

## Taxic diversity and ecology of Mesozoic bony fish assemblages from the Khorat Group, NE Thailand

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**Abstract** - Environmental drivers shape freshwater alpha-diversities. The Khorat Group in northeastern Thailand is a succession of five continental formations ranging from the Middle? Jurassic with the lower part of the Phu Kradung to the Aptian with the Khok Kruat Formation. In order to identify ecological traits of the palaeocenoses, we focus here on biological and taphonomical features rather than on the sedimentological context of each assemblage. The major distinction that can be made in the succession of bony fish assemblages within the Khorat Group is between the Late Jurassic – basal Cretaceous Phu Kradung Formation on the one hand and the Early Cretaceous Sao Khua and Khok Kruat formations on the other hand.

**Keywords:** Taxic diversity, Khorat Group, alpha-diversity, Palaeocenoses, ginglymodians

### 1. Introduction

Environmental drivers shape freshwater alpha-diversities. In a monsoonal tropical stream, for example, there are positive relationships between species richness and stream width, substrate heterogeneity, pH, dissolved oxygen and a negative relationship with altitude (Shukla and Bhat, 2017). At the global scale, terrestrial primary productivity, annual precipitation, isothermality and mean annual temperature seem to be the most important of variables affecting the alpha-diversity but historical factors, in particular their role as refuge areas or centers of diversification, seem to have played a more important role than physical parameters (Pelayo-Villamil *et al.*, 2015).

The Khorat Group in northeastern Thailand is a succession of five continental formations ranging from the Middle? Jurassic with the lower part of the Phu Kradung to the Aptian with the Khok Kruat Formation. Three of these formations (Phu Kradung, Sao Khua and Khok Kruat) have yielded bony fish remains in about 20 different localities. Here, we compare some taphonomic features and taxonomic traits of the main fish localities. Although still very superficial, this study is a preliminary attempt to identify ecological traits, which characterize these palaeocenoses. It is expected that this approach will allow comparison with modern fish assemblages in order to identify links between biological traits (alpha diversity, taxic composition) and environmental drivers

### 2. Material and methods

In order to identify ecological traits of the palaeocenoses, we focus here on biological and taphonomical features rather than on the sedimentological context of each assemblage. Sedimentology will be used in a second step to test the results obtained here. Among the easily identified parameters of a fossil assemblage are its taxic composition, and the mode of preservation and the abundance of specimens for each species. These data have been collected on the basis of literature (in particular on an update of Cavin *et al.*, 2009) and personal observations by the authors. Some sites with only a few and little informative fish remains are not included in this study, such as Phra Pong (Sra Keaw), Khok Kong (Kalasin), Na Krai (Kalasin), Dan Luang (Mukdahan) and Dan Kaeng (Mukdahan). In one of the fossil fish sites, Phu Nam Jun, a taphonomical analysis of the fish assemblages has been performed (Deesri *et al.*, 2009). We also recorded on a three-level scale (low, middle, high) the alpha diversities of tetrapods and sharks in each site by simply counting species of taxa.

### 3. Results

Table 1 presents the compilation of data for 15 sites and Figure 1 shows a general view of the fish taxa in the three examined formations. The stratigraphical succession within each formation in Table 1 is generally unknown, except in the Phu Kradung Formation (Cuny *et al.*, 2014).

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In this formation, the Phu Nam Jun site appears to be at the top of the formation and is probably Berriasian in age. The stratigraphic position of the Phu Din Dang site is

uncertain, either at the base of the Khok Kruat Formation or at the top of the Sao Khua Formation (position retained in Table 1).

