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Llandovery (lower Silurian) graptolites from the Sepon Mine, Truong Son Terrane, central Laos and their palaeogeographical significance

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ABSTRACT

Graptolites are described from the Llandovery of the Sepon mine area, central Laos, part of the Truong Son Terrane. The palaeobiogeographical affinities of the Rhuddanian graptolites are with peri-Gondwanan Europe and Arabia rather than equatorial regions such as South China and Laurentia (Arctic Canada). A review of previous palaeontological research on the middle Palaeozoic of the Indochina terranes reveals an often contradictory picture with vertebrates suggesting close proximity of South China to the Truong Son Terrane in the Devonian and invertebrates and radiolarians providing evidence for a palaeogeographical barrier between the two. Graptolites from the Mojiang area, Yunnan are typical of low latitude Silurian faunas and suggest that this area (Simao or Loei Terrane) was separate from the Truong Son Terrane.

1. Introduction

Today South-East Asia comprises a highly complex patchwork of terranes bounded by fault and shear zones, sutures and fold belts (Figs. 1 and 2). Unravelling the geological history of the region requires interdisciplinary studies utilizing all available evidence. Here we provide some palaeobiogeographical constraints on the early Silurian location of the Truong Son Terrane (one of the Indochina terranes) based upon graptolite faunas from the Sepon Mine area, central Laos. We discuss also previous palaeogeographical work on the middle Palaeozoic of the Truong Son Terrane as well as published sporomorph and graptolite data from that part of Yunnan (China) that has been widely portrayed as part of the combined Indochina Terrane. The importance of such palaeobiogeographical studies is considerable given the paucity/absence of reliable palaeomagnetic data for much of South-East Asia (Metcalf, 2005, p. 172; Burrett et al., 2014, p. 33).

2. Location of the Indochina terranes in the Ordovician–Devonian: Discussion of previous suggestions

The vast majority of published palaeogeographical reconstructions have treated Indochina (sometimes referred to as Annamia, e.g. Torsvik and Cocks, 2009) as a single entity. Many recent terrane maps of South-East Asia (e.g. Burrett et al., 2014; Khin Zaw et al., 2014; Lai et al., 2014; Fig. 1), however, recognise that Indochina itself is a composite of

a number of terranes, each with its own distinctive tectonic, stratigraphical and magmatic history. These include the Truong Son Terrane from which the Laotian graptolites discussed herein originate. For this reason, we discuss separately in Section 3 the published evidence for the palaeogeographical position of the Mojiang region, Yunnan, on the basis that it may not have been part of a geographically contiguous block with the Truong Son Terrane during the early mid-Palaeozoic.

With the exception of Young and Janvier (1999), palaeogeographical reconstructions show Indochina lying to the west of Eastern Gondwana (= much of Australia, India and Antarctica) during the early mid-Palaeozoic. Young and Janvier (1999) felt that the distinctiveness of the vertebrates from the South China-Tarim-Indochina composite Terrane necessitated giving it “complete continental isolation” in the Pacific Ocean, east of Eastern Gondwana. There is much less agreement, however, with regard to Indochina’s palaeolatitude and its location in relation to South China. Some indication of the range of published proposals for the Ordovician to Devonian is given by the brief review that follows.

Usuki et al. (2013, Fig. 6) placed Indochina on the south-west margin of Eastern Gondwana in the Ordovician at a palaeolatitude of 28–18° S, bounded to the north by South China and to the east by the Qiangtang (spelt Qiantang by some authors) Terrane (northern Tibet). Their study was based upon U-Pb and Hf isotope analyses of detrital zircons from the Truong Son Belt. Wang et al. (2014) showed similar relationships between Indochina, South China and Qiangtang in their

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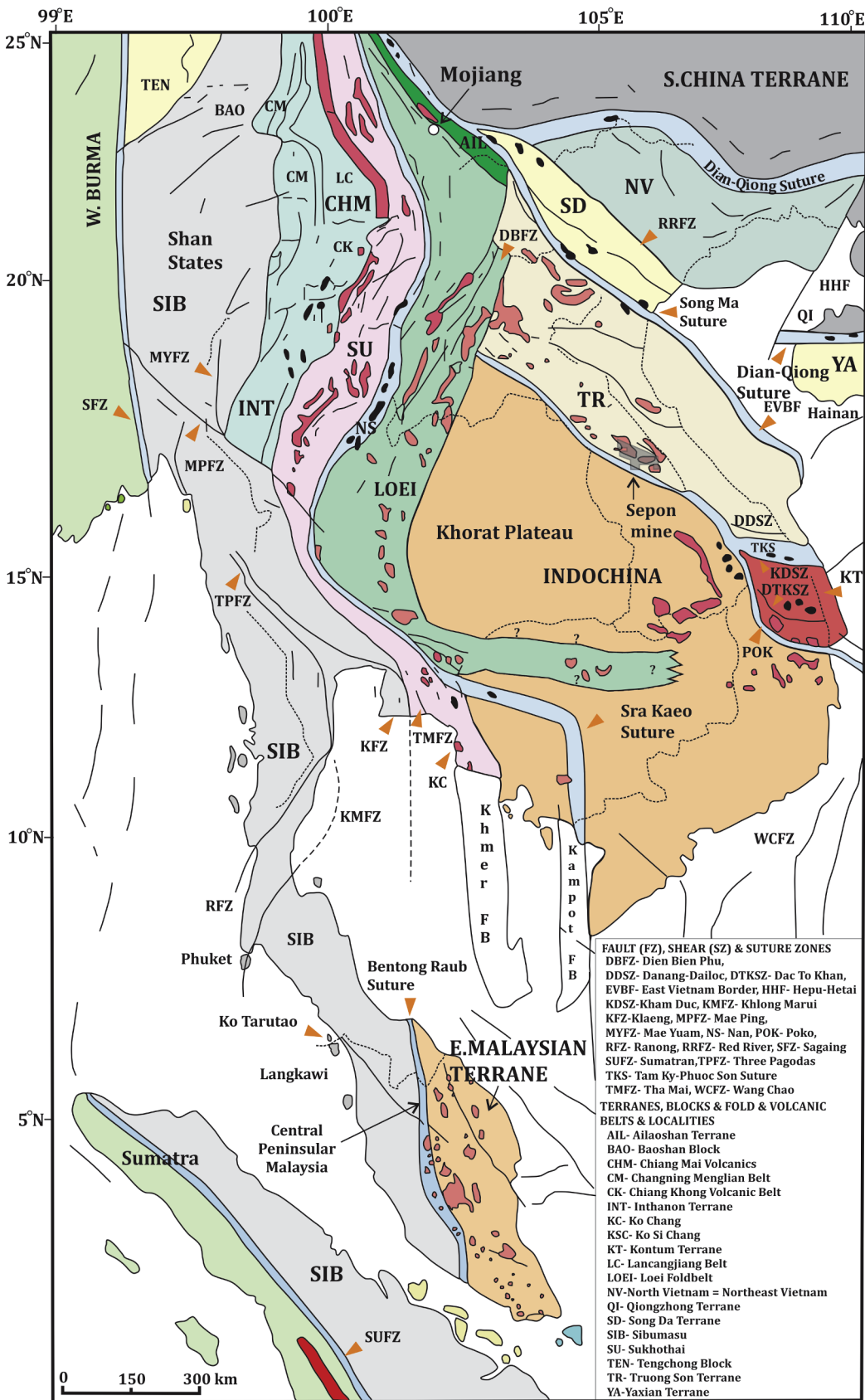


