

A review of the hybodont sharks from the Mesozoic of Thailand

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ABSTRACT

We propose here a quick review of the hybodont assemblages from the Mesozoic of Thailand, both from the Indochina and Sibumasu (Shan-Thai) terranes. The faunas from the Triassic and the Jurassic are still imperfectly known. The faunas from the Cretaceous, found so far only in the Indochina terrane, represent an assemblage endemic to Asia and well adapted to life in freshwater. Current data suggest that they originated from a European stock sometimes during the Jurassic. These Thai assemblages seem also to suggest that the marine ptychodontids emerged from a freshwater lonchidiid lineage at the beginning of the Cretaceous.

Keywords: Jurassic, Cretaceous, Thailand, Chondrichthyes

1. INTRODUCTION

Since 1998, an intensive screen-washing programme has been part of the Dano-Franco-Thai collaboration aiming at the study of the Mesozoic vertebrate palaeobiodiversity of Thailand. This programme recovered a great number of hybodont shark teeth, many of them belonging to new species, and representing also new genera. This work was first focused on the Lower Cretaceous of the Khorat Plateau, but our work was extended to the Jurassic of the same area as early as 1999. In 2003, we started screen-washing in the Jurassic of the South part of Thailand. This article aims at presenting the current state of our knowledge concerning the hybodont sharks recovered so far in the Jurassic and the Cretaceous of Thailand and at highlighting their palaeogeographic and evolutionary relevance. Full descriptions of the fossils are, or will be, provided elsewhere (Cuny *et al.*, 2003, in press).

To protect the fossiliferous sites, their exact locations are not provided in this article. For scientific purposes, these locations can however be obtained on request from the second author. The material mentioned in this work is housed in the Phu Kum Khao Dinosaur Research and Education Center (Department of Mineral Resources, Kalasin Province), as well as in the Srisuk House Museum, a private museum in Khao Yoi (Phetchaburi Province).

2. REVIEW OF THE FAUNAS

2.1. Indochina Terrane

2.1.1. Phu Kradung Formation (Late Jurassic – Early Cretaceous)

Class: Chondrichthyes Huxley, 1880
Subclass: Elasmobranchii Bonaparte, 1838

Order: Hybodontiformes Maisey, 1987
Family: Hybodontidae Owen, 1846

Subfamily: Hybodontinae Owen, 1846 *sensu* Maisey, 1989
Genus: *Hybodus* Agassiz, 1839
Hybodus sp.

Occurrences: Chong Chat, Nong Bua Lamphu Province (Cuny *et al.*, 2003); Phu Nam Jun, Kalasin province; Wang Din So, Phitsanulok Province (Srisuk, 2002).

Note: The material is so far quite scanty and represented mainly by broken teeth. It is probable that more than one species is represented, but this cannot be ascertained for the time being. More collection efforts are needed.

Subfamily: Acrodontinae Casier, 1959 *sensu* Maisey, 1989
Genus: *Acrodus* Agassiz, 1837
Acrodus sp.

Occurrences: Chong Chat, Nong Bua Lamphu Province; Wang Din So, Phitsanulok Province (Cuny *et al.*, 2003).

Family: Lonchidiidae Herman, 1977
Genus: *Lonchidion* Estes, 1964
Lonchidion sp.

Occurrence: Wang Din So, Phitsanulok Province (Srisuk, 2002).

Note: This material, consisting of 17 teeth, was originally described as *Lissodus* by Srisuk (2002), but the constricted base of the crown and narrow labial peg would rather favour an identification of these teeth as belonging to the genus *Lonchidion*. The four finspines attributed by the same author to *Lissodus* are not diagnostic at the generic level, and could belong to any of the three genera mentioned at Wang Din So (*Hybodus*, *Acrodus*, or *Lonchidion*).

Family: Lonchidiidae Herman, 1977
Lonchidiidae indet.

Occurrence: Khok Sanam, Kalasin Province.

Note: Only five fragmented crowns have been recovered so far, which do not allow a more precise identification to be made.