Form.	Sites	Bony fish taxa	1	2	3	4	Reconstructed environment
Khok Kruat	Ban Saphan Hin (Nakhon Ratchasima)	<i>Ginglymodi</i> nov. gen. nov. sp.	■	■	■	■	Channel (conglomerate)
	Ban Sam Ran (Khon Kaen)	<i>Ginglymodi</i> indet.	■	■	■	■	Channel (conglomerate)
	Lam Pao Dam (Kalasin)	<i>Ginglymodi</i> indet. *	■	■	■	■	Channel (clastic sandstone)
	Khok Pha Suam (Ubon Ratchathani)	<i>Ginglymodi</i> indet. <i>Ginglymodi</i> nov. gen. nov. sp. <i>Siamamia</i> sp.	■	■	■	■	Flood plain (siltstone)
Sao Khua	Phu Din Dang (Sakhon Nakhon)	<i>Siamamia</i> sp.	■	■	■	■	Flood plain (siltstone)
	Phu Phok (Sakhon Nakhon)	<i>Siamamia naga</i> <i>Ginglymodi</i> indet. *	■	■	■	■	Flood plain (siltstone)
	Phu Wiang (Khon Kaen)	<i>Ginglymodi</i> indet. *	■	■	■	■	Flood plain (siltstone)
	Phu Phan Thong (Nong Bua Lamphu)	<i>Siamamia</i> sp. cf. <i>Anomoeodus</i> <i>Ginglymodi</i> indet. *	■	■	■	■	Paralic environment? (presence of cf. <i>Anomoeodus</i> )
	Nong Sung (Mukdahan)	<i>Siamamia</i> sp. Pycnodontiformes indet. <i>Ginglymodi</i> indet.	■	■	■	■	Channel (clastic sandstone)
Phu Kradung	Kham Phok (Mukdahan)	<i>Thaichthys buddhabutrensis</i>	■	■	■	■	Flood plain (siltstone)
	Phu Nam Jun (Kalasin)	<i>Thaichthys buddhabutrensis</i> <i>Isanichthys palustris</i> <i>Ferganoceratodus martini</i>	■	■	■	■	Dried pond (mudstone-siltstone)
	Chong Chat (Nong Bua Lamphu)	cf. <i>Thaichthys</i> <i>Ferganoceratodus</i> sp.	■	■	■	■	Channel (sandstone)
	Phu Noi (Kalasin)	<i>Isanichthys lertboosi</i> <i>Ferganoceratodus</i> sp.	■	■	■	■	Channel (bottom) floodplain (top)
	Khok Sanam (Kalasin)	<i>Ginglymodi</i> sp. A cf. <i>Ptycholepis</i> <i>Ferganoceratodus</i> sp.	■	■	■	■	Flood plain (siltstone)
	Khao-Phu Luang (Nakhon Ratchasima)	<i>Khoratichthys gibbus</i>	■	■	■	■	

degree of articulation 1 ■ high  
 Abundance of fishes 2 ■ middle  
 Shark alpha-diversity 3 ■ low  
 Tetrapod alpha-diversity 4 ■ \* with crushing teeth

**Table 1.** Occurrences of bony fish taxa in 15 localities of the Late Jurassic – Early Cretaceous Khorat Group, NE Thailand. Main references for bony fishes are Cavin and Suteethorn (2006), Cavin *et al.* (2007a, b; 2009; 2013), Deesri *et al.* (2009; 2014; 2016).