Fig. 1. Provisional terrane map of mainland South East Asia, modified from Burrett et al. (2014). Note that the Sepon Mine area (from which the graptolite fauna described herein was collected), is close to the southwest margin of the Truong Son Terrane. The graptolite fauna and sporomorph flora from Mojiang in Yunnan Province, China are provisionally placed on an extension of the Loei Terrane. However, the area between the Ailaoshan and the Changning-Menglian area may belong to a separate terrane known as the Simao Terrane (see Wang et al., 2014). Main constituents of the composite Indochina Terrane are the Loei Terrane (or foldbelt), the Truong Son Terrane, the Kontum Terrane and the rocks beneath the Khorat Plateau and much of Cambodia which are assigned to the general composite Indochina Terrane.

late Silurian palaeogeographical reconstruction, with Indochina now at a southern tropical latitude (15–8°S). Burrett et al.'s (2014) Early–Middle Ordovician (Floian–Dapingian, c. 470 Ma) reconstruction

(also based upon U–Pb isotope analyses of zircons) placed the Indochina terranes at about 40° S, sandwiched between South China to the west-northwest and the Qiangtang Terrane to the east. Iran is shown due

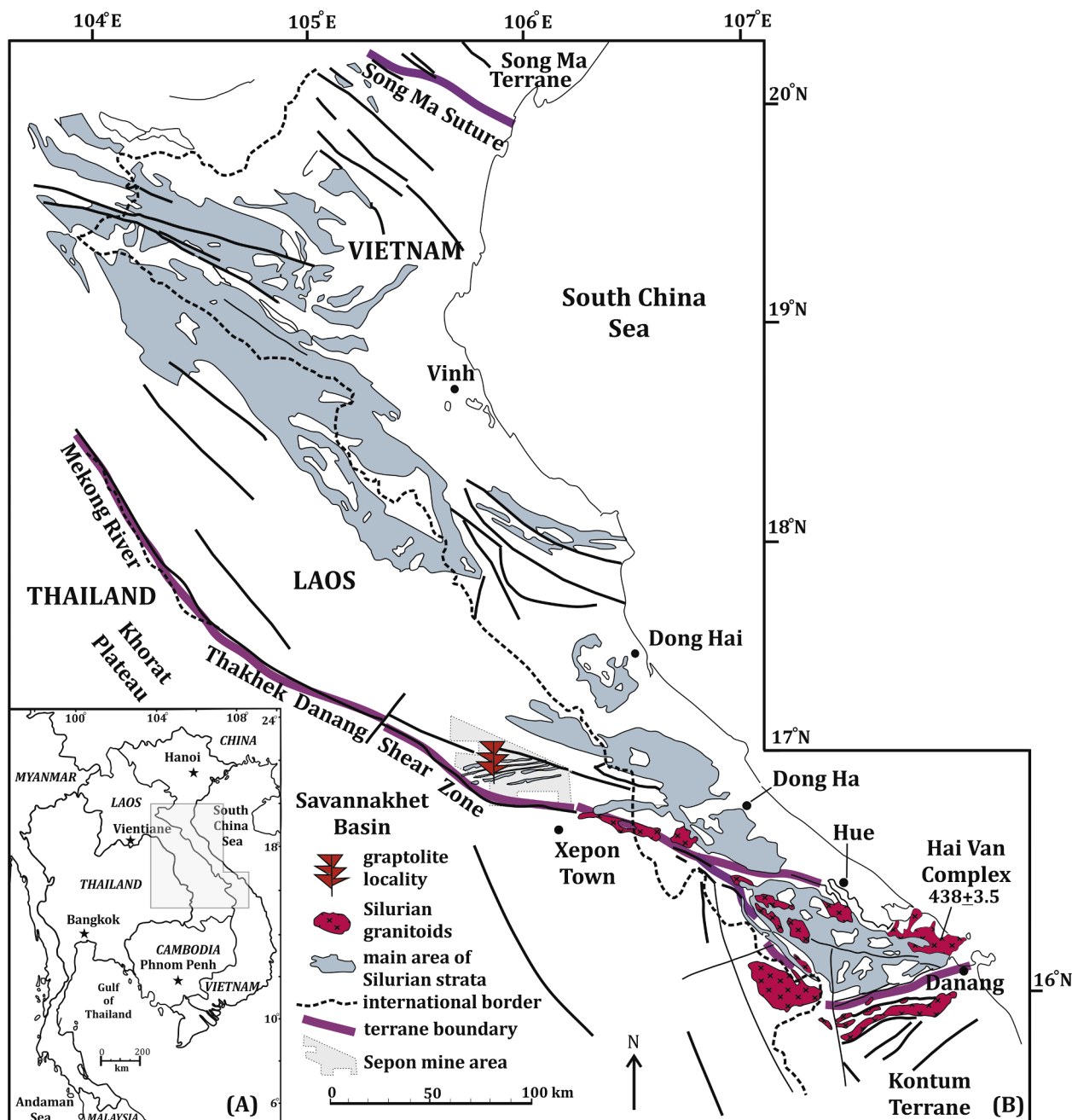


Fig. 2. (A) Location of Truong Son Terrane of Fig. 2B in South East Asia. (B) Distribution of Silurian strata on the Truong Son Terrane (from Thassanapak et al., 2018). Area shown may include some Upper Ordovician and Lower Devonian strata. Graptolite locality in Sepon Mine Area is shown to the northwest of Xepon Town. The Truong Son Terrane is bordered by the Song Ma suture in the north, which extends offshore (see Fig. 1) and to the south and west by the still active Thakhek-Danang Shear Zone. The Mekong River, which defines the border of Laos (Lao PDR) and Thailand, follows this shear zone. The Truong Son Terrane covers parts of Vietnam and Laos and the international border between them is shown as a dotted line which in part, follows the heavily forested and, in places, impenetrable, highlands of the Annamitic Chain.

south of Indochina.

By contrast, Metcalfe (2005) had located Indochina straddling the equator during the Tremadocian (earliest Ordovician) and at a very low northerly palaeolatitude during the mid-late Silurian. Rather than lying on the Gondwanan margin, Indochina is shown situated between Tarim and Sibumasu and to the north to north-east of South China.

Torsvik and Cocks (2009), referring to Indochina as Annamia, concluded that this may not have been part of core Gondwana during the early Palaeozoic. Subsequently, Annamia was considered by the same authors possibly to be “integrated with South China as a unified continent from the Neoproterozoic to the Middle Devonian” (Cocks and

Torsvik, 2013; Torsvik and Cocks, 2016). Annamia plus South China are shown attached to Gondwana in the mid-Cambrian (Cocks and Torsvik, 2013, Fig. 3), but the development of a spreading ridge is shown to have led to their separation from Gondwana in the Early Ordovician. Annamia’s latitude is shown as about 40°S in the late Tremadocian from whence it drifted (still attached to South China, which is shown to the NNE of Annamia) steadily northwards parallel to the western margin of Gondwana; by the Silurian it had reached the equator. In the same year the same authors (Torsvik and Cocks, 2013) show Annamia as already rifted from Gondwana by the early-Cambrian and portray it as separate from South China throughout the early Palaeozoic. They noted that the

