

Research paper

A brief review of the Middle Palaeozoic vertebrates from Southeast Asia

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Abstract

Here we review the Silurian and Devonian vertebrates from Southeast Asia and their biogeographic affinities. These vertebrate remains are distributed in the Shan-Thai and Indochina terranes as well as the South China block, including the fossil fishes from western Yunnan (a part of the Shan-Thai terrane). The Devonian vertebrates from the Si Ka, Bac Bun and Mia Le formations of northern Vietnam resemble those from the Xitun Formation of Yunnan, South China, and thus belong to the Xitun fauna. The Late Silurian vertebrates from the Dia Giang Formation of My Duc (central Vietnam) are suggestive of the Xiaoxiang fauna of South China. Fossil vertebrate evidence shows the proximity between the South China block and the Indochina terrane in the Middle Palaeozoic and the close relationship between Shan-Thai and east Gondwana in the Middle Devonian.

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1. Introduction

The Middle Palaeozoic vertebrate remains from Southeast Asia are distributed in the Shan-Thai (Sibumasu) and Indochina terranes as well as the South China block (Fig. 1) (Long, 1993). The South China block lies to the north of the Shan-Thai and Indochina terranes, borders the Shan-Thai terrane by the Ailaoshan suture (Suture 1, Fig. 1), and the Indochina terrane by the Song Ma suture (Suture 2, Fig. 1). The Shan-Thai terrane is bordered to the west by the Shan Boundary (Suture 3, Fig. 1) and to the east by Nan-Uttaradit (Suture 4, Fig. 1), Sra Kaeo (Suture 5, Fig. 1), and Raub-Bentong sutures, which mark the boundary between the Shan-Thai and Indochina terranes (Metcalf, 1998). The vertebrate fauna of the Shan-Thai terrane discussed here also includes fishes from western Yunnan of China, which is a part of the Shan-Thai terrane.

The fragments of galeaspids and antiarchs in the Lung Co-Mia Le (Lung Co-Si Ka) section of northern Vietnam described by Mansuy (1915) represent the first finding of Middle Palaeozoic vertebrates from Southeast Asia (Janvier and Phuong,

1999; Tông-Dzuy and Janvier, 1987). During the 20th century, early vertebrates from Southeast Asia, including agnathans (galeaspids and thelodonts) and gnathostomes (placoderms, acanthodians, chondrichthyans, and osteichthyans), were found in a number of Siluro-Devonian localities. Long (1993), Janvier and Tông-Dzuy (1998) and Young and Janvier (1999) reviewed all these vertebrate remains from Southeast Asia, and discussed their palaeogeographic framework.

During the last decade, some new findings have been reported from Vietnam, including remains from the localities of the South China block (Tong Vai, Ban Nhuan, Dong Mo, Trang Xa and Lung Co-Mia Le section) and the Indochina terrane (Tra Ban, Ly Hoa and Cau Rong) (Janvier and Phuong, 1999; Janvier et al., 2003, 2009; Racheboeuf et al., 2005, 2006). To facilitate comparisons with the coeval Chinese faunas (Zhao and Zhu, 2010), a review of Middle Palaeozoic vertebrates from Southeast Asia is presented here and organized by localities.

2. Shan-Thai (Sibumasu) Terrane

The Shan-Thai terrane includes parts of Burma, Indonesia, Malaysia, Thailand, small segments of China and Vietnam (Krobicki et al., 2008; Metcalfe, 1998). All Middle Palaeozoic vertebrate remains from this terrane are microfossils, except

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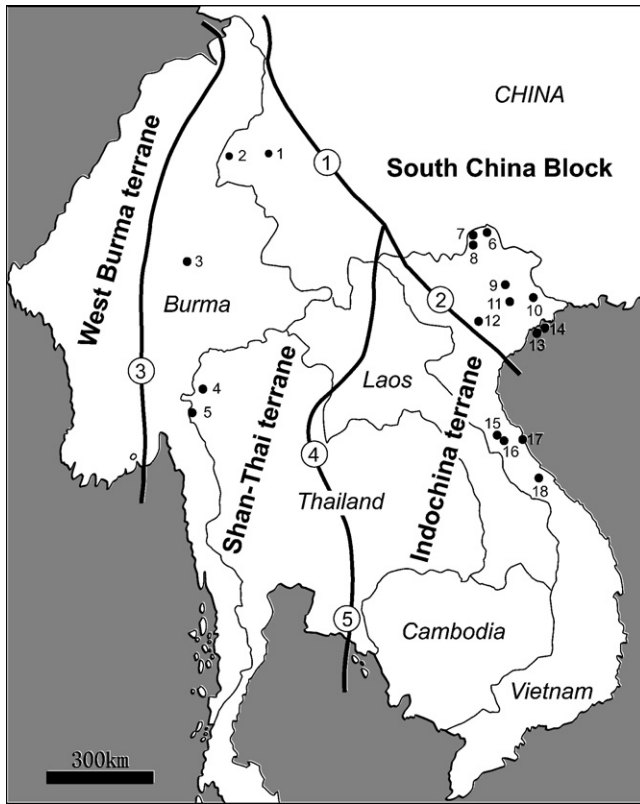


Fig. 1. Distribution of Siluro-Devonian vertebrate fossil localities in Southeast Asia and western Yunnan (updated from Long, 1993). Labelled sutures (circles)—1: Ailaoshan; 2: Song Ma; 3: Shan Boundary; 4: Nan-Uttaradit; 5: Sra Kaeo. Siluro-Devonian vertebrate fossil localities—1: Shidian; 2: Yingjiang; 3: Maymyo; 4: Mae Sariang; 5: Mae Sam Lap; 6: Long Co-Mia Le section; 7: Tong Vai; 8: Khao Loc; 9: Ban Nhuan; 10: Dong Mo; 11: Trang Xa; 12: lower Song Da area; 13: Do Son; 14: Tra Ban; 15: Cau Rong; 16: Qui Dat; 17: Ly Hoa; 18: My Duc.

an incomplete placoderm skull roof from Yingjiang, western Yunnan (Wang and Cao, 1988).

2.1. Shidian, western Yunnan, China (locality 1, Fig. 1)

Wang et al. (1986) described some thelodont microfossils from the Malutang and Heyuanzhai sections in Shidian County of western Yunnan, China. Among these are *Turinia pagoda* from the lower part of the Heyuanzhai Formation (upper Givetian), and *Turinia* spp. from the Eifelian Malutang Formation (Fig. 2A–C). The occurrence of *T. pagoda* from western Yunnan, with the contemporaneous record of *Turinia* cf. *T. pagoda* from South Australia (Long et al., 1988), may indicate a close relationship between Shan-Thai and east Gondwana (Young and Janvier, 1999).

