Ginglymodian fishes (Actinopterygii, Holostei) from Thailand: An overview

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Abstract

Isolated ganoid fish scales are not uncommon in Mesozoic deposits of Thailand. Traditionally referred to 'semionotiform' or *Lepidotes*-like fishes, they were not assigned to well-defined taxa and are of little use for palaeontological reconstructions. During the last fifteen years, however, the discovery of well-preserved articulated fish specimens, with ganoid squamations, allowed us to properly define new taxa, to search for phylogenetic relationships and to address the place of these fishes in palaeoenvironments. So far two genera and three species of ginglymodians have been named on the basis on material from the Phu Kradung Formation, but at least nine different taxa have been recognized ranging from the Late Triassic to the Aptian. Phylogenetic analyses of *Thaiichthys* and *Isanichthys* indicate that they belong, or are closely related, to the Lepisosteiformes. The palaeogeographical distribution of the four known *Isanichthys* species is restricted to the northern margin of the Tethys during the Middle Jurassic to the basal Cretaceous. The palaeobiogeographical signal of *Thaiichthys* is more ambiguous, its closest relatives having been found in the early Late Cretaceous of western Gondwana (South America and Africa).

Keywords: Cretaceous, Ginglymodi, palaeobiogeography, phylogeny

Introduction

Mesozoic deposits worldwide, both marine and freshwater in origin, have yielded isolated ganoid scales commonly referred to 'semionotiforms' or *Lepidotes*-like fishes. These scales can generally be distinguished from ganoid scales of non-neopterygian fishes (the 'palaeonisciforms') because the abdominal flank scales usually bear a pair of processes on their anterior margin in complement to the dorsal process[1,2]. Their abundance in the fossil record is due in part to their strong mineralization, being constituted of a bony basal plate cover with an enamel layer. Except some research that attempt to identify the systematic affinities of isolated scales on the basis of the micro-ornamentation of the enamel layer[3,4,5,6], a taxonomical assignment is usually not possible with no articulated material, in particular if no articulated cranial material is preserved. Relatively complete specimens in anatomical connexion of ginglymodians, however, are known for a long time in various Lagerstätten worldwide, and their study have enabled researchers to propose phylogenetic relationships within the group, and to consider relationships of these fishes with other actinopterygians. Classically, the Holostei gathered the living Amiiformes and Lepisosteidae, together with some extinct groups. Patterson (1973)[7] questioned this concept: he regarded the Holostei as a non-monophyletic group and considered the Semionotidae as Halecostomi, i.e. as closer to teleosts than to gars (Lepisosteidae). Alternatively, Olsen and McCune (1991)[8] regarded the Halecomorphi and the Lepisosteidae as forming a clade with the Macrosemiidae

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(the Semionotiformes), which is resolved as the sister-group of teleosts. In their scheme, Halecomorphi (*Amia* and relatives) are located as the sister-group of Semionotiformes + Teleostei. During the last decades, however, most molecular phylogenetic studies have resuscitated the Holostei (for instance Venkatesh et al. 2001[9] , Inoue et al. 2003[10], Near et al. 2012[11]; Betancur et al. 2013[12]), and this configuration was subsequently also found in morphological studies, which included fossil taxa[13,14]. In his review of the Lepisosteiformes Grande (2010)[13] proposed a classification, in which the Holostei include the Halecomorphi and a clade called Ginglymodi, which gathers gars together with several extinct taxa. Most recent studies have found the monophyly of Ginglymodi containing the Lepisosteiformes, 'macrosemiiformes' and 'semionotiformes', but there is still no consensus about the respective composition and relationships of the latter two groups (compared for instance López-Arbarello 2012[2] with Cavin et al. 2013[14] and Deesri et al. 2014[15]).

An overview of Jurassic and Cretaceous bony fish record from Thailand has been published in 2009[1]. However, new discoveries and new analyses of the data have been made during the last years, and a new synthesis is now necessary. Here, we present an overview of the discoveries of ginglymodians in Thailand, and we discuss their impact in the evolutionary history of the group within the frame recent phylogenies.