Palaeozoic locations of the terrane are “poorly constrained”. A combined Annamia and South China are shown still attached to Gondwana throughout the Silurian by [Torsvik and Cocks \(2016, Fig. 7.1\)](#), but separated from Gondwana by a transform plate margin in a later figure ([Torsvik and Cocks, 2016, Fig. 7.4](#)).

A further variant is provided by [Rong et al. \(2003, Fig. 34\)](#) whose global palaeogeographical reconstruction for the Silurian shows Indochina just south of the equator, adjacent to north-west Australia and still part of Gondwana. South China is shown immediately east of Indochina. Yet another palaeocontinental configuration is presented by [Agematsu et al. \(2008\)](#) with Indochina at a southern tropical palaeolatitude in the Late Ordovician, close to North China and more than 2000 km north-east of South China. Finally, [Rong and Cocks \(2014, Fig. 15\)](#) provide a reconstruction for the early Silurian which shows Indochina as a separate entity with the Western South Equatorial Current (WSEC) flowing between it and South China. South China is shown to the east of Indochina.

The above review of palaeogeographical reconstructions gives some indication of the uncertainty surrounding Indochina’s location in the early Palaeozoic with different maps showing it to the east, west, south or north of South China and varying in proximity to South China from being physically attached to separation by more than 2000 km.

3. Previous palaeobiogeographical studies concerning the location of the Indochina terranes in the mid Palaeozoic

The palaeobiogeographical significance of the various fossil groups that have been recorded from the middle Palaeozoic of the Indochina terranes is discussed below. As will be seen, in some cases the conclusions drawn are poorly supported by the evidence provided or are contradictory.

We discuss separately the published palaeobiogeographical evidence (1) from localities that are part of the Truong Son Terrane as shown in [Fig. 1](#) and (2) from that part of central and southern Yunnan which may belong to a different terrane or sub-terrane (Simao, Loei or Ailaoshan: [Sone and Metcalfe, 2008](#); [Burrett et al., 2014](#); [Khin Zaw et al., 2014](#); [Wang et al., 2014](#)) and therefore may have had a different geological history from the Truong Son Terrane.

3.1. Vertebrates from the Truong Son Terrane

3.1.1. The Ly Hoa fauna (Devonian)

[Janvier et al. \(1997, p. 403\)](#) emphasized the considerable palaeogeographical significance of certain mid Palaeozoic vertebrate groups, stating that they “can practically be treated as continental organisms for palaeobiogeographical reconstructions.” One of the key lines of evidence for the close proximity of Indochina and South China during the mid Palaeozoic has been the record of a yunnanolepidoid-like antiarch (*Vukhuclepis lyhoaensis*) and a youngolepidid-like sarcopterygian from the Givetian of Ly Hoa, central Vietnam (Indochina) ([Tong-Dzuy Thanh et al., 1996a](#); [Janvier et al., 1997](#) and references therein). Yunnanolepiforms had been recorded previously only from South China. [Tong-Dzuy Thanh et al. \(1996a\)](#) considered it very unlikely that a continental margin-bound fish could have dispersed across a wide ocean (hence the necessary proximity of South China and Indochina), but noted also that there were marked differences in the invertebrate faunas of north Vietnam (South China Terrane) and central Vietnam (Indochina Terrane) which are interpreted to indicate some palaeogeographical barrier between South China and Indochina in the Devonian. These differences they stated remained a “riddle”.