2.2. Yingjiang, western Yunnan, China (locality 2, Fig. 1)

Wang and Cao (1988) described a partial placoderm skull roof from the lower part of the Early Devonian Guanshang Formation in the Shizishan section of Yingjiang County, western Yunnan, resembling the macropetalichthyid *Wijdeaspis* from the Early Devonian of North Europe, Spitsbergen, and Australia. It is associated with some invertebrate fossils including *Lingula*, *Petzia*, *Howellella*, *Primitia*, *Ultichia*, *Trochiliscens*, and *Holopea* (Wang and Cao, 1988), suggesting an age of Lochkovian (Wang, 1993). However, this age assignment is tentative, mainly based on the brachiopod *Howellella* sp., and further field work in this area is needed.

2.3. Maymyo, central Burma (locality 3, Fig. 1)

The Devonian locality in the Wetwin Shale, about 20 km east of Maymyo, lies to the east of the Shan Boundary separating the West Burma and Shan-Thai terranes, thus belonging to the Shan-Thai terrane (Metcalf, 1998). The only Middle Palaeozoic

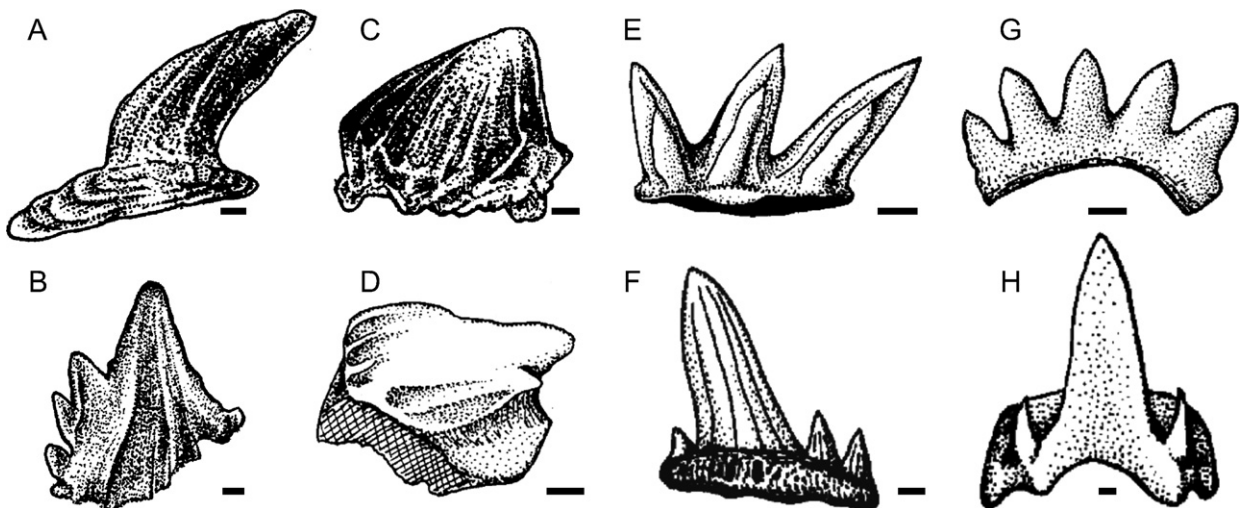


Fig. 2. Siluro-Devonian vertebrates from the Shan-Thai terrane. (A–C) Thelodont scales from the Middle Devonian of western Yunnan (from Wang et al., 1986). (A) *Turinia* sp., (B) *Turinia pagoda*, (C) *Turinia* sp., (D) Late Silurian–Early Devonian acanthodian scale, *Nostolepis* sp., from north of Mae Sariang, Thailand (from Long, 1993 redrawn after Blicek et al., 1984). (E–H) Late Famennian chondrichthyan teeth from near Mae Sam Lap northern Thailand (from Long, 1990). (E) *Phoeobodus australiensis*, (F) *Cladodus* cf. *C. acutus*, (G) *Siamodus janvieri*, (H) *Symmorium* sp. Scale bar = 0.1 mm.

vertebrate fossil is an “ichthyodorulite” (fossil spine) reported by Chhibber (1936).

2.4. Mae Sariang district, northern Thailand (locality 4, Fig. 1)

The Middle Palaeozoic vertebrate record from this region comprises isolated acanthodian (Blieck and Goujet, 1978) and thelodont (Blieck et al., 1984) scales from an Uppermost Silurian–Lowermost Devonian locality situated north of Mae Sariang. The acanthodian scale was referred to *Nostolepis* sp. (Fig. 2D) and the thelodont scale was indeterminate.

2.5. Mae Sam Lap, northern Thailand (locality 5, Fig. 1)

Limestone samples from along the road south of Mae Sariang to Mae Sam Lap have yielded many vertebrate microfossils, mainly chondrichthyan teeth (Long, 1989, 1990; Long and Burrett, 1989), dated as late Famennian by associated conodonts (Long, 1990). The chondrichthyans include *Phoebodus australiensis*, *Siamodus janvieri*, *Thrinacodus ferox*, *Symmorium* sp., and *Cladodus* cf. *C. acutus* (Fig. 2E–H). *T. ferox* (Turner, 1982) was a widespread taxon of the Late Devonian to earliest Carboniferous with fossils discovered in Australia, Thailand, China, Europe, and the USA (Turner, 1993; Young and Janvier, 1999). Other remains include some indeterminate acanthodian and actinopterygian scales.

3. South China block

Northern Vietnam, which lies to the north of the Song Ma suture, is a small extension of the South China block. The Siluro-Devonian vertebrate fauna of this region, including endemic galeaspids, yunnanolepiforms, and the sarcopterygian *Youngolepis*, is notable for displaying a striking similarity to broadly contemporaneous assemblages from Yunnan and Guangxi, China. Janvier and Tông-Dzuy (1998) reviewed the Middle Palaeozoic vertebrates from northern Vietnam. Since then, new discoveries from this region have further confirmed its geographic affinity to the South China block.