Geological setting

Thailand consists of two continental blocks or microcontinents: the eastern part, on which is located the Khorat Plateau, belongs to the Indochina block, and the western part, including the southern Peninsula, belongs to the 'Shan-Thai' or 'Sibumasu'. The Shan-Thai block has yielded very few ginglyomodian fish remains so far, except scales and fragmentary elements found in the Mab Ching locality in the Khlong Min Formation, Middle or Late Jurassic in age[1]. Most of the ginglymodian remains have been found in the Khorat Plateau in NE Thailand, which contains non-marine sediments deposited during the Mesozoic. Racey (2009)[16] and Racey and Goodall (2009)[17] restricteded the Khorat Group to five formations: the Phu Kradung, Phra Wihan, Sao Khua, Phu Phan and Khok Kruat formations, in ascending order. Chonglakmani (2011)[18] included in Khorat Group the underlaying Nam Phong Formation. Ginglymodians have been found in the Phu Kradung, the Sao Khua and the Khok Kruat formations, as well as in the underlying Late Triassic Huai Hin Lat Formation. The Phu Kradung Formation comprises fluvial channel sandstone, siltstone and mudstone with intermittent calcretes. The formation was deposited in a mainly lake-dominated floodplain cut by meandering and occasionally braided river channels. The formation is sandier in its upper part. The age of most of this formation is considered to be Late Jurassic on the basis of recent vertebrate discoveries[19,20,21] but the upper part, however, is now regarded as basal Cretaceous in age based on palynological evidence[17]. Similar ages have been established on the basis of the shark assemblages[22]. The Sao Khua Formation comprises dominantly floodplain deposits including sandstone, siltstone and mudstone, together with common calcretes, and was deposited in a low-energy fluvial setting comprising meandering channels and extensive flood plains. Based on palynomorphs, a Berriasian- early Barremian age is suggested for this formation[17]. The Khok Kruat Formation comprises sandstone, conglomerate, siltstone, shale and intermittent palaeosols deposited in a dominantly fluvial environment. This formation is considered as Aptian in age on the basis of palynomorphs[23] and vertebrates[24,25].

The Ginglymodian Thai fossil record

Since thirty years, the Thai-French collaboration team has studied non marine vertebrate fossils from Thailand, ranging in age from the Late Triassic to the late Early Cretaceous. Bony fishes have been discovered regularly, and were mostly represents by isolated ganoid scales referred to semionotid-like fishes[25]. From 2002 to 2007, excavations were repeatedly conducted in the site of Phu Nam Jun, Tambon Lao Yai, Kalasin Province, a locality disco vered some years before by local people[26]. So far this site has yielded only bony fishes, and this discovery triggered specific researches on this group of vertebrates. Most of the specimens belong to a ginglymodian fish, *Thaiich-*