2.1.2. Sao Khua Formation (Early Cretaceous)

Family: Hybodontidae Owen, 1846

Subfamily: Hybodontinae Owen, 1846 *sensu* Maisey, 1989

Genus: *Hybodus* Agassiz, 1837

Hybodus sp. A

Hybodus sp. B

Occurrence: Phu Phan Thong and Phu Wat, Nong Bua Lamphu Province (Cuny *et al.*, 2005, in press)

Hybodus sp.

Occurrence: Phu Noi, Sakhon Nakhon Province.

Note: The material consists of a single tooth of a rather large size (9 mm in height) kept at the Srisuk's private museum. This is insufficient to allow a determination at the species level, and difficult to compare with the much smaller and fragmented material from Phu Phan Thong. At least two hybodont fin spines were recovered from the same site, but may belong to either of the two other genera discovered in this locality (*Heteroptychodus* and *Isanodus*, see below) as well as to *Hybodus* since a determination at the generic level of these spines is impossible.

Family: Lonchidiidae Herman, 1977

Genus: *Lonchidion* Estes, 1964

Lonchidion khoratensis Cuny *et al.*, in press

Occurrence: Phu Phan Thong, Nong Bua Lamphu Province (Cuny *et al.*, 2005, in press)

Genus: *Parvodus* Rees & Underwood, 2002

Parvodus sp.

Occurrence: Phu Phan Thong, Nong Bua Lamphu Province (Cuny *et al.*, 2005, in press).

Genus: *Isanodus* Cuny *et al.*, in press

Isanodus paladeji Cuny *et al.*, in press

Occurrences: Phu Phan Thong, Nong Bua Lamphu Province (Cuny *et al.*, 2005, in press); Phu Noi?, Sakhon Nakhon Province

Note: The presence of *Isanodus* in Phu Noi is only suggested by a single tooth kept in Srisuk's private museum at this time, but more material from this site has been recently collected and seems to contain more *Isanodus* teeth (Claude, pers. Comm., 2005).

Family: Ptychodontidae Jaekel, 1898

Genus: *Heteroptychodus* Yabe & Obata, 1930

Heteroptychodus steinmanni Yabe & Obata, 1930

Occurrences: Phu Phan Thong, Phu Wat and Huai Lao Yang, Nong Bua Lamphu Province (Cuny *et al.*, 2005, in press); Phu Wiang 1A, Khon Kaen Province; Phu Kum Khao and Phu Mai Paw, Kalasin Province; Phu Phok and

Phu Noi, Sakhon Nakhon Province; Non Liam, Chaiya Phum Province (Cuny *et al.*, 2003).

2.1.3. Khok Kruat Formation (Aptian-Albian)

Family: Hybodontidae Owen, 1846

Subfamily: Hybodontinae Owen, 1846 *sensu* Maisey, 1989
“*Hybodus*” sp.

Occurrence: Khok Pha Suam, Ubon Ratchathani province (Cuny *et al.*, 2003).

Note: These teeth are quite unusual for *Hybodus* with their very dense ornamentation and the first pair of lateral cusplets almost as high as the main cusp. They probably represent a new genus.

Family: Ptychodontidae Jaekel, 1898

Genus: *Heteroptychodus* Yabe & Obata, 1930

Heteroptychodus steinmanni Yabe & Obata, 1930

Occurrences: Khok Pha Suam, Ubon Ratchathani province (Cuny *et al.*, 2003); San Ram, Khon Kaen Province.

Note: Teeth belonging to juvenile specimens of *Heteroptychodus steinmanni* have been recovered from Khok Pha Suam (Cuny *et al.*, 2003).

Family: *incertae sedis*

Genus: *Thaiodus* Cappetta, Buffetaut & Suteethorn, 1990

Thaiodus ruchae Cappetta, Buffetaut & Suteethorn, 1990

Occurrences: Khok Pha Suam, Ubon Ratchathani province, Ban Khok Kruat and Ban Sapan Hin, Nakhon Ratchasima Province (Cuny *et al.*, 2003); San Ram, Khon Kaen Province.