Assignment of vertebrate material by [Tong-Dzuy Thanh et al. \(1996a\)](#) to the yunnanolepiforms (or closely related group) was based upon a single characteristic plate similar to that of *Yunnanolepis*, but remarkably short and broad and certainly belonging to a new species

(which was formally described as *Vukhuclepis lyhoaensis* by [Janvier et al., 1997](#)). [Janvier et al.’s \(1997\)](#) detailed description and discussion of the material initially indicates that assignment to Yunnanolepidae is not certain. For example, they stated (p. 396) that “none of these characters (characterizing Yunnanolepidae) are preserved in the available material of *Vukhuclepis* from Ly Hoa, with the possible exception of a minute structure that may be evidence for some kind of ventrolateral recess, thus suggesting affinities with the Yunnanolepidae.” Similarly, on the same page it is stated: “Assuming that *V. lyhoaensis* can be referred to the Yunnanolepidae, which is fairly probable, it differs from all other genera of the group...”. Later in the same paper, however, [Janvier et al. \(1997, p. 401\)](#) concluded that “*Vukhuclepis lyhoaensis* clearly shows closest resemblances to the Yunnanolepidoidei and other non-euantiarch antiarchs from the South China Block” and that two characters in *V. lyhoaensis* “suggest reliably that this species belongs to the Yunnanolepidoidei or even the Yunnanolepidae”.

The sarcopterygian material from Ly Hoa was assigned by [Janvier et al. \(1997\)](#) to ?Dipnomorpha. The fragmentary bones could not be identified, but some had a cosmine layer particularly “suggestive” of *Youngolepis* and they had a size and thickness in agreement with bones from this genus. The pattern of grooves and pores on a single scale impression was stated to be “strikingly similar” to that of some body scales of *Youngolepis* from the South China Terrane.

It is important to recognise, as pointed out by [Tong-Dzuy Thanh et al. \(1996a\)](#) and [Janvier et al. \(1997\)](#), that in South China yunnanolepiforms are recorded only from the Lower Devonian (in particular the Lochkovian and Pragian), whereas the central Vietnamese material is anachronistic in being from the Givetian. Similarly, *Youngolepis* is known elsewhere only from the Lower Devonian. To explain this, [Janvier et al. \(1997\)](#) proposed that Indo-China and South China were “united in the Silurian and Early Devonian”, which contrasts considerably with proposals based upon geological evidence that Indochina and China did not collide until the Late Devonian–Early Carboniferous ([Metcalfe, 1998](#)) or as late as the Triassic ([Sone and Metcalfe, 2008](#); [Rossignol et al., 2018](#)), but agrees with [Cocks and Torsvik’s \(2013\)](#) portrayal of Indochina and South China being united until the Mid Devonian. [Wang et al. \(2010, p. 35\)](#) stated that the Ly Hoa vertebrate fauna is of Emsian age, but earlier in the same paper had noted that the fossil flora from the Ly Hoa Formation suggests a Middle Devonian (probably Givetian) age.

Further vertebrates from Ly Hoa were described by [Racheboeuf et al. \(2006\)](#), including new sarcopterygian material. Two specimens were described: a dermal plate the identity of which was “quite difficult to determine”; and a jaw bone which had fields of denticles on its lateral margin as seen in jaw bones of *Youngolepis*. Scales found in the vertebrate assemblage “As a whole... agree with those of *Youngolepis*.” [Racheboeuf et al. \(2006\)](#) describe material (“strange tuberculate fragments”) that they refer “with reservation” to a galeaspid (it is described in the systematic palaeontology section as “Galeaspida? gen. et sp. indet.”. [Wang et al. \(2010\)](#) in their review of Southeast Asia middle Palaeozoic vertebrates simply refer to this material as “The galeaspid agnathan” from Ly Hoa and cite it as additional evidence for the proximity of Indochina and South China. Indeed, they state (a Philippe Janvier, pers. comm.) that “The vertebrate fossil evidence supports that the (Song Ma) suture (between Indochina and South China) was formed during the Late Silurian to Early Devonian, or at least the two (Indochina and South China) were very close to each other.”

In summary, the vertebrates described from the Devonian of central Vietnam do not make as strong a case for the proximity of South China and Indochina as if identical taxa were found on both terranes. The central Vietnamese material that is stated to demonstrate biogeographical affinities is all described as similar to or “-like” a vertebrate described from South China and in many cases is questionably identified or with

differences from the taxon with which the material is being compared. This contrasts considerably with the vertebrates recorded from the Devonian of northern Vietnam, which are very similar indeed to those from other localities on the South China Terrane (Wang et al., 2010).

3.1.2. The My Duc fauna (Silurian)

The palaeobiogeographical significance of the faunas recovered by Tong-Dzuy Thanh et al. (1997) from the upper Silurian of My Duc in central Vietnam (Indochina) was stated to be the reverse of that referred to in Tong-Dzuy Thanh et al. (1996a) for the Givetian. Here the invertebrate fauna (see further discussion of brachiopods, below), is stated to be most similar to that of the Miaokao Formation of northeast Yunnan (South China), whereas, apart from one doubtful *Youngolepis*-like fragment, “none of these Silurian vertebrates [from My Duc] suggest particular affinities with the endemic Silurian and Devonian vertebrate taxa of the South China Plate.” Racheboeuf et al. (2006, p. 33) refer to the “South Chinese affinities” of the My Duc fauna, quoting Tong-Dzuy Thanh et al. (1997) as the reference for this, but, as can be seen from the quote above, this is not what Tong-Dzuy Thanh et al. (1997) had stated.