thys buddhabutrensis (Cavin, Suteethorn, Khansubha, Buffetaut & Tong, 2003)[27], which was described in detail only recently[14]. A taphonomical and morphometric study of the *T. buddhabutrensis* assemblage was published by Deesri et al.[28] in 2009. In the meantime, a single specimen from the Phu Nam Jun site was referred to another ginglymodian, *Isanichthys palustris* Cavin and Suteethorn, 2006. In 2008, a new site called Phu Noi, situated in the Phu Kradung Formation but located stratigraphically lower than the site of Phu Nam Jun[22] has been regularly excavated. A very rich vertebrate assemblage, compri sing sharks, turtles, crocodiles and different dinosaurs, has been discovered[22]. Several ginglymodian specimens were also recovered. Although they show some variability in their skull bone pattern, they have been all referred to a species of *Isanichthys* distinct from *I. palustris*, *I. lertboosi* Deesri, Lauprasert, Suteethorn, Wongko and Cavin (2014)[15]. Isolated discoveries of articulated ginglymodians have been done in other localities from the Phu Kradung Formation. An almost complete specimen was discovered in the Ban Nong Rua site, Wang Nam Khiao District, Nakhon Ratchasima Province, and has been described in a PhD Thesis[29]. It likely represents a new taxon and its phylogenetic relationships are currently investigated. Two specimens closely related to *Thaiichthys* have been discovered in localities other than Phu Nam Jun: a specimen referred to *Thaiichthys* cf. *buddhabutrensis* was found in the locality of Chong Chat, Non Sung District, Nong Bua Lamphu Province[29] and one specimen from the locality of Kham Phok, Nong Sung District, Mukdahan Province, was regarded as a juvenile of *T. buddhabutrensis*[30]. It should be noticed here that both specimens show differences with individuals from the type locality, but because this species possesses a wide range of morphological variability, and because only one specimen from each locality is available, we prefer to avoid erecting new taxa pending the discovery of new material. Other localities from the Phu Kradung Formation, such as Khok Sanam, Dan Luang, Phu Dan Kaeng, Lam Payang (Phu Klang) and Wan Din So contain smooth ganoid scales, but we are not able so far to determine if they can be referred to one of the taxon from this Formation known by articulated material (*Thaiichthys* and *Isanichthys*) or if they correspond to new taxa. Outside the Phu Kradung Formation, numerous other localities from the Mesozoic of Thailand have yielded isolated ginglymodian remains from different stratigraphic horizons. The locality of Huai Pha Pheng, in the Late Triassic Huai Hin Lat Formation, is one of the rare localities, which has yielded articulated material with the recent discovery of several subcomplete ray-finned fishes. Some of these specimens are probably ginglymodians, but their study is too preliminary to permit well-supported assignations. Other discoveries are mostly isolated scales, rare teeth and skull ossifications. Although this kind of preservation precludes the recognition of taxa, we can assess the diversity on the basis of the association of teeth and scales, and on the morphology of the latters. The locality of Mab Ching, in the Khlong Min Formation, has yielded an association of large ganoid smooth scales with a conical tooth, which indicate the occurrence of a ginglymodian taxon likely different from those of the other localities (Ginglymodi indet. 1 in table 1). Two localities from the Sao Khua Formation (Phu Phan Thong and Phu Wiang) have yielded smooth ganoid scales associated with button-like teeth. This kind of teeth has never been found in the Phu Kradung Formation so far, and it likely indicates the occurrence of another taxon of ginglymodian in this formation (Ginglymodi indet. 2 in table 1). In the Khok Kruat Formation, two kinds of scales have been found in the Khok Pha Suam locality: one kind has a smooth ganoine surface and the other has parallel ridges on the surface. These scales, never found associated with button-like teeth, indicates the occurrence of two taxa in this locality (Ginglymodi indet. 3 and 4 in table 1). The site of Lam Pao Dam, in the Khok Kruat Formation, has yielded large ganoid scales ornamented with parallel rows of small pits, as well as a large button-like tooth (Ginglymodi indet. 5 in table 1). The locality of Ban Saphan Hin in the Khok Kruat Formation, Mueang Nakhon Ratchasima District, Nakhon Ratchasima Province, has yielded the posterior part of an articulated fish, as well as numerous isolated skull bones[29]. We cannot determine so far if these elements correspond to one of the three other taxa pre

sent in other localities of the Khok Kruat Formation, or if they correspond to a new taxon. Thus, at least three ginglymodian taxa are present in the Khok Kruat Formation. The study of the micro-ornamentation of the ena mel surface of these scales is a research in progress[29], which should allow assessing more effectively the diversity of ginglymodians in each formation. So far ten distinct ginglymodian species can be distinguished in Thailand ranging from the Late Triassic Huai Hin Lat Formation to the Aptian Khok Kruat Formation. Three species have been named from the Phu Kradung Formation, and a forth is pending. The diversity in the Khok Kruat Formation is apparently also rather important; although the material is not complete enough for erec ting new taxa. Strangely enough, the lowest diversity is observed in the Sao Khua Formation, which otherwise has yielded the most diverse tetrapod assemblages[31]. This paucity is possibly related to taphonomical features of the vertebrate localities that have been excavated in this formation until now. One exception is the locality of Phu Phok (Sakhon Nakhon Province), which is the type locality of the sinamiid *Siamamia*, a halecomorph fish represented by isolated bones and some articulated cranial material[32].