3.1. Lung Co-Mia Le section, Dong Van District, Ha Giang Province, northern Vietnam (locality 6, Fig. 1)

The Lung Co-Mia Le (Lung Co-Si Ka) section in Dong Van of Ha Giang Province, from Lung Cu to Mia Le via Si Ka, is a classical Devonian section where the first Palaeozoic vertebrate remains of Vietnam were found (Janvier and Phuong, 1999; Mansuy, 1915). Those remains were from the Lower Devonian (Lochkovian) Bac Bun Formation in the Yen Minh area (Janvier and Tông-Dzuy, 1998; Tông-Dzuy and Janvier, 1987), and include a few fragments of galeaspid dermoskeleton referred to *?Bannhuanaspis*, antiarchs referred to *?Chuchinolepis dongmoensis*, and Yunnanolepiformes gen. et sp. indet. (Janvier and Tông-Dzuy, 1998; Tông-Dzuy and Janvier, 1994). Janvier and Phuong (1999) and Janvier et al. (2009) reported new vertebrate findings (Fig. 3A) from the Si Ka, Bac Bun and Mia Le for-

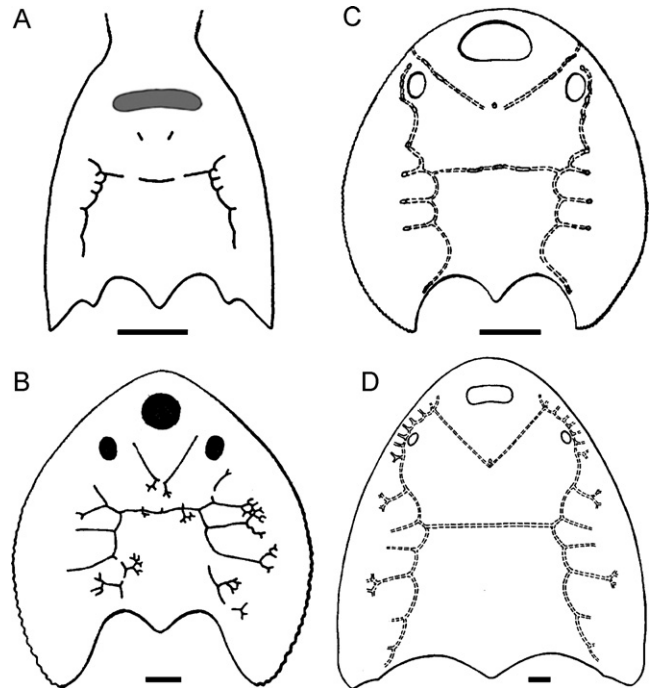


Fig. 3. Devonian galeaspids from North Vietnam of the South China block. (A) *Sanqiaspis vietnamensis*, from the Si Ka Formation of Lung Co-Mia Le section (from Janvier et al., 2009). (B and C) Galeaspids from the Khao Loc Formation of Tong Vai. (B) *Laxaspis yulongssus* (from Janvier and Phuong, 1999). (C) *Polybranchiaspis liaojiaoshanensis* (from Tông-Dzuy et al., 1995). (D) *Bannhuanaspis vukhuci*, from the Bac Bun Formation of Ban Nhuann (from Janvier et al., 1993). Scale bar = 1 cm.

mations (Lower Devonian, Lochkovian-Pragian). The current faunal list is as follows:

Si Ka Formation:

Galeaspids: *Sanqiaspis vietnamensis*, *Polybranchiaspis* sp., Galeaspida gen. et sp. indet.
Antiarchs: *Heteroyunnanolepis* sp., *Yunnanolepis* cf. *Y. spinulosa*, *Chuchinolepis* sp., *Yunnanolepis* sp., Yunnanolepidoidei gen. et sp. indet.
Sarcopterygian: Sarcopterygii gen. et sp. indet.

Bac Bun Formation:

Galeaspid: *?Bannhuanaspis* sp.
Antiarchs: *Minicrania* sp., *?C. dongmoensis*, Antiarcha? gen. et sp. indet.
Arthrodire: Brachythoraci?
Petalichthyids: *Tongdzuyalepis vietnamensis*, Petalichthyida gen. et sp. indet.
Ptectodontid: Ptectodontida? gen. et sp. indet.

Mia Le Formation:

Galeaspid: Galeaspida gen. et sp. indet.
Placoderm: Placodermi gen. et sp. indet.

3.2. Tong Vai Valley, Dong Van district, Ha Giang Province, northern Vietnam (locality 7, Fig. 1)

The Tong Vai area, west of the Quan Ba hamlet, in Dong Van, Ha Giang Province, has produced several Devonian vertebrate localities (Janvier and Tông-Dzuy, 1998; Tông-Dzuy et al., 1995). The vertebrate remains (Figs. 3B and C, and 4A–C) come from the basal part of the Early Devonian Khao Loc Formation. This fauna is in accord with that from the upper part of the Xishancun Formation and the lower part of the Xitun Formation of South China, indicating an age from the middle to late Lochko-

