowermost Cretaceous Purbeck Group of Dorset, southern England. *Special Papers in Palaeontology*, **68**, 83-101.

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