Evolutionary history

The resurrection of Holostei on the basis of morphological characters, including data from fossil taxa, was first proposed by Grande (2005, 2010)[33,13]. This clade includes the Halecomorphi and the Ginglymodi, the latter comprising the Macrosemiiformes, the Semionotiformes and the Lepisosteiformes. In Grande's study, the Semionotiformes consist of the genus *Semionotus* (represented by *S. elegans* (Newberry, 1888)[34] only. Cavin (2010)[35] proposed a phylogenetic analysis of a set of Mesozoic ginglymodians, and found that several Cretaceous taxa are stem lepisosteids, a pattern also found in López-Arbarello (2012)[2], although different taxa are placed as stem lepisosteids. In López-Arbarello's analysis[2], the Semionotiformes are monophyletic and gathers genera ranging from the Triassic to the Cretaceous, and includes the Macrosemiidae (which, consequently, lost an ordinal rank as part of the Semionotiformes). Recent analyses[14,36,15] recover the monophyletic Lepisosteiformes, but the taxa placed in the Semionotiformes in López-Arbarello's study are not resolved as a clade, but are situated in various positions as 'basal' ginglymodians. Most of the recent phylogenetic analyses resolve the genera *Scheenstia* and *Lepidotes* as basal Lepisosteiformes (Figure 1). Cladistic analyses that include both genera defined on the basis of Thai material, *Thaiichthys* and *Isanichthys*, indicate 1) that *Thaiichthys* is a Lepisosteiformes situated as the sister-group of the Western Gondwanian pair *Pliodetes* and *Araripelepidotes*[14,15], and 2) that *Isanichthys*, is resolved either in a polytomy with other ginglymodians[14,15,36,37] or as basal Lepisosteiformes[2,15]. It is interesting to note that both Thai genera belong to the Lepisosteiformes (or are closely related to Lepisosteiformes for *Isanichthys* in some of the studies), a clade containing the living gars restricted now to North and Central America. '*Lepidotes' luchowensis* Wang, 1974, from the Middle Jurassic of Sichuan, China, and '*Lepidotes' latifrons* Woodward, 1893 from the Middle Jurassic of UK are included in the genus *Isanichthys*[15]. The palaeogeographical distribution of the four species of *Isanichthys* is broad, but it is concentrated to the northern margin of the Tethys from the Middle Jurassic to the basal Cretaceous (Figure 1). The palaeobiogeographical pattern associated with *Thaiichthys* is more confuse. This genus appears to be related to a lineage from western Gondwana, which split into the pair genera *Pliodetes* and *Araripelepidotes* in the early Late Cretaceous, probably in connection with the opening of the South Atlantic. Because these three genera are freshwater, or possibly brackish for *Araripelepidotes*, we suggest that the observed phylogenetic pattern is related to the fragmentation of Pangea and that the split should be as old as Triassic in age. Vicariant events associated with the opening of the South Atlantic are also observed in other Lepisosteiformes, in particular the split of sister species within both obaichthyid genera, *Obaichthys* and *Dentilepisosteus* (Figure 1). It is worth noting that the general patterns proposed here are still weakly supported because their rest on few taxa and on a weakly supported phylogeny. But they constitute hypotheses to be tested in further studies.

Conclusion

Ginglymodian fishes are relatively common in the Mesozoic sediments of Thailand. Although only two genera and three species have been properly identified so far, new material currently studied and recent field disco veries indicate that much more taxa were present. The knowledge of the Thai ginglymodian fossil record has twofold impacts: 1) It allows to better understand the palaeoecology of the vertebrates assemblages in the Mesozoic of South-East Asia, in particular by showing the existence of ginglymodian fishes with peculiar positions within the trophic web: *Thaiichthys* was probably a grazing herbivorous or detritus feeder, while *Isanichthys* was likely a predator; 2) It contributes to depict the evolutionary history of the ginglymodians as a whole, which were fishes with a wide variety of morphology, ecology and complex palaeobiogeographical history.