Note: *Thaiodus ruchae* is normally found together with *Heteroptychodus steinmanni*, except in Nakhon Ratchasima Province. There is currently no explanation for this oddity.

New genus and species # 1 (Cuny *et al.*, 2003)

Occurrence: Khok Pha Suam, Ubon Ratchathani province (Cuny *et al.*, 2003).

New genus and species # 2 (Cuny *et al.*, 2003)

Occurrence: Khok Pha Suam, Ubon Ratchathani province (Cuny *et al.*, 2003).

New genus and species # 3 (Cuny *et al.*, 2003)

Occurrence: Khok Pha Suam, Ubon Ratchathani province (Cuny *et al.*, 2003).

2.1.4. Diversity of the Cretaceous freshwater hybodonts.

The freshwater hybodonts from the Sao Khua and Khok Kruat Formations are diverse and show adaptation to a wide range of diets. *Hybodus* spp., genus #2 and *Parvodus* sp. were probably opportunistic feeders, feeding on rather soft preys while the grinding dentition of *Lonchidion khoratensis* *Heteroptychodus steinmanni*, genus #1, and genus #3 indicate more durophagous sharks. *Isanodus paladeji*, with a clutching-grinding dentition represents another type of

durophagous shark. Finally, the cutting dentition of *Thaiodus* suggests a diet mainly consisting of large, soft-bodied preys. These sharks thus represented an important and diverse component of the freshwater ecosystems of the Khorat Plateau, but the majority of them, both in terms of number of species and number of individuals were durophagous.

2.2. Sibumasu (Shan-Thai) Terrane

2.2.1. Huai Hin Formation (Tithonian)

Family: Hybodontidae Owen, 1846

Subfamily: Acrodontinae Casier, 1959 *sensu* Maisey, 1989

Genus: *Asteracanthus* Agassiz, 1837
Asteracanthus sp.

Occurrence: Pha Dang Zinc Mine, Tak Province (Fig. 1).

Note: The Huai Hin formation was dated as Tithonian by ammonites (Fontaine, 1990).



Figure 1. *Asteracanthus* tooth from Pha Dang in apical view.

2.2.2. Khlong Min Formation (Mid to Late Jurassic)

Family: Hybodontidae Owen, 1846

Subfamily: Hybodontinae Owen, 1846 *sensu* Maisey, 1989

Genus: *Hybodus* Agassiz, 1837
Hybodus sp.

Occurrences: Mab Ching, Nakhon Si Thammarat Province (Tong *et al.*, 2002); Khlong Thom, Krabi Province (buffetaut *et al.*, 2005).



Figure 2. Hybodont fin spine from Mab Ching in lateral view.

Note: The teeth found at Mab Ching are rare, minute and incomplete, but show crown morphology in accordance with that of the genus *Hybodus*. On the same site, two rather large finspines have been recovered, the largest one being 145 mm in length, the smallest one being 135 mm in length. They appear to be too large to belong to the same animal as the minute teeth. However, their ornamentation is made of tubercles in the lower part of the spines, and of costae in the upper part (fig. 2). According to Maisey (1978), this would indicate that these spines belong to old, large animals, maybe explaining the size discrepancy with the teeth, which might belong to younger individuals. However, also at the same site, some dermal denticles of unusual shape (fig. 3) have been recovered. To the best knowledge of the authors, such dermal denticles have never been described in *Hybodus*, which would indicate that probably more than a single hybodont genus is present at Mab Ching.

A single crown has been recovered from Khlong Thom. It appears larger and more acute than the ones recovered at Mab Ching.



Figure 3. Hybodont dermal denticle from Mab Ching in apical view.

Subfamily: Acrodontinae Casier, 1959 *sensu* Maisey, 1989

Genus: *Asteracanthus* Agassiz, 1837
Asteracanthus sp.

Occurrences: Ao Luk, Krabi Province; Mab Ching, Nakhon Si Thammarat Province.



Figure 4. *Asteracanthus* tooth from Ao Luk in apical view.