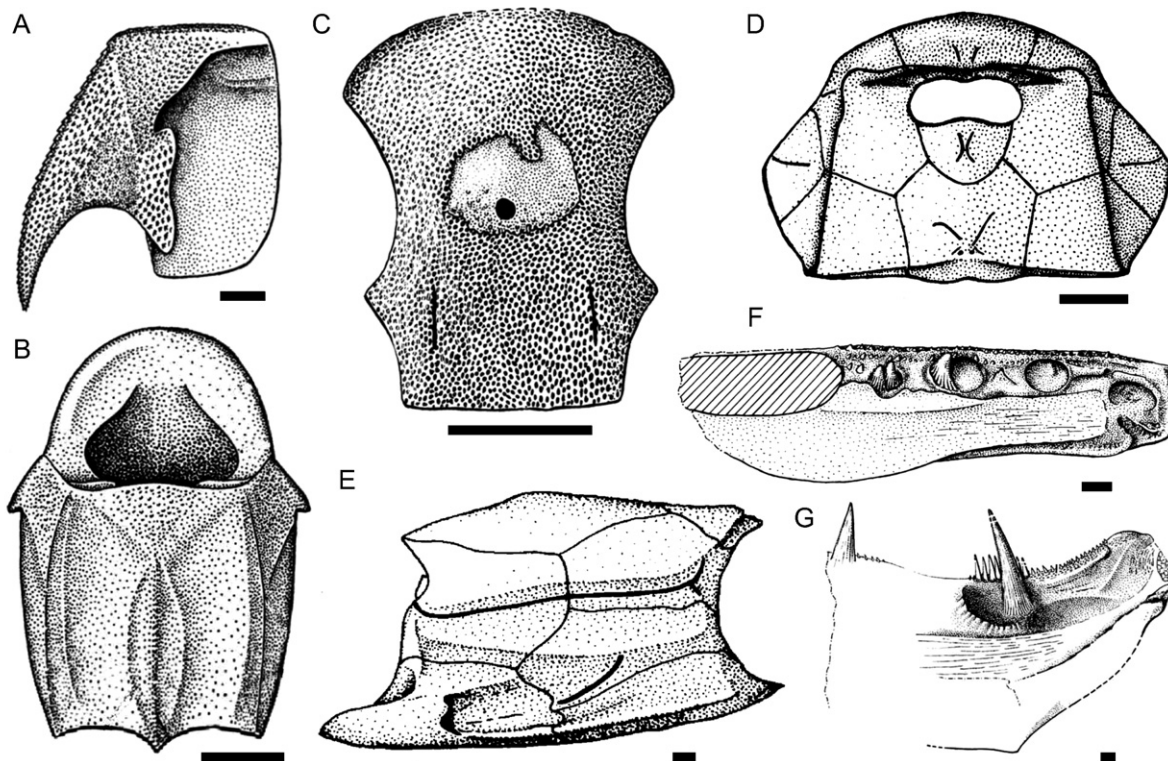


Fig. 4. Placoderms and sarcopterygians from North Vietnam of the South China block. (A–C) From the Khao Loc Formation of Tong Vai. (A) *Hagiangella goujeti* (after Racheboeuf et al., 2005). (B) *Minicrania lissa* (after Janvier and Phuong, 1999). (C) Youngolepididae gen. et sp. indet. (after Racheboeuf et al., 2005). (D and E) From the Bac Bun Formation of Dong Mo. (D) *Chuchinolepis dongmoensis* (after Tông-Dzuy and Janvier, 1990). (E) *Yunnanolepis bacboensis* (after Tông-Dzuy and Janvier, 1990). (F) *Youngolepis* cf. *Y. praecursor*, from the Si ka Formation of Dong Mo (after Tông-Dzuy and Janvier, 1990). (G) *Langdenia campylognatha*, from the Bac Bun Formation of Trang Xa (after Janvier and Phuong, 1999). Scale bar = 2 mm.

vian (Janvier and Phuong, 1999; Racheboeuf et al., 2005). The fauna includes galeaspids *Polybranchiaspis liaojiaoshanensis*, *Laxaspis yulongssus*, the acanthothoracid *Hagiangella goujeti*, antiarchs *Zhanjilepis aspratilis*, *Heteroyunnanolepis qujingensis*, *Minicrania lissa*, Yunnanolepidoidei gen. et sp. indet., petalichthyids *Diandongpetalichthys?* sp., Quasipetalichthyidae gen. et sp. indet., and sarcopterygian Youngolepididae gen. et sp. indet. (Janvier and Phuong, 1999; Racheboeuf et al., 2005; Tông-Dzuy et al., 1995).

3.3. Khao Loc, Ha Giang Province, northern Vietnam (locality 8, Fig. 1)

Tông-Dzuy and Janvier (1987) reported the galeaspid *Polybranchiaspis* sp. from the Early Devonian (Lochkovian) Si Ka Formation in Khao Loc, Yen Minh area of Ha Giang Province, northern Vietnam.

3.4. Ban Nhuan, Phu Luong district, Bac Thai Province, northern Vietnam (locality 9, Fig. 1)

The locality of Ban Nhuan, northeast of Du, in the Phu Luong District, has yielded Lower Devonian vertebrate fossils (Fig. 3D) from near the boundary between the Si Ka Formation and the Bac Bun Formation (late Lochkovian to early Pragian) (Janvier and Tông-Dzuy, 1998; Janvier et al., 1993). The

fauna includes the galeaspid *Bannhuanaspis vukhuci*, antiarchs *Y. spinulosa*, *Yunnanolepis* sp., *C. dongmoensis*, and the sarcopterygian *Youngolepis* sp. (Janvier and Phuong, 1999; Janvier et al., 1993).

3.5. Dong Mo, Lang Son Province, northern Vietnam (locality 10, Fig. 1)

The fauna from Dong Mo in Lang Son Province of northern Vietnam is similar to that of the Xitun Formation of Yunnan, China. It can be dated as late Lochkovian, which is slightly younger than faunas of the Khao Loc Formation in the Tong Vai area of northern Vietnam and the Xishancun Formation in Yunnan, China (Janvier, 1990; Janvier and Phuong, 1999; Janvier and Tông-Dzuy, 1998; Tông-Dzuy and Janvier, 1990). Dong Mo provides a remarkably preserved fauna, which includes (Fig. 4D–F):

Si Ka Formation:

Galeaspid: Galeaspida gen. et sp. indet.

Antiarchs: *Yunnanolepis* cf. *Y. porifera*. Antiarcha gen. et sp. indet.

Sarcopterygian: *Youngolepis* cf. *Y. praecursor*.

Bac Bun Formation:

Galeaspid: Galeaspida gen. et sp. indet.

Antiarchs: *C. dongmoensis*, *Yunnanolepis bacboensis*, *Yunnanolepis deprati*, *Yunnanolepis* sp., *Vanchienolepis langsonensis*, Antiarcha gen. et sp. indet.

Sarcopterygians: *Youngolepis* cf. *Y. praecursor*, Dipnoi gen. et sp. indet., *Psarolepis* sp.

3.6. Trang Xa, Bac Thai Province, Vietnam (locality 11, Fig. 1)

The locality of Trang Xa, south of Dinh Ca, is on the main road from Thai Nguyen to Vo Nhai, in the Bac Thai Province (Tông-Dzuy and Janvier, 1994), and has yielded Early Devonian vertebrates in the uppermost part of the Si Ka Formation and the lower part of the Bac Bun Formation (Fig. 4G) (Janvier and Phuong, 1999; Janvier and Tông-Dzuy, 1998; Tông-Dzuy and Janvier, 1987, 1990, 1994). The fauna from Trang Xa includes:

Si Ka Formation:

Sarcopterygian: *Youngolepis* sp.

Bac Bun Formation:

Galeaspid: Galeaspida gen. et sp. indet.

Antiarchs: *Yunnanolepis* sp., *Chuchinolepis* sp., *Heteroyunnanolepis?* *meemanae*

Petalichthyid: Petalichthyida gen. et sp. indet.

Acanthodian: *Nostolepis* sp.

Sarcopterygians: *Youngolepis* cf. *Y. praecursor*, *Youngolepis* sp., Dipnoi gen. et sp. indet., *Langdenia campylognatha*.

L. campylognatha (Fig. 4G) was first described by Janvier and Phuong (1999) as a dipnomorph fish, but Zhu and Yu (2004) recognized that it may represent a basal onychodont.

3.7. Lower Song Da area, Son La Province, northern Vietnam (locality 12, Fig. 1)

The Early Devonian vertebrate locality in the lower Song Da area is in the Van Yen District, eastern Son La Province, northern Vietnam (Janvier et al., 1996). The vertebrate fauna from the presumably Lochkovian Nam Pia Formation contains Galeaspida gen. et sp. indet., the antiarch *Songdalepis pustulata*, Petalichthyida gen. et sp. indet., Actinolepida? gen. et sp. indet., and the sarcopterygian *Youngolepis?* sp.