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References

1. Cavin L, Deesri U, Suteethorn V. The Jurassic and Cretaceous bony fish record (Actinopterygii, Dipnoi) from Thailand. In: Buffetaut, E., Cuny, G., Le Loeuff, J. and Suteethorn, V. Late Palaeozoic and Mesozoic Continental Ecosystems of SE Asia. Geological Society of London, Special Publication 2009; 315: 123-137.
2. López-Arbarello A. Phylogenetic interrelationships of ginglymodian fishes (Actinopterygii, Neopterygii). PLoS ONE 2012; 7(7), e39370. doi,10.1371/journal.pone.0039370.
3. Gayet M, Meunier F. Apport à l'étude de l'ornementation de la ganoïne dans la détermination de l'appartenance générique et/ou spécifique des écailles isolées. Comptes Rendus de l'Académie des Sciences, Paris 1986; 303, sér. II, 13, 1259-1262.
4. Gayet M, Meunier F. A propos du genre Paralepidosteus (Ginglymodi, Lepisosteidae) du Crétacé Gondwanien. Cybium 2001; 25 (2): 153-159.
5. Brito P, Meunier F. The morphology and histology of the scales of Aspidorhynchidae (Actinopterygii, Halecostomi). Geobios 2000; 33(1): 105-111.
6. Meunier F. The Osteichthyes, from the Paleozoic to the extant time, through histology and palaeohistology of bony tissues. Comptes Rendus Paleovol 2011; 10: 347-355.
7. Patterson C. Interrelationships of holosteans. In: Greenwood, P. H., Miles, R. S. and C. Patterson (eds) Interrelationships of fishes, Academic Press, London 1973; 233-305.
8. Olsen PE, McCune AR. Morphology of the Semionotus elegans group from the Early Jurassic part of the Newark Supergroup of Eastern North Americ with comments on the family Semionotidae (Neopterygii). Journal of Vertebrate Paleontology 1991; 11(3): 269-292.
9. Venkatesh B, Erdmann MV, Brenner S. Molecular synapomorphies resolve evolutionary relationships of extant jawed vertebrates. PNAS 2001; 98(20): 11382–11387.
10. Inoue JG, Miya M, Tsukamoto K, Nishida M. Basal actinopterygian relationships, a mitogenomic perspective on the phylogeny of the 'ancient fish'. Molecular Phylogenetics and Evolution 2003; 26: 110–120.
11. Near TJ, Eytan RI, Dornburg A, Kuhn, KL, Moore JA, Davis MP, Wainwright PC, Friedman M, Smith WL. Resolution of ray-fined fish phylogeny and timing of diversification. PNAS 2012; 109(34): 13698-13703.