Janvier and Tong-Dzuy Thanh (1998) described an additional placoderm specimen from My Duc. This was described as possibly related to an undescribed genus (“*Wangolepis*”) from Yunnan (South China), although “its ornamentation is quite different”. The My Duc specimen was refigured by Wang et al. (2010, Fig. 1B, in which it was referred to as a “*Wangolepis*”-like placoderm) as were two other “*Wangolepis*”-like specimens from Yunnan (South China). Janvier and Tong-Dzuy Thanh (1998) concluded that the Silurian vertebrate fauna of central Vietnam “shows closest affinities to the South Chinese Silurian vertebrate faunas, in particular by the abundance of placoderms and sarcopterygians, which are not known elsewhere in the Silurian.” Both groups are geographically widespread in the Devonian (e.g. Young, 2010), so this restriction to their geographical distribution is limited to the Silurian.

Wang et al. (2010, p. 35) stated that the Dai Giang Formation at My Duc contains the same late Silurian vertebrates as the Xiaoxiang fauna of South China, listing in addition to the “*Wangolepis*”-like placoderm, *Psarolepis*-like and *Guiyu*-like osteichthyans. They concluded that the “vertebrates of My Duc should be assigned to the Xiaoxiang fauna” and that the “evidence strongly supports close contact between the Indochina Terrane and South China block as early as [the] Ludlow.” This is very different from Tong-Dzuy Thanh et al.’s (1997) original assertion that the My Duc and South China vertebrate faunas had little in common. It is not clear which publication the *Psarolepis*-like and *Guiyu*-like osteichthyan identifications are from. In the two papers cited on the My Duc fauna by Wang et al. (2010), Tong-Dzuy Thanh et al. (1997) referred their material only questionably to the Osteichthyes, referring to it as “gen. et sp. indet.” and Janvier and Tong-Dzuy Thanh (1998) recorded no osteichthyans in their new collections from the location.

In their review of early mid-Palaeozoic vertebrates from Eastern Gondwana and various Asian terranes, Young and Janvier (1999) considered that South China, Tarim and Indochina formed a composite terrane by the early Silurian. They emphasized the significance of the endemism of the diverse South China vertebrate assemblages seeing this as key evidence for “complete continental isolation” of South China (and associated terranes) from Gondwana and Laurentia/Euramerica. As noted above, their preferred location for this Asian composite terrane in the mid Palaeozoic is to the east of Eastern Gondwana within the Pacific, as opposed to a position west of Australia as shown on almost all other palaeogeographical reconstructions.

3.1.3. Summary

Overall, much of the vertebrate material from the Silurian and Devonian of the Indochina terranes is fragmentary and only questionably identified. The key palaeobiogeographical observation seems

to be that of Janvier and Tong-Dzuy Thanh (1998) that placoderms and sarcopterygians of Silurian age have been recorded only from South China and Indochina, suggesting proximity of the two areas at this time. It is worth noting that the My Duc vertebrate fossils were associated with very common brachiopods (their palaeobiogeographical significance is discussed below) interpreted as indicating Benthic Assemblage (BA) 2 or shallow 3 and thus clearly are from a shallow, fully marine environment (water depth 10–30+ m according to Brett et al., 1993). Whether the fish were living in this marine environment or were in fact “primary division” fishes (= exclusively freshwater taxa; see Young and Janvier, 1999), their remains having been transported presumably from some nearby estuary, is clearly significant in terms of how far these fish could disperse and thus how close South China and the Truong Son Terrane need to be on late Silurian reconstructions. Unfortunately, the environmental distribution of Silurian placoderms and sarcopterygians is not (and probably cannot) be known with certainty (Young and Janvier, 1999).

3.2. Brachiopods from the Truong Son Terrane

As noted above, Tong-Dzuy Thanh et al. (1996a) stated that the marked differences in the invertebrate faunas from the Devonian of north Vietnam (South China) and central Vietnam (Indochina) can be interpreted to indicate some palaeogeographical barrier between South China and Indochina at this time. Janvier et al. (1997, p. 403) provided a useful summary of the differences between the Devonian brachiopod “communities” of the South China and Indochina terranes, noting that these differences become less pronounced after the Early Devonian and non-existent after the Givetian. Tong-Dzuy Thanh et al. (1996b) gave a detailed account of the brachiopod and other shelly faunas of the Devonian of South-East Asia as a whole, emphasizing again the differences between the Indochina and South China Terrane invertebrate faunas, in particular the presence of the “*tonkinensis* fauna” in the latter and its absence from the former. Tong-Dzuy Thanh et al. (1996b) also commented on the very limited similarity (3% of stromatoporoids, 3.8% of brachiopods and 8% of corals) with faunas from Australia and emphasized that South-East Asian Devonian faunas as a whole show the greatest similarity with those from Bohemia (part of peri-Gondwanan Europe).

By contrast, the similarities between the late Silurian brachiopods from Kien An (South China Terrane) and My Duc (Truong Son Terrane, Indochina) in Vietnam indicated to Tong-Dzuy Thanh et al. (2001) that they “were probably fairly close geographically to each other.” This had been stated previously also by Tong-Dzuy Thanh et al. (1997) who noted that the brachiopod fauna from the Dai Giang Formation of My Duc was most similar to that of the Ludlow–Přídolí of the Miaokao Formation of the Qujing area, north-east Yunnan (South China Terrane). Tong-Dzuy Thanh et al. (2001) noted, however, that “Trying to work out the paleogeographic and lithofacies relations of the Chinese and Vietnamese *Retziella* fauna localities is difficult owing to lack of truly compelling data.” The My Duc brachiopod collection described by Tong-Dzuy Thanh et al. (2001) comprised 3203 specimens, with four species (*Retziella weberi*, *Nikiforovaena vietnamensis*, ‘*Howellella*’ *lynxoides* and *Retziella alaica*) making up 98.5% of the specimens. This is a typical assemblage from the biogeographically significant “*Retziella* Fauna” of Rong et al. (1995) that is used to define the “Sino-Australian Province” which included North China, Tarim, South China, Indochina, Eastern Australia and possibly parts of the central Asian tectonic collage in Tadjikistan and Uzbekistan. However, the Tadjik *Retziella* specimens are placed into four other genera by Dzhaliyev (1991, pp. 96–99) and the palaeobiogeographical significance of the Central Asian brachiopods is unclear (Fig. 9).