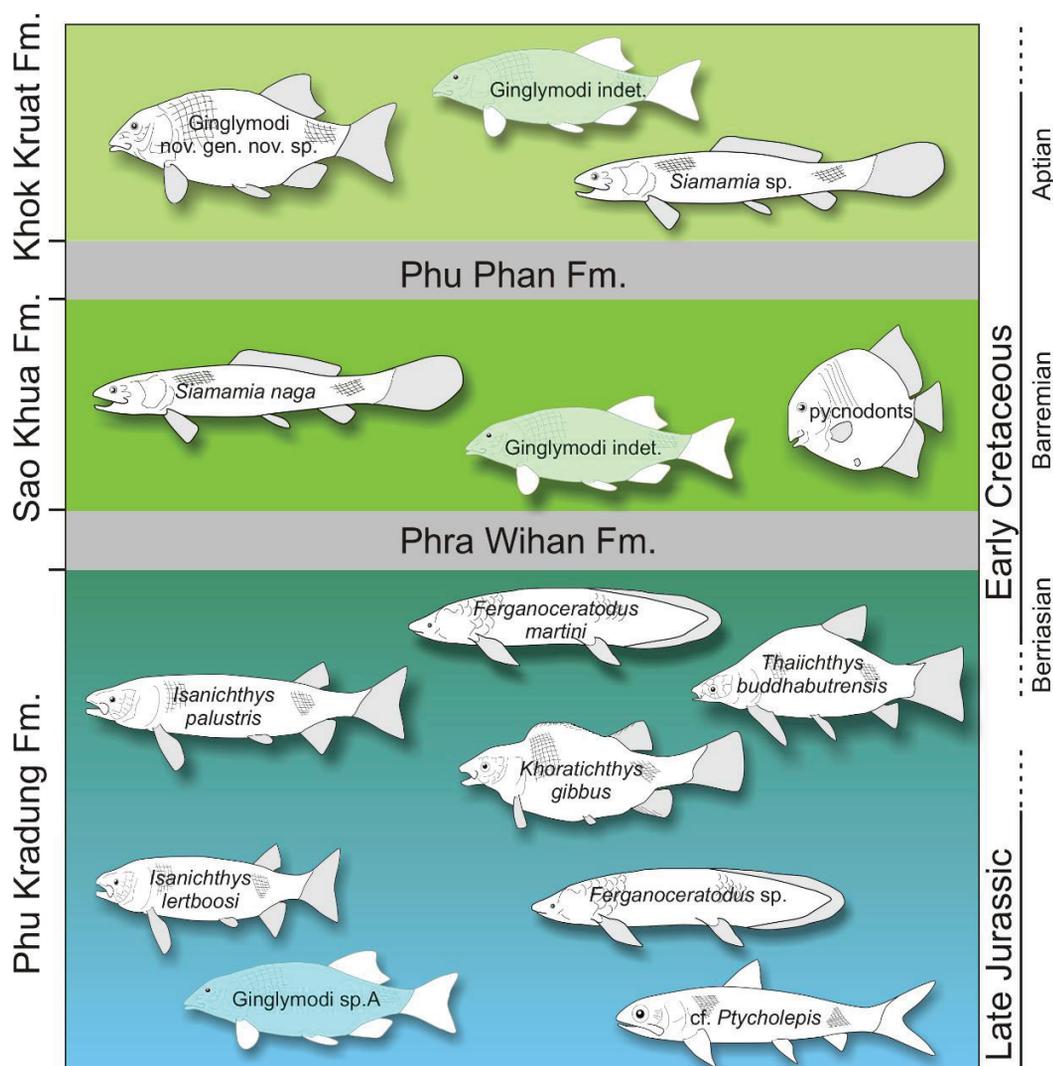
**4. Discussion**

**4.1 Taxic diversity**

For actinopterygians, all assemblages are characterized by a single non-neopterygian ray-finned fishes found in one of the oldest site, i.e. cf. *Ptycholepis* from Khok Sanam, by very rare remains of pycnodonts in two localities of the Sao Khua Fm, by the general absence of teleosts and by the largest diversity being found in the holosteans. One of the pycnodonts was referred to cf. *Anomoeodus*, which is a Cretaceous genus generally found in marine environment. Halecomorphs are present only in the younger formations, with the sinamiid *Siamamia naga* in the Sao Khua Fm and a probable other but closely related species in the Khok Kruat Fm. Ginglymodians are the most abundant and the most diversified, and they are present in all formations and in almost all localities. Distinctions can be done between the ginglymodians from the different formations. In the Phu Kradung Fm one of the oldest most site, Khok Sanam, has yielded an unnamed ginglymodian, which differs from those found in other Late Jurassic sites (e.g. Phu Noi with *Isanichthys lertboosi*) and those from the basal Cretaceous sites (e.g. Phu Nam Jun with *I. palustris* and *Thaichthys*

*buddhabutrensis*). In the Sao Khua Fm., the ginglymodians are poorly preserved but they differ from taxa found in the Phu Kradung Fm, notably because they occur together with button-like crushing teeth (in Phu Wiang and Phu Phan Thong sites). In the Khok Kruat Fm, different ginglymodians occur. A new taxon currently under description from Ban Saphan Hin and Khok Pha Suam is characterized by a very deep skull. This form, or a closely related one is also known in the Grès Supérieurs Fm in Laos. Another taxon, with button-like crushing teeth, is present in at least one locality (Lam Pao Dam).

Lungfishes are known in Phu Nam Jun with *Ferganoceratodus martini* and in Phu Noi with a closely related species under description, both species represented by semi-articulated skulls. Isolated tooth plates referred to *Ferganoceratodus* sp. were found in other localities from the Phu Kradung Formation as well as in Triassic localities in NE Thailand, which are not discussed here because these sites are not included in the Khorat Group. So far, lungfishes are absent in the Sao Khua and Khok Kruat formations.