12. Betancur-R R, Broughton RE, Wiley EO, Carpenter K, López JA, Li C et al. The tree of life and a new classification of bony fishes. PLOS Currents Tree of Life. DOI, 10.1371/currents.tol.53ba26640df0ccaee 75bb165c8c26288. 2013.
13. Grande L. An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeleton anatomy. The resurrection of Holostei. Copeia 10. American Society of Ichthyologists and Herpetologists, special Publication 2010; 6 (suppl. 2a): 1-871.
14. Cavin L, Deesri U, Suteethorn V. Osteology and relationships of Thaiichthys nov. gen., a ginglymodi from the Late Jurassic – Early Cretaceous of Thailand. Palaeontology 2013; 56(1): 183-208.
15. Deesri U, Lauprasert K, Suteethorn V, Wongko K, Cavin L. A new species of the ginglymodian fish Isanichthys from the Late Jurassic Phu Kradung Formation, northeastern Thailand. Acta Palaeontologica Polonica 2014; 59(2): 313-331.
16. Racey A. Mesozoic red bed sequences from SE Asia and the significance of the Khorat Group of NE Thailand. In: Buffetaut, E., Cuny, G., Le Loeuff, J. and Suteethorn, V. (eds) LatePalaeozoic and Mesozoic Ecosystems in SE Asia. Geological Society, London, Special Publications 2009; 315: 41-67.
17. Racey A, Goodall J. Palynology and stratigraphy of the Mesozoic Khorat Group red bed sequences from Thailand. In: B Buffetaut, E., Cuny, G., Le Loeuff, J. and Suteethorn, V. (eds) Late Palaeozoic and Mesozoic in SE Asia. Geological Society, London, Special Publications 2009; 315: 69-83.
18. Chonglakmani C. Chapter 6 Triassic. In: Ridd, M.F., Barber, A.J. and Crow, M.J. (eds) The Geology of Thailand. Geological Society, London 2011; 137-150.
19. Buffetaut E, Suteethorn V, Tong H. The first thyreo phoran dinosaur from Southeast Asia, a stegosaur vertebra from the Late Jurassic Phu Kradung Formation of Thailand. Neues Jahrbuch für Geologie und Paläontologie Monatshefte 2001; 95-102.
20. Buffetaut E, Suteethorn V. A sinraptorid theropod (Dinosauria, Saurischia) from the Phu Kradung Formation of northeastern Thailand. Bulletin de la Société Géologique de France 2007; 178: 497-502.
21. Tong H, Claude J, Naksri W, Suteethorn V, Buffetaut E, Khansubha S, Wongko K, Yuangdetkla P. Basilochelys macrobios n. ge. and n. sp., a large cryptodiran turtle from the Phu Kradung Formation (latest Jurassic-earliest Cretaceous) of the Khorat Plateau, NE Thailand. In: Buffetaut, E., Cuny, G., Le Loeuff, J. and Suteethorn, V. (eds) Late Palaeozoic and Mesozoic Ecosystem in SE Asia. Geological Society, London, Special Publications 2009; 315: 151-170.
22. Cuny G, Liard R, Deesri U, Liard T, Khamha S, Suteethorn V. Shark faunas from the Late Jurassic-Early Cretaceous of northeastern Thailand. Paläontologische Zeitschrift. DOI 10.1007/s12542-013-0206-0. 2013.
23. Sattayarak N, Srigulawong S, Pataramethа M. Subsurface stratigraphy of the non-marine Mesozoic Khorat Group, northeastern Thailand. GEOSEA VII Abstracts, Bangkok, 1991; p.36.
24. Cappetta H, Buffetaut E, Suteethorn V. A new hybodont from the Lower Cretaceous of Thailand. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 1990; 11: 659-666.
25. Buffetaut E, Suteethorn V. The biogeographical significance of the Mesozoic vertebrates from Thailand. In: Hall, R. and Holloway, J.D. (eds), Biogeography and Geological Evolution of SE Asia, Backhuys, Leiden 1998; 83-90.
26. Cavin L, Suteethorn V, Buffetaut E, Chitsing S, Lauprasert K, Le Loeuff J, Lutat P, Philippe M, Richter U, Tong H. A new fish locality from the continental Late Jurassic–Early Cretaceous of Northeastern Thailand. Revue de Paléobiologie 2004; 9: 161-167.
27. Cavin L, Suteethorn V, Khansubha S, Buffetaut E, Tong H. A new Semionotid (Actinopterygii, Neopterygii) from the Late Jurassic–Early Cretaceous of Thailand. Comptes Rendus Palévol 2003; 2: 291-297.
28. Deesri U, Cavin L, Claude J, Suteethorn V, Yuangdetkla P. Morphometric and taphonomic study of a ray-finned fish assemblage (Lepidotes buddhabutrensis,

Semionotidae) from the Late Jurassic-earliest Cretaceous of NE Thailand. In: Buffetaut, E., Cuny, G., Le Loeuff, J. and Suteethorn, V. (eds) Late Palaeozoic and Mesozoic Ecosystems in SE Asia. Geological Society, London, Special Publications 2009; 315: 115-124.