Note: the complete crown found at Ao Luk (Fig. 4) is very similar to the incomplete *Asteracanthus* tooth found in the Tak Province (Fig. 1), and is likely to belong to the same species, although more material will be needed to get identification at the species level. This, if confirmed, would suggest a Late Jurassic age for the upper part of the Khlong Min Formation. The tooth from Mab Ching is very fragmentary and its identification should be considered tentative. Moreover, It was found well below the levels that yielded the *Asteracanthus* teeth in Ao Luk and the *Hybodus* teeth in Mab Ching.

2.2.3. Other reports

Srisuk (2003) reported a hybodont fauna from Ao Min (Nakhon Si Thammarat Province) including teeth of *Hybodus*, *Lissodus*, *Asteracanthus?* (identified as *Palaeobates* by Srisuk) as well as dermal denticles very similar to those found at Mab Ching. The age of this fauna is currently unclear (Srisuk, 2003), although it looks very similar to the fauna previously recovered from the Khlong Min Formation.

Srisuk (2005) also described the first Triassic hybodont assemblage from Thailand, found at Khao Ok Thalu, Phatthalung Province. This fauna is likely to contain only lonchidiid teeth, and not *Acrodus* and *Polyacrodus* as stated by the author, because all the teeth figured seem to show a well-developed labial peg. Further study of this fauna is needed.

3. PALAEOGEOGRAPHY

From a palaeobiogeographical point of view, The Cretaceous faunas of the Indochina terrane are much more informative than the Jurassic faunas, whether from the Indochina or Sibumasu terranes, because the latter are still imperfectly known. The faunas from the Sao Khua Formation include *Hybodus*, which possesses a worldwide distribution, but the exact affinities of the material from Phu Phan Thong and Phu Noi are unclear. *Parvodus* was so far restricted to Europe (Rees & Underwood, 2002). *Isanodus paladeji* and *Lonchidion khoratensis* are known only from Thailand. Prior to the Late Jurassic, the genus *Lonchidion* was restricted to North America, Europe and Africa (Rees & Underwood, 2002). *Heteroptychodus* has been recorded in Thailand, Japan, Kirghisia, and Mongolia, under the generic name of *Asiadontus* in these two latter countries (Yabe & Obata, 1930; Nessov, 1997; Tanimoto & Tanaka, 1998; Cuny *et al.*, 2003). Compared with the hybodont fauna from the Aptian-Albian Khok Kruat Formation of Thailand, the Sao Khua fauna appears much less endemic, at least at the generic level (Cuny *et al.*, 2003). This fauna appears to be dominated by Lonchidiidae, but this family is so far unknown from the Khok Kruat Formation (Cuny *et al.*, 2003). This would indicate some dramatic changes in the shark faunas between the depositions of these two formations, although *Heteroptychodus steinmanni* was not affected.

In the Khok Kruat Formation, genera #1, #2, and #3 appear endemic to the Khorat Plateau and likely to have been restricted to freshwaters, hence their endemism. "*Hybodus*" probably belong to a new genus that appears again to be endemic to the Khorat Plateau. *Thaiodus* is known only from the Khorat Plateau and Tibet, where it has been found in a deltaic environment (Cappetta *et al.*, 1990). *Heteroptychodus* is known in several Asian localities (see above).

Maisey (1989) suggested that many hybodont genera (*Hamiltonichthys*, *Hybodus*, *Lissodus*) were euryhaline. Such a mode of life would explain the distribution of *Heteroptychodus* and *Thaiodus* around the Asian continent, following the coastline to invade several freshwater systems. A similar strategy is seen today among the sawfish *Pristis perotteti*, which has colonized several lakes along the Atlantic coast of Central and South America (Thorson, 1982) or among the freshwater ray *Himantura chaophraya* which is found in several rivers from Thailand in the North to Australia in the South (Last & Stevens, 1994). Following a similar pattern, the spreading of *Thaiodus* and *Heteroptychodus-Asiadontus* would have been favoured by the Late Aptian sea transgression (Averianov & Skutschas, 2000). However, as these sharks are unknown outside Asia, they were probably unable to face open water. The presence of *Parvodus*, and also *Lonchidion*, in the Sao Khua Formation seems to indicate a European origin for the Thai hybodonts. It is possible that they reached Thailand following the coast sometimes in the Jurassic and then settled in freshwater environments where they diversified.