This fauna can be referred undoubtedly to the Devonian “galeaspid-yunanolepiform” province, thus confirming that the lower Song Da area was on the southern edge of the South China block in the Early Devonian time (Janvier et al., 1996; Janvier and Tông-Dzuy, 1998). This also confirms that a separate “Song Da terrane” did not exist in the Devonian (Janvier et al., 1996; Young and Janvier, 1999).

3.8. Do Son Peninsula, south of Haiphong, Vietnam (locality 13, Fig. 1)

The Do Son sandstone exposed in the Do Son Peninsula, southwest of Haiphong, was first compared to the Early Devonian Si Ka Formation of northern Vietnam (Janvier et al., 1987; Tông-Dzuy, 1986). Further investigation in the southeastern part of the peninsula unearthed vertebrate remains including the antiarchs *Bothriolepis* sp., *Vietnamaspis trii* Long et al., 1990, and *Arthrodira?* gen. et sp. indet. (Fig. 5A and B). With the associated plant remains, these indicated a younger age (Givetian) for the Do Son Formation (Janvier et al., 1989; Long et al., 1990; Tông-Dzuy, 1993).

However, the subsequent discovery of vertebrate, eurypterid and plant remains from a nearby locality of the peninsula makes

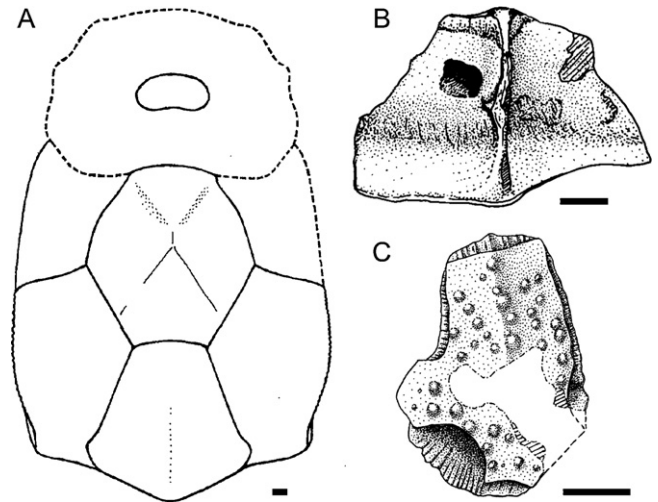


Fig. 5. Vertebrates from the Do Son Peninsula. (A and B) From the Upper Member of the Do Son Formation, Middle Devonian (Givetian), Petite Baie fossil site. (A) *Bothriolepis* sp. (after Janvier et al., 1989), (B) *Vietnamaspis trii* (after Long et al., 1990). (C) Yunnanolepiform-like antiarch, resembling *Zhanjilepis*, from the Lower Member of the Do Son Formation, Late Silurian, Ngoc Xuyen quarry (after Janvier and Tông-Dzuy, 1998). Scale bar = 5 mm.

the age of the Do Son Formation an enigma (Tông-Dzuy et al., 1994a). This locality is at Ngoc Xuyen, in the northwestern part of Do Son Peninsula, less than 1 km northwest of the previous vertebrate and plant locality. The occurrence of plant remains typical of the Late Silurian–Early Devonian interval and well-preserved eurypterids referred to a taxon hitherto known only from the Late Silurian of North America supports a Late Silurian–Early Devonian age. Placoderms found in association with the eurypterids include an indeterminate antiarch (Fig. 5C) resembling *Zhanjilepis* from the Early Lochkovian Xishancun Formation of China (Zhang, 1978; Zhu, 1996) and a plate (Fig. 6A) showing some antiarch-like characters and close similarities to an undescribed Silurian placoderm “*Wangolepis*” from China (Janvier and Tông-Dzuy, 1998; Tông-Dzuy et al., 1994a).

The age of the Do Son Formation has been enigmatic for a long time (Janvier and Tông-Dzuy, 1998), but new evidence in the southwest of Dong Thon on the Do Son Peninsula indicates unconformities within the formation rather than interpreting the Do Son Formation as diachronous (Janvier et al., 2003). Also the material found from Tra Ban Island (see next section) supports the opinion that the Do Son Formation probably includes two parts of different age—the lower part being Late Silurian (Ludlow-Pridoli) and the upper part being Middle Devonian (Givetian).

Whether the Do Son Peninsula belongs to the South China block or the Indochina terrane is not resolved. Long et al. (1990) suggested that Do Son and the area between the Red River Fault and the Song Ma suture were in close affinity. But the fish fauna from the Song Da area suggests that this area was on the southern edge of the South China block in Early Devonian time (Janvier et al., 1996). In this case, given Do Son’s affinity to the Song Da-Song Ma area, the peninsula should also belong to the South China block. Young and Janvier (1999) pointed out that Do Son

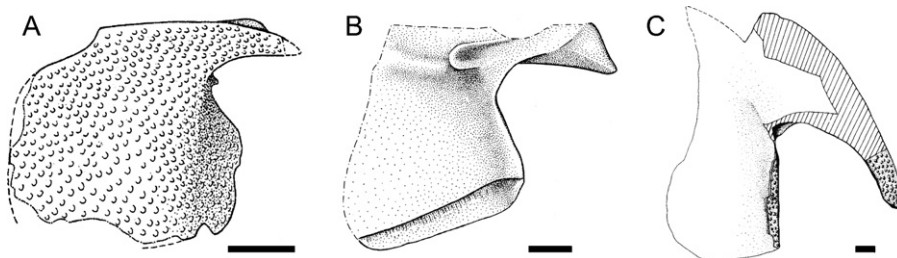


Fig. 6. “*Wangolepis*”-like placoderms from Do Son of North Vietnam (A, after Janvier et al., 1994), My Duc of central Vietnam (B, after Janvier and Tông-Dzuy, 1998) and Yunnan of South China (C). Scale bar = 5 mm.

should be referred to the South China block with its position north of Song Ma suture, but similarities of lithology and fauna with those of Ly Hoa also indicate affinity to the Indochina terrane (Young and Janvier, 1999). Yet the occurrence of the endemic *Vietnamaspis* and *Lyhoalepis* in Ly Hoa cannot sufficiently indicate proximity between Do Son and the Indochina terrane (Ly Hoa). In this paper, we refer Do Son to northern Vietnam of South China block considering its position north of Song Ma suture, after Tong-Dzuy et al. (2007).

3.9. Tra Ban Island, south of Haiphong, Vietnam (locality 14, Fig. 1)

This locality in the Do Son Formation, about 80 km north-east of Do Son Peninsula (Janvier et al., 2003), has produced vertebrate remains strongly suggestive of the European genus *Asterolepis* Eichwald, 1840, which was also recorded from North America with uncertain records from Iran, Australia, and Colombia (Janvier, 1979; Janvier and Villarroel, 2000; Lyarskaya, 1981; Young, 1993). If the vertebrate remains belong to the genus *Asterolepis*, it would be the first occurrence of *Asterolepis* from the South China block (Janvier et al., 2003). The invertebrate fauna of the overlying Trang Kenh Formation indicates a late Givetian assemblage, suggesting a Givetian age for the placoderm.