29. Deesri U. Osteology and scale microstructure of Late Jurassic-Early Cretaceous Ginglymodians from Thailand, Evolutionary, Taxonomical and Palaeogeographical implicantions. PhD Thesis. Mahasarakham University. Thailand. 2013; 266 pp.
30. Deesri U, Suteethorn V, Liard R, Cavin L. First discovery of a juvenile Thaiichthys (Actinopterygii, Holostei) from the Late Jurassic - Early Cretaceous of Thailand. Journal of Science and Technology, Mahasarakham University. In press.
31. Buffetaut E, Cuny G, Le Loeuff J, Suteethorn V. Late Palaeozoic and Mesozoic continental ecosystems of SE Asia, an introduction. Geological Society, London, Special Publications 2009; 315: 1-5.
32. Cavin L, Suteethorn V, Buffetaut E, Claude J, Cuny G, Le Loeuff J, Tong H. The first sinamiid fish (Holostei, Halecomorpha) from South-east Asia (Early Cretaceous of Thailand). Journal of Vertebrate Paleontology 2007; 27(4): 827-837.
33. Grande L. Phylogenetic study of gars and closely related species, based mostly on skeletal morphology. The resurrection of Holostei. In: Poyato-Ariza, F.J. (ed.) Fourth International Meeting on Mesozoic Fishes - Systematics, homology and Nomenclature. UAM, Miraflores de la Sierra, Madrid, Spain 2005; 119-121.
34. Newberry JS. Fossil fishes and fossil plants of the Triassic rocks of New Jersey and the Connecticut Valley. Monographs of the United States Geological Survey 188; 14: xiv+152 pp., pls. 1-26.
35. Cavin L. Diversity of Mesozoic semionotiform fishes and the origin of gars (Lepisosteidae). Naturwissenschaften 2010; 97: 1035-1040.
36. Gibson SZ. Biodiversity and Evolutionary History of Lophionotus (Neopterygii: Semionotiformes) from the Western United States. Copeia 2013; 4: 582–603.
37. Cavin L, Suteethorn V. A new Semionotiform (Actinopterygii, Neopterygii) from Upper Jurassic–Lower Cretaceous deposits of North-East Thailand, with comments on the relationships of Semionotiforms. Palaeontology 2006; 49: 339-353.

Table 1 Thai fossil record of ginglymodians based on data from Cavin et al. (2009: fig. 6 and table 1)[1] with inclusion of new discoveries.

Fms	Localities	Articulated material	Isolated remains
KK	Ban Saphan Hin	Posterior part of a body	Various skull bones
	Lam Pao Dam		Large pitted scales (Ginglymodi indet. 5) — Large button-like tooth
	Khok Pha Suam		Ridged scales (Ginglymodi indet. 4) Smooth scales (Ginglymodi indet. 3)
SK	Phu Wiang		Smooth scales (Ginglymodi indet. 2) — Button-like teeth
PK	Phu Nam Jun	*Thaiichthys buddhabutrensis* — *Isanichthys palustris*	
	Kham Phok	*T. buddhabutrensis* (juvenile)	
	Chong Chat	*T.* cf. *buddhabutrensis*	
	Phu Noi	*Isanichthys lertboosi*	
	Ban Nong Rua	New taxon	
	Khok Sanam, etc.		Smooth scales
KM	Mab Ching		Large smooth scales (Ginglymodi indet. 1) — Conical tooth
HHL	Huai Pha Pheng	Ginglymodi indet.	