To summarize, the late Silurian brachiopod faunas of Indochina and South China indicate that both were part of the broad “Sino-Australian

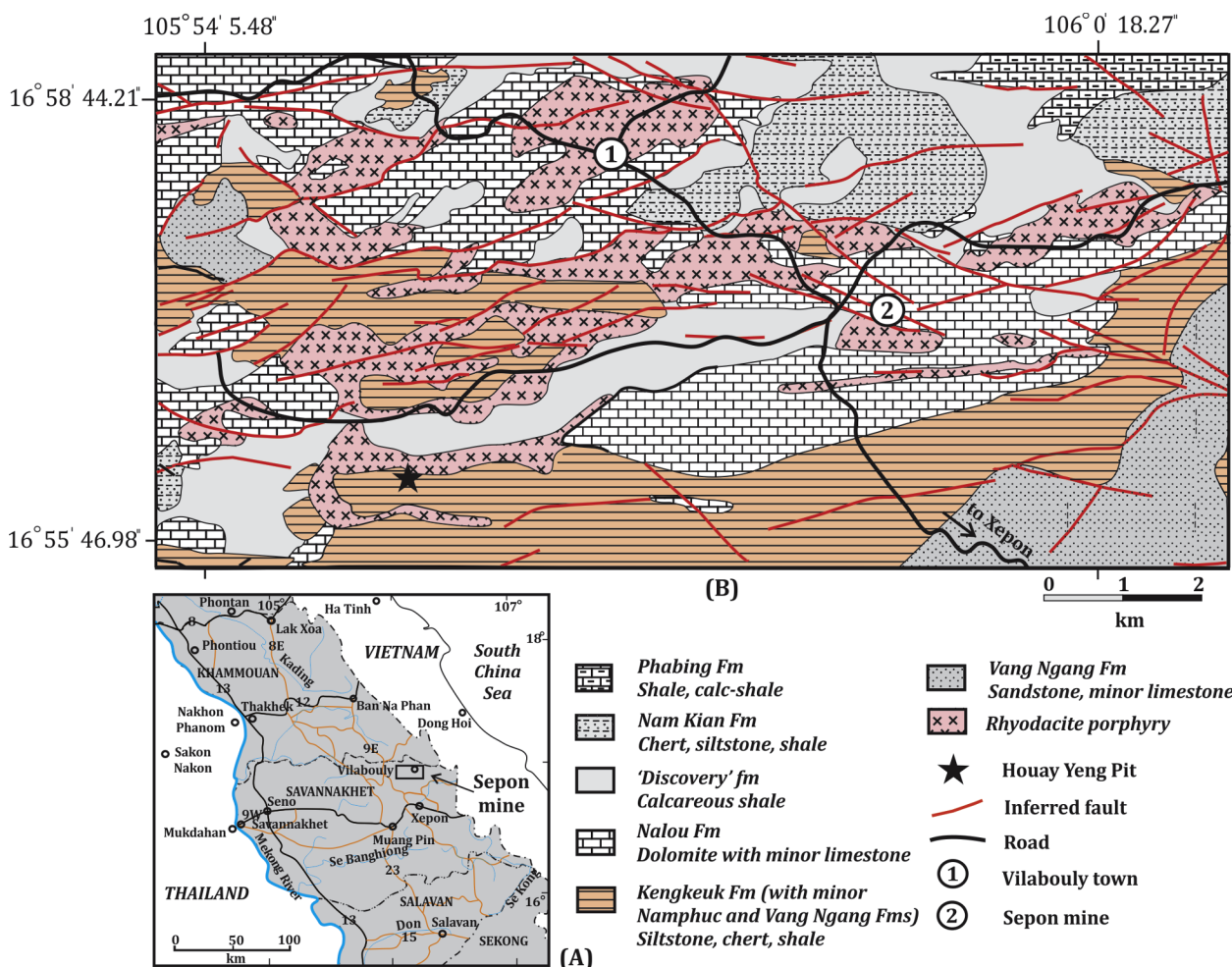


Fig. 3. (A) Road and provincial map of southern central Laos showing area of Sepon Mine next to the town of Vilabouly. (B) Geological map of Sepon Mine region (from Boutathap, 2013, Cannell et al., 2015 and other sources) showing area containing the Houay Yeng Pit. The intrusive Rhyodacite Porphyry (or RDP) is Permian and is thought to be a major source of the copper that is mined. The formations are shown on a geological column in Fig. 4A.

Province”, but provide no greater geographical precision than this, whilst Early Devonian brachiopod faunas are sufficiently different to suggest that Indochina and South China are unlikely to have been in close proximity at this time.

3.3. Tentaculitids from the Truong Son Terrane

Thassanapak et al. (2012) described tentaculitids from the Frasnian of Ban Phonxai, central Laos. Those specimens identified to species level were assigned to *Homoctenus ultimus*, which is widely geographically distributed, and *Costulatostylionina vesca*, previously recorded only from the South China Terrane. The same two tentaculitid species were recorded from Vilabouly, 150 km SE of Ban Phonxai, Laos (Fig. 3) by Udchachon et al. (2017a).

3.4. Radiolarians from the Truong Son Terrane and Loei fold belt

The radiolarians that have been described recently from central Laos and north-east Thailand (Thassanapak et al., 2012, 2018; Udchachon et al., 2017a, 2017b) provide useful biostratigraphical constraints on the strata from which they have been extracted, but the taxa recorded appear to have been geographically widespread and thus do not assist with palaeogeographical reconstructions in terms of palaeolatitude or faunal provincialism. They do, however, provide

extremely important evidence for regional palaeoenvironmental interpretations which have a bearing on the questions of the unity or proximity of the Indochina terranes and South China in the mid Palaeozoic.

Udchachon et al. (2017a) recorded Frasnian radiolarian cherts from Vilabouly area of central Laos (Truong Son Terrane) deposited in “relatively deep marine environments” and in their palaeogeographical reconstruction of the region show the radiolarian-bearing sediments being deposited between an emergent part of Indochina and another small landmass termed Phu Hoat with a marine strait approximately 250 km wide separating Phu Hoat from South China. Udchachon et al. (2017a, p. 155) noted that that during the Frasnian Indochina was “separated from the South China Block and from Gondwana by oceanic lithosphere.”

3.5. Graptolites from the Truong Son Terrane

Graptolitic strata are exposed in many sections within the Truong Son Terrane, most notably in central Vietnam from which Nguyen Van Phuc (2002) recorded many Llandovery graptolite biozones, with generally more sporadic records of Wenlock to Devonian biozones. In the same paper are details also of graptolitic sections from northern Vietnam (South China Terrane). Further lists of graptolites identified from Vietnam are provided by Tong-Dzuy Thanh et al. (2013). Nguyen

Van Phuc (1981) had previously described and illustrated a small number of graptolites from both central and northern Vietnam, but in the absence of more detailed descriptive studies it is not possible to draw any palaeogeographical conclusions.

More recently, Williams et al. (2016a) described a small collection (25 specimens identifiable to genus level) from a single horizon in the Long Dai Formation at Lam Thuy in central Vietnam. In addition to a retiolitid (*Pseudoplegmograptus*) and fragmentary material of *Pristiograptus* and *Monograptus* that could not be identified confidently to species level, *Oktavites spiralis* (Geinitz) and *O. bodentoerlensis* Loydell were identified. The former is extremely widespread and gives its name to the Telychian *spiralis* Biozone whilst the latter was first described from the lower *spiralis* Biozone of Austria (Loydell, 2003) and subsequently from New South Wales, Australia (Rickards et al., 2005) and thus appears also to have been widely distributed.

3.6. Sporomorphs from Yunnan (Indochina)

Wang and Zhang (2010) studied the sporomorphs from Mojiang County (Fig. 1), Yunnan, China and concluded: “Based on the sporomorph evidence, it is probable that the South China and Indo-China palaeoplates could have been in close proximity (maybe with some continental bridges linking them) at least in the Llandovery.” This view was reiterated by Zhang et al. (2014, p. 28). However, as Wang and Zhang (2010) acknowledged, Silurian cryptospore species are cosmopolitan – every one of the seven species recorded by Wang and Zhang (2010) has a very wide distribution, from high southern palaeolatitudes (sites in North Africa and Argentina) through to localities on Laurentia and South China widely accepted to have been at tropical palaeolatitudes. On the basis that it is thought that spores could not be distributed across wide oceans, Steemans and Pereira (2002) concluded that the uniformity of Upper Ordovician and Llandovery sporomorph assemblages could be best explained using palaeogeographical reconstructions with only narrow oceans separating the continents. Thus, all that the sporomorphs are telling us is that the Mojiang area (Indochina) was not widely distant from another (which could be any other) continent.

3.7. Graptolites from Yunnan (Indochina)

Telychian (upper Llandovery) graptolites from Mojiang County were initially illustrated and discussed briefly by Wang and Zhang (2010), then described in detail (with some different identifications from those in Wang and Zhang, 2010) by Zhang et al. (2013), with a few species re-illustrated by Zhang et al. (2014, Fig. 3.12). Two horizons within the Manbo Formation yielded graptolites assigned by Zhang et al. (2013) to the *crenulata* Biozone. The lower horizon (MJ101) yielded a moderately diverse assemblage of retiolitids and monograptids. A new species, *Oktavites kewanensis*, was erected, the illustrated material of which includes specimens (e.g. Figs. 3A and 5A) indistinguishable from *O. bodentoerlensis* Loydell, 2003 and others (e.g. Fig. 3K) that match *O. falx* (Suess), whilst another (Fig. 3C) is much broader than the maximum width (1.3 mm) stated for *O. kewanensis* and appears to be a fragment of *O. spiralis*. It seems likely that the assemblage is of similar age to that described by Williams et al. (2016a) from Vietnam and is from the lower *spiralis* Biozone. The widespread appearance globally of graptolitic strata at this level is a reflection of high sea-levels at this time (Loydell, 1998). It is worth pointing out here also that the specimens identified by Zhang et al. (2013) as *Stimulograptus clintonensis* (Hall) show clear thecal overlap and are not this species, but are *Monograptus parapriodon* Bouček and thus the “biostratigraphical enigma” presented by the Williamson Shale of New York State (Loydell et al., 2007) has not been solved. Also, the specimens attributed to *Retiolites* by Zhang et al. (2013, 2014) lack the parallel-sided rhabdosomes typical of this genus and in several specimens (e.g.

Fig. 9K–N) stomata can be seen indicating that they should be assigned to *Stomatograptus*.

It is difficult to make palaeobiogeographical comparisons of graptolite assemblages from the *spiralis* Biozone for a number of reasons. The *spiralis* Biozone clearly represents a longer period of time than other Telychian biozones (Loydell, 1998) and wherever it has been studied there are significant changes in assemblages between different levels within the biozone (e.g. Spain, Loydell et al., 2009; Wales, Loydell and Cave, 1993; Latvia, Loydell et al., 2003). With the exception of the Corral de Calatrava section, Spain (Loydell et al., 2009), recently published graptolite assemblages from the *spiralis* Biozone occur in thin black shale horizons within otherwise non-graptolitic strata (see e.g. Loydell et al., 2017, Fig. 5) and thus are sampling only very small portions of the biozone as a whole. Deciding upon whether differences in assemblages between localities reflect biogeography and/or palaeoenvironment rather than simply being samples from horizons representing slightly different time intervals within the zone and thus with some different species present (alongside long-ranging and cosmopolitan taxa such as *O. spiralis* and *Monograptus priodon* (Bronn)) therefore can be difficult. Having said this, the Mojiang graptolite assemblage is different from that from the continuously graptolitic lower *spiralis* Biozone in Corral de Calatrava, Spain (Loydell et al., 2009), part of peri-Gondwanan Europe, lacking for example the genera *Euroclimacis* and *Retiolites*. Interestingly, the common retiolitid specimens from Mojiang appear very similar indeed to *Stomatograptus canadensis* Lenz (see Lenz and Kozłowska, 2007, Fig. 4), a species recorded only from the Northwest Territories, Canada (Lenz, 1988) and from Arctic Canada (Lenz and Melchin, 1987; Lenz and Kozłowska, 2007) and thus only from Silurian equatorial regions. Nothing comparable was recorded by Bouček and Münch (1943) in their review of retiolitids from central (=peri-Gondwanan) Europe or has been encountered there since.