Interestingly, terrestrial tetrapods appear to show a rather different pattern: many of the dinosaurs from the Sao Khua Formation belong to groups endemic to eastern Asia, whereas the Khok Kruat Formation contains forms (such as iguanodontids) suggesting faunal interchange with other parts of the world, including Europe (Buffetaut & Suteethorn, 1998). The cause for this discrepancy is not easily explainable in palaeobiogeographical terms, unless the freshwater sharks and the dinosaurs with European affinities belong to two distinct dispersal episodes. The peculiar freshwater sharks of the Khok Kruat Formation may represent the result of endemic evolution from a basal stock which became isolated from the assemblages of other land masses at an early period (Jurassic ?). In this case, the older shark fauna from the Sao Khua Formation could reflect an intermediate stage of differentiation, at which resemblances with shark faunas from other regions were still perceptible. The episode of faunal interchange reflected by the non-endemic dinosaurs from the Khok Kruat Formation apparently did not include freshwater sharks. The Lonchidiidae were replaced in Thailand by more endemic hybodonts (Cuny *et al.*, 2003), which may suggest that the link with Europe was cut at that time. The reason of the disappearance of the Lonchidiidae in Thailand sometime during the Early Cretaceous remains unclear in the present stage of our knowledge.

4. THE ORIGIN OF *PTYCHODUS*

Ptychodus is a large shark possessing a crushing dentition with a global distribution during most of the Cretaceous (Cappetta, 1987). It is thought by some authors to be a hybodont shark (Cappetta, 1987), while others consider it likely to be a neoselachian shark (Maisey *et al.*, 2004), mostly because some calcified vertebral centra have been found together with its teeth (Everhart & Caggiano, 2004). Its teeth are very characteristic, but quite different from any other sharks, hence the difficulty of deciphering its phylogenetic relationships. The teeth of *Heteroptychodus* shows however a pattern of ornamentation quite similar to those of *Ptychodus*, differing only by a reduced marginal area and a denser pattern of parallel longitudinal ridges

ornamenting the crown, and is thus included in the family Ptychodontidae (Cuny *et al.*, 2003, in press).

The resemblance in the pattern of ornamentation and shape of the posterior teeth between *Isanodus paladeji* and *Heteroptychodus steinmanni* may also suggest that these two genera are closely related (Cuny *et al.*, in press). *Heteroptychodus steinmanni* is so far the oldest member of the family Ptychodontidae, being known as early as the ?Berriasian in Thailand and Japan (Cuny *et al.*, 2003; Goto & Kuga, 1982), while *Ptychodus* is unknown before the Albian and already shows a very specific tooth morphology (Cappetta, 1987; Siverson, 1999). It may thus be tempting to interpret the Ptychodontidae as having originated from Lonchidiidae that became increasingly adapted to durophagy, such as *Isanodus paladeji* with its large grinding posterolateral teeth. Moreover, the teeth of *Isanodus* show the development of ridges parallel to the longitudinal crest, a pattern very characteristic of the Ptychodontidae. The current data would thus favour an origin of the Ptychodontidae in the Early Cretaceous of Asia, possibly in freshwater environments, and would definitely indicate that *Ptychodus* is indeed a hybodont shark. However, this hypothesis needs further evidence to be formally accepted, and a cladistic analysis is in preparation by one of us (S.K.).

5. CONCLUSION

Thailand has yielded diverse faunas of Mesozoic hybodont sharks. The faunas from the Triassic and the Jurassic are still imperfectly known, and more fieldworks to recover more fossils are needed before to propose an evolutionary and palaeogeographic scenario for these faunas. The faunas from the Cretaceous, found so far only in the Indochina terrane, represent endemic assemblages well adapted to life in freshwater. Current data suggest that they originated from a European stock sometimes during the Jurassic. These Thai assemblages seem also to suggest that the ptychodontids emerged from a freshwater lonchidiid lineage sometimes at the beginning of the Cretaceous.

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