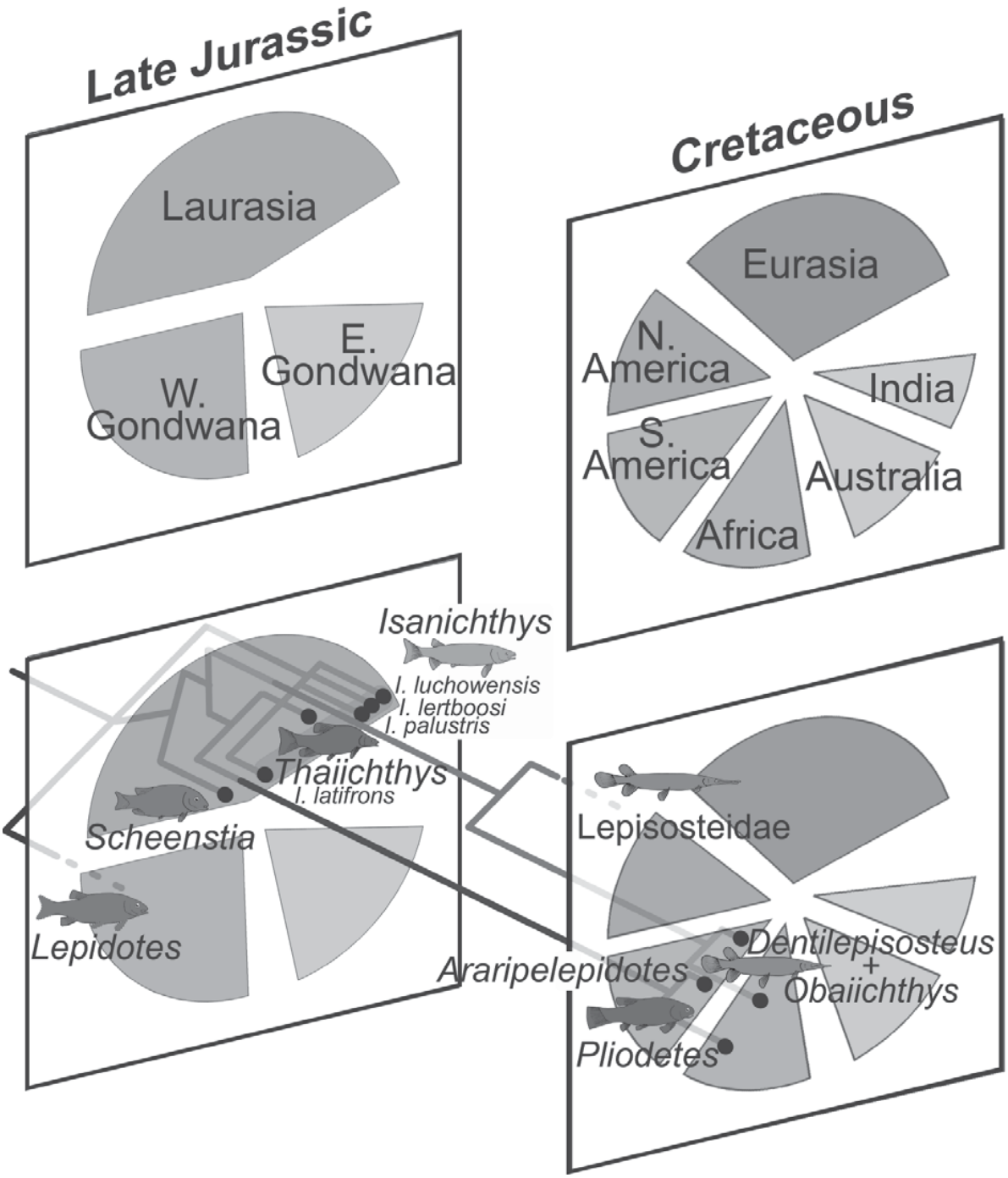

Figure 1 Plot of the phylogenetic tree of the Lepisosteiformes (from Deesri et al. 2014[15]) against palaeogeography. The upper row shows schematic evolution of the palaeogeographical pattern in the Late Jurassic and in the Cretaceous. The lower row shows the phylogenetic tree included in the palaeogeography. Vicariant events are favoured over dispersal events.