4. Indochina terrane

The Indochina terrane includes east Thailand, Vietnam south-west of the Song Ma suture, Cambodia, a large portion of Laos, and small parts of Malaysia and Indonesia. Middle Palaeozoic vertebrate remains are only known from the Vietnamese part of the Indochina terrane.

4.1. Cau Rong, Quang Binh Province, central Vietnam (locality 15, Fig. 1)

Fish remains attributed to the antiarch *Bothriolepis* sp. were recovered from the lowermost part of the Dong Tho Formation at Cau Rong in the western part of the Quang Binh Province (Racheboeuf et al., 2006). Although poorly preserved, these materials do not resemble those of the Ly Hoa Formation. The associated charophyte *Sycidium haikouense* and the brachiopod *Holynetes caurongensis* suggest a Givetian age (Racheboeuf et al., 2006; Tong-Dzuy et al., 2007).

4.2. Qui Dat, Quang Binh Province, central Vietnam (locality 16, Fig. 1)

Long (1993) described the faunas from the Muc Bai (=Qui Dat) Formation (Givetian) and the Xom Nha Formation (late Famennian) in Quang Binh Province, central Vietnam. The fauna of the Muc Bai Formation includes: Osteolepiformes gen. et sp. indet., Actinopterygii gen. et sp. indet., Placodermi gen. et sp. indet. The Xom Nha Formation comprises indeterminate osteichthyan material and the following chondrichthyans (Long, 1993): Stethacanthid gen. et sp. indet., *Phoebodus* cf. *P. gothicus*, *Cladodus* cf. *C. acutus* (Fig. 7A).

4.3. Ly Hoa, Quang Binh Province, central Vietnam (locality 17, Fig. 1)

The Devonian terrigenous deposits at Cape Ly Hoa, in Quang Binh Province of central Vietnam (formerly “Ly Hoa Sandstones”; now known as the Ly Hoa Formation; Pham Huy et al., 1999), were regarded as a lateral facies of the Dong Tho Formation (Tông-Dzuy et al., 1994b). Racheboeuf et al. (2006), based on new findings from Ly Hoa and Cau Rong, pointed out that the Ly Hoa Formation cannot be a lateral facies of the Dong Tho Formation. Fish remains from Ly Hoa include Galeaspida? gen. et sp. indet., arthrodires *Lyhoalepis duckhoai* (Fig. 7B), Holonematidae? gen. et sp. indet., Brachythoraci gen. et sp. indet., the antiarch *Vukhuclepis lyhoaensis* (Fig. 7C), Acanthothoraci gen. et sp. indet., Petalichthyida gen. et sp. indet., and sarcopterygians Youngolepididae gen. et sp. indet. (Fig. 7D) and Sarcopterygii gen. et sp. indet. (Janvier et al., 1997; Racheboeuf et al., 2006; Tông-Dzuy et al., 1994b, 1996).

Yunnanolepid antiarchs were known exclusively from the Lower Devonian of the South China block until the antiarch *V. lyhoaensis* was recorded from the Ly Hoa Formation of Quang Binh Province (Racheboeuf et al., 2006; Tông-Dzuy et al., 1996). The discovery of *V. lyhoaensis*, with Youngolepididae and possibly galeaspids from the Indochina terrane, provides strong evidence for geographical proximity between the South China block and the Indochina terrane in the Devonian (Racheboeuf et al., 2006).

The vertebrate remains suggest an Early Devonian (probably Emsian) age, yet the fossil flora of the Ly Hoa Formation suggests a Middle Devonian (probably Givetian) age. To explain this, Racheboeuf et al. (2006) suggested that the Ly Hoa Formation might be diachronous. Alternatively, the Ly Hoa Formation

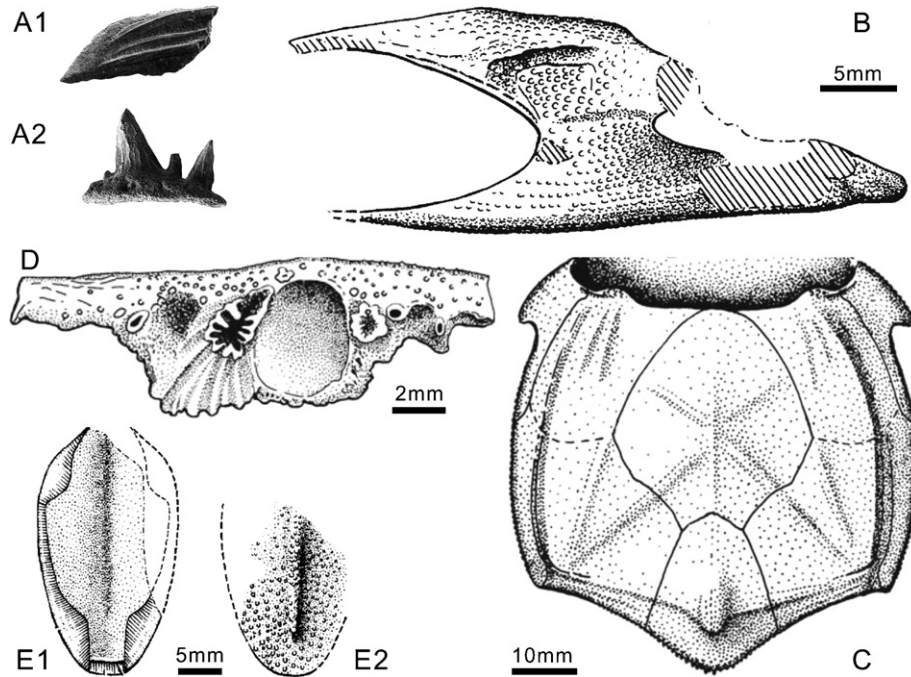


Fig. 7. Vertebrates from central Vietnam of the Indochina terrane. (A) Microvertebrates from the Xom Nha Formation of Qui Dat (after Long, 1993). (A1) cf. *Moythomasia*, (A2) *Cladodus* cf. *C. acutus*. (B–D) Vertebrates from the Ly Hoa Formation of Ly Hoa (after Tông-Dzuy et al., 1994b and Racheboeuf et al., 2006). (B) *Lyhoalepis duckhoai*, (C) *Vukhuclepis lyhoaensis*, (D) Youngolepididae gen. et sp. indet. (E) *Mydocosteus anmaensis* in internal (E1) and external view (E2), from Dai Giang Formation of My Duc (after Tông-Dzuy et al., 1997).

could be divided into two parts, as for the Do Son Formation in the Do Son Peninsula, but further fieldwork is needed to resolve this problem.

The galeaspid agnathan recently reported from Ly Hoa (Racheboeuf et al., 2006) is of particular interest. Young and Janvier (1999) mentioned that galeaspid would be expected if Indochina and South China had a close relationship. Thus far, endemic taxa of the Pan-Cathaysian landmass such as galeaspid, yunnanolepid antiarchs, and basal sarcopterygians (Zhao and Zhu, 2010) have been recorded from central Vietnam (Indochina terrane). This provides additional evidence on the formation of the Song Ma suture. The vertebrate fossil evidence supports that the suture was formed during the Late Silurian to Early Devonian, or at least the two were very close to each other (Janvier, personal communication). The evidence suggests that the Indochina terrane also belonged to the Pan-Cathaysian landmass.

4.4. My Duc, in Quang Binh Province, central Vietnam (locality 18, Fig. 1)

Tông-Dzuy et al. (1997) described Silurian vertebrates from this locality in the late Ludlow–early Pridoli Dai Giang Formation, near My Duc (Quang Binh Province). The locality has yielded abundant placoderm, acanthodian, and sarcopterygian remains (Figs. 6B and 7E), including the placoderms (*Mydocosteus anmaensis*, *Acanthothoraci* gen. et sp. indet.), the acanthodians (*Climatiida* gen. et sp. indet.), and Osteichthyes gen. et sp. indet.

The placoderm *M. anmaensis* cannot be referred to any of the major placoderm groups known to date, although it shares

some characters with arthrodires and antiarchs. One specimen (Fig. 6B) closely resembles “*Wangolepis*” from the Silurian of Yunnan in overall shape; however, the ornamentation of large, scattered tubercles differs from sinuous ridges of “*Wangolepis*” (Janvier and Tông-Dzuy, 1998; Tông-Dzuy et al., 1997). Recent findings of a similar specimen (Figs. 6C and 8) from the Ludlow Kuanti Formation, at the same locality as *Guiyu oneiros* (Zhu et al., 2009), also has ornamentation of scattered tubercles. To date, Late Silurian “*Wangolepis*”-like materials have been recorded only from South China (Yunnan), North Vietnam (Do Son Peninsula), and central Vietnam (My Duc).

The My Duc osteichthyans include at least two types. Dermal bone with ornamentation of cosmine pierced by large pores is similar to that of the basal osteichthyan *Psarolepis* from Yunnan, hitherto known only from the Late Silurian–Early Devonian of South China and Vietnam (Janvier and Tông-Dzuy, 1998; Tông-Dzuy et al., 1997; Yu, 1998; Zhu and Schultze, 1997; Zhu et al., 1999). Another dermal bone fragment and a scale ornamented with parallel ridges resemble the basal osteichthyan *Guiyu*, a recently discovered taxon from Yunnan that displays mosaic gnathostome characters (Zhu et al., 2009). *Guiyu*, *Psarolepis*, *Naxilepis*, and *Ligulalepis* constitute the osteichthyans of the Xiaoxiang fauna in Yunnan.

Distinctive placoderms (*M. anmaensis*) and basal osteichthyans (material similar to *Psarolepis* and *Guiyu*) from My Duc highlight strong similarities with the Xiaoxiang fauna and strongly imply that the My Duc vertebrate assemblage belongs within the Xiaoxiang fauna. This further indicates that the South China block and the Indochina terrane were near each other during the Late Silurian, as already suggested by Young and Janvier (1999). Comparisons of the invertebrate fauna from My Duc

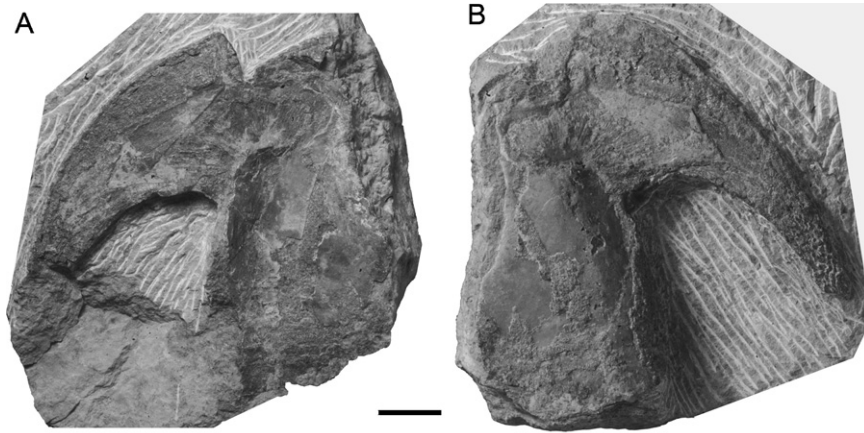


Fig. 8. Placoderm from the Ludlow Kuantu Formation near Xiaoxiang Reservoir of Qujing, Yunnan, resembling the undescribed “Wangolepis”, IVPP V 17039, A and B, in part and counterpart. Scale bar = 1 cm.

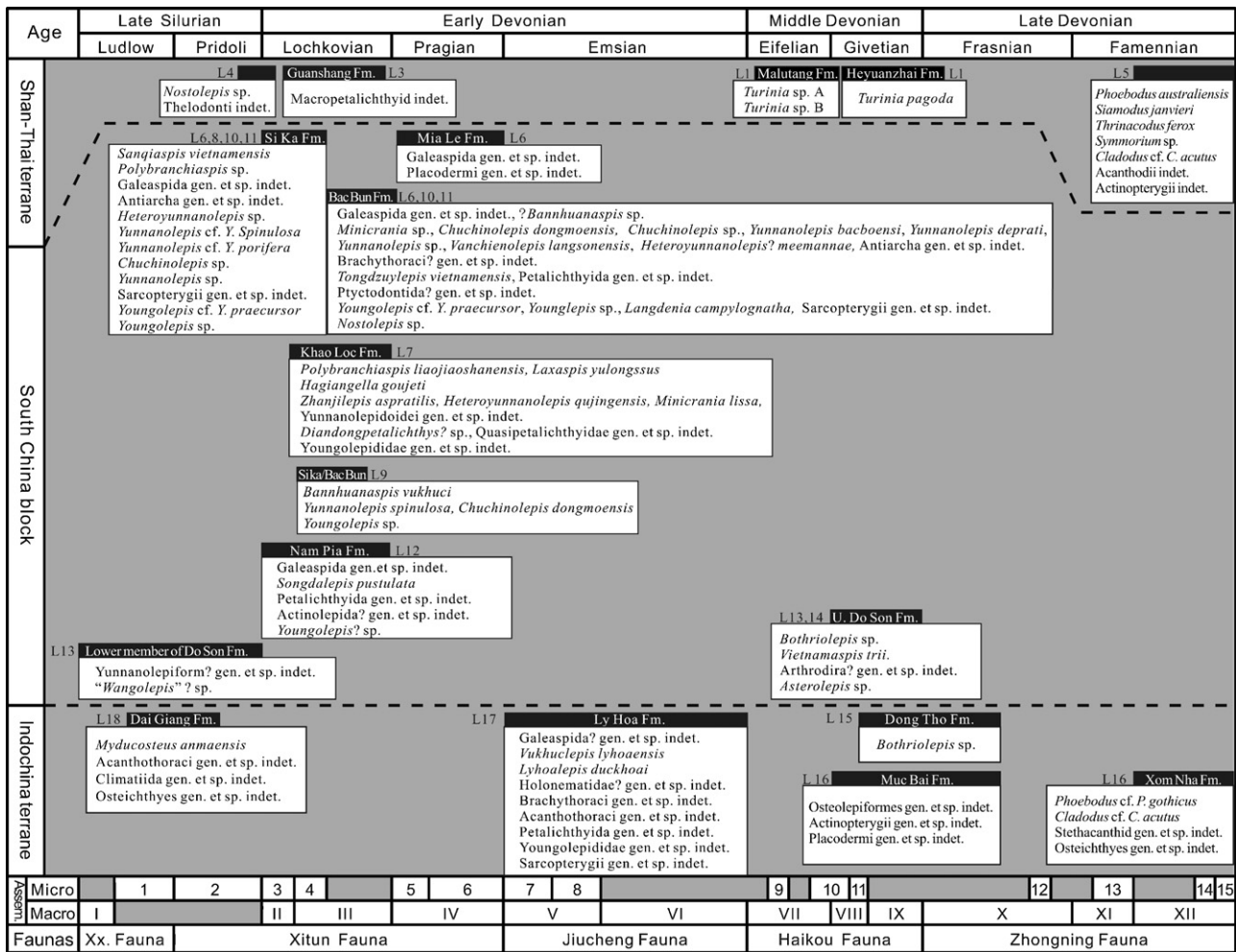


Fig. 9. Siluro-Devonian vertebrate distribution of Southeast Asia and western Yunnan, with the coeval Chinese assemblages and faunas. Abbreviations: Assem: assemblage; Fm: Formation, L1–18: Siluro-Devonian vertebrate fossil localities labelled in Fig. 1; Si Ka/Bac Bun: near the boundary of the Si Ka and Bac Bun formations; U: upper member; Xx: Xiaoxiang. Microvertebrate assemblages (after Zhu and Wang, 2000; Zhu et al., 2000)—1: *Ligulalepis yunnanensis*; 2: *Nostolepis sinica*; 3: *Poracanthodes zoigenensis*; 4: *Poracanthodes* cf. *P. porosus*; 5: *Gomphonchus liujingensis*; 6: *Cheiracanthoides dolosus*; 7: *Cheiracanthoides wangi*; 8: *Wuxuanichthys wangi*; 9: *Dangdouchthys liui*; 10: *Acanthodes dublinensis*; 11: *Acanthodes - Ohiolpis*; 12: *Phoeobodus bifurcatus*; 13: *Acanthodes - Ctenacanthus*, 14: *Phoeobodus - tenacanthus*; 15: *Phoeobodus* cf. *Ph. limpidus*. Macrovertebrate assemblages (after Zhu and Wang, 2000; Zhu et al., 2000)—I: *Silurolepis*; II: *Polybranchiaspis*; III: *Diabolepis - Nanpanaspis*; IV: *Sanchaspis - Asiaspis*; V: *Kueichowlepis - Sinopetalichthys*; VI: *Wudinolepis - Yinosteus*; VII: *Bothriolepis sinensis - Hunanolepis*; VIII: *Bothriolepis kwangtungensis - B. lochangensis*; IX: *Panxiosteus - Eastmanosteus*; X: *Changyanophytom - Chirodipterus*; XI: *Remigolepis*; XII: *Sinolepis*.

(central Vietnam) and Kien An (North Vietnam) also support this conclusion (Tông-Dzuy et al., 2001).

5. Discussion and conclusion

The Siluro-Devonian vertebrate distribution in the strata of Southeast Asia and western Yunnan is summarized (Fig. 9), with the comparable Chinese assemblages and faunas (Zhao and Zhu, 2010; Zhu and Wang, 2000; Zhu et al., 2000).

The Middle Palaeozoic vertebrates from northern Vietnam accord with those from Yunnan and Guangxi of South China. The Si Ka and Bac Bun formations of Bac Bo (Lung co-Mia Le section, Dong Mo, Trang Xa, Ban Nhuan and Khao Loc) and the Khao Loc Formation of Tong Vai yield galeaspids, antiarchs, arthrodires, acanthothoracids, petalichthyids, ptyctodontids, acanthodians, and sarcopterygians. This fauna accords with the coeval Xitun fauna from China, which is characterized by the radiation of Polybranchiaspidiformes, Huannanaspisiformes, Yunnanolepididae, and crown sarcopterygians (Zhao and Zhu, 2010). Hence, the vertebrates from the Si Ka, Bac Bun and Khao Loc formations of northern Vietnam (also a part of South China block) can be referred to the Xitun fauna.

The vertebrate fauna from lower Song Da area can be referred to the Devonian “galeaspid-yunanolepiform” province undoubtedly, thus confirming that a separate “Song Da terrane” did not exist in Devonian time. The Do Son Formation can be divided into two distinct sections of Late Silurian and Givetian ages.

Central Vietnam of the Indochina terrane yields vertebrates with South China affinities from the Emsian Ly Hoa Formation and the late Ludlow–early Pridoli Dai Giang Formation. The Dia Giang Formation of My Duc contains the same Late Silurian members, the “*Wangolepis*”-like placoderm, *Psarolepis*-like and *Guiyu*-like osteichthyans, with the Xiaoxiang fauna of China, which is characterized by the early diversification of gnathostomes, in particular the occurrence and divergence of osteichthyans (Zhao and Zhu, 2010; Zhu et al., 2009). Therefore, the vertebrates of My Duc should be assigned to the Xiaoxiang fauna, as for those from the lower member of the Do Son Formation. The evidence strongly supports close contact between the Indochina terrane and South China block as early as Ludlow.

The occurrence of thelodont microfossils *T. pagoda* from Shidian of western Yunnan on the Shan-Thai terrane, with the contemporaneous record of *Turinia* cf. *T. pagoda* from South Australia, may indicate a close relationship between Shan-Thai and east Gondwana during the Middle Devonian.

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