Zhang and Lenz (1997) described upper Wenlock–Ludlow graptolites (from the *praedeubeli-leintwardinensis* biozones [note that *Saetograptus fritschii linearis* (Bouček) as recorded by Zhang and Lenz is a junior synonym of *S. leintwardinensis*; Štorch et al., 2014]) from Mojiang County, Yunnan (Indochina Terrane). Graptolite faunas at this time were considered to show little provincialism and the authors observed that the sequence studied correlated well with those in northern Canada, Britain and the Czech Republic, the only noteworthy absentees from Yunnan being *Neodiversograptus nilssoni* (Lapworth) and *Monograptus* [now *Uncinograptus*] *uncinatus* (Tullberg). These absences perhaps take on greater significance when it is noted that these species are distinctive components of lower Ludlow graptolite assemblages from Great Britain, Bohemia and Poland but are absent also from Arctic Canada (Lenz and Kozłowska-Dawidziuk, 2004), which had an equatorial location at this time.

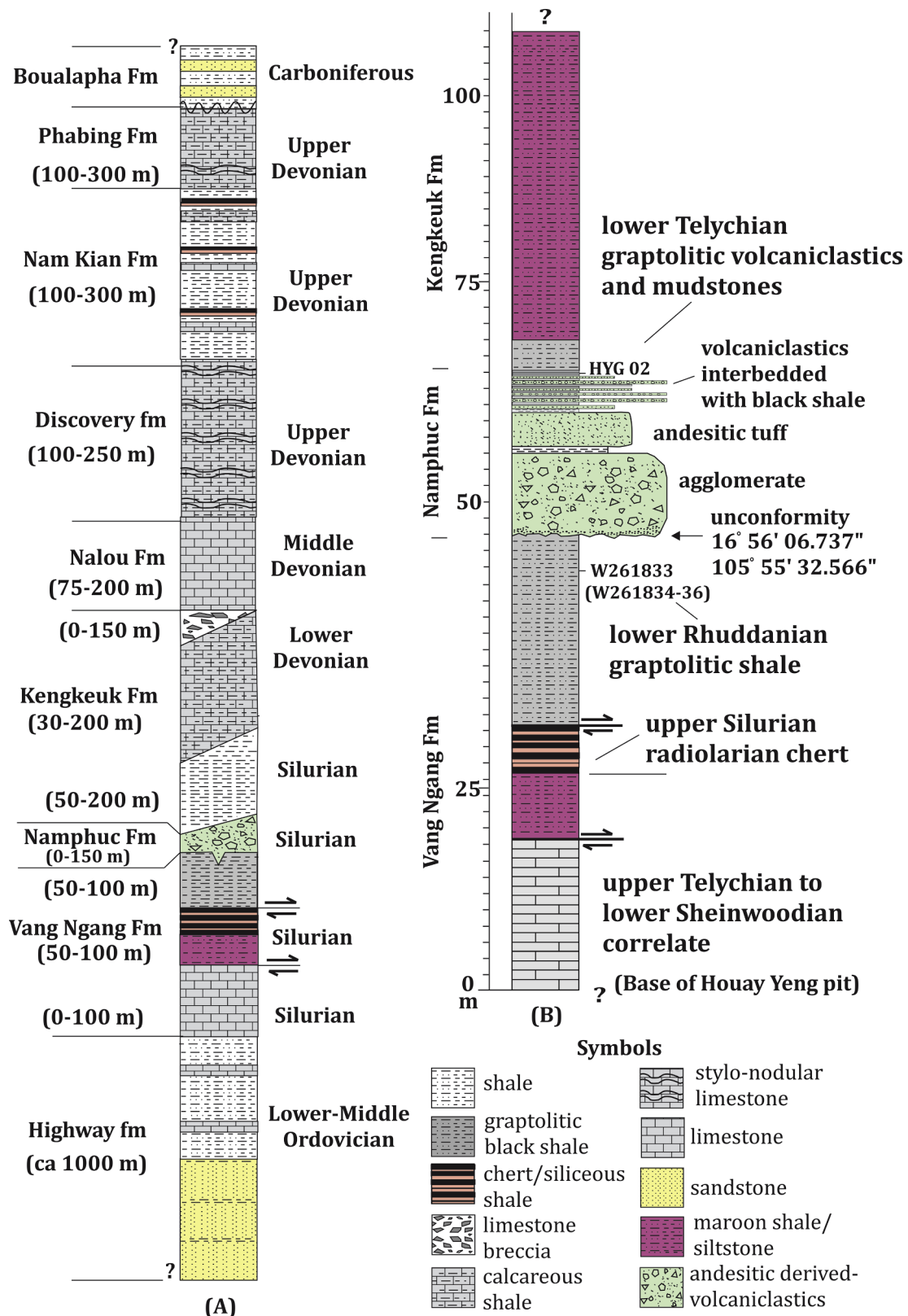
3.8. Palaeobiogeographical conclusions based upon published work

It is difficult to draw firm conclusions from the published palaeobiogeographical data. Similarities between the vertebrate faunas from the Devonian of South China and the Truong Son Terrane suggest that these two continental blocks may have been close to each other or were connected. Prior to this time there is no palaeobiogeographical evidence for the two necessarily being particularly close to each other and at times in the Devonian differences in the fossil assemblages (particularly brachiopods) and the palaeoenvironmental significance of the fossils themselves (especially the radiolarians) suggests that a palaeogeographical barrier existed between South China and the Truong Son Terrane.

With regard to the palaeobiogeographical significance of the Llandovery graptolite assemblages from Laos described and discussed below, the Givetian (the age of the vertebrates from the