**Figure 1.** General view of the bony fish assemblages from the three formations of the Khorat Group, NE Thailand.

#### 4.2 Taphonomy

The Phu Kradung Fm contains some sites with fish specimens found articulated, while the two younger formations have yielded fish remains represented by isolated and fragmentary remains only. The only exceptions is the Phu Phok site in the Sao Khua Fm which has yielded a few sub-articulated skulls of sinamiids and the Ban Saphan Hin site, in the Khok Kruat Fm, which has yielded a single articulated portion of a body of a ginglymodian.

#### 4.3 Palaeoenvironments

Deposits of the Khorat Group are considered to have been deposited in continental environments and yielded freshwater and terrestrial vertebrate assemblages. Bony fishes found in these deposits confirm this observation, or at least does not contradict it. The only possible exception is the occurrence of cf. *Anomoeodus* in Phu Phan Thong, which may indicate proximity of marine influences. However, some pycnodonts are known in freshwater environment, in particular during the Early Cretaceous such as in Montsech and Las Hoyas in Spain (Poyato-Ariza *et al.*, 1998).

The data presented here are strongly affected by preservational biases. It is obvious that the thick ganoid

scales and teeth, which are strongly mineralized and dense, are more easily preserved than more fragile bones, in particular bones of supposed teleosts. This fact also explains the low taxic diversity observed in the various fish assemblages compared to modern freshwater fish communities. Having stated this, are there differences between the fish assemblages, which indicate possible differences of environments? Several of the Phu Kradung sites correspond to concentrated accumulations. In the case of Phu Noi, with a high diversity of tetrapods and most of the specimens semi-articulated, the accumulation was probably the result of transportation by a stream on a short distance followed by deposition in an area with low energy, such as a meander in a floodplain (Martin *et al.*, 2016). In the case of Phu Nam Jun, with fishes well-preserved and absence of tetrapods, the accumulation was probably the result of a fish population trapped in a drying pond. Most of the sites in the Sao Khua and Khok Kruat formations yielded isolated fish bones, which generally do not form accumulations. Most of them correspond probably to deposits in fluvial floodplains. Smith *et al.* (1988) provided an interesting discussion of the Cenozoic freshwater fish fossil record from North America. Although unstable at a short, ecolog-

ical-scale level, the fluvial floodplain habitats are regarded as stable on longer time scales, i.e. on a geological-scale level. In this environment, in which biological cycles of fishes are closely associated with fluctuation of flooding and desiccation, Smith *et al.* (1988) suggested that the fossil record is strongly affected by spawning migrations and predator-prey relationships. In particular, they postulated that the impact of piscivorous predators may cause important non-fossilizable mortality of the fishes at the base of the food-chain. Only these predators and associated scavengers may be fossilized at the end of the cycle (represented mostly by gars, bowfins and catfishes in the case of the Palaeogene of North America). Interestingly, it is in these formations that sites with abundant remains of *Sinamia* occur, which was a piscivorous predator.

The sites with the highest alpha diversities in tetrapods are often those with the highest shark alpha diversity (Phu Noi, Kham Phok and Phu Wiang), but differ from those with the highest bony fish diversity (although this diversity is always very low). Further studies will identify if these distinction is caused by ecological differences, taphonomical biases, sampling biases (shark remains are mostly found by sieving sediment) or, more probably, by combination of these factors.

## 5. Conclusions

The major distinction that can be made in the succession of bony fish assemblages within the Khorat Group is between the Late Jurassic – basal Cretaceous Phu Kradung Formation on the one hand and the Early Cretaceous Sao Khua and Khok Kruat formations on the other hand. In the former, fishes are often rather well-preserved and represented mostly by abundant plant or detritus-eaters together with a few piscivorous taxa diversified among ginglymodians. This association and the body morphologies of these taxa are reminiscent of recent fish faunas mainly composed of cypriniforms. In the latter two formations, ginglymodians are represented by forms with crushing dentition and by a specialized deep-headed form. They are accompanied by rare pycnodonts and relatively common carnivorous sinamiids, at least in some localities. It is interesting to note that the bivalve diversity, which is potential prey for ginglymodians with crushing dentition and for pycnodonts, is higher in these younger formations (Tumpeesuwan *et al.*, 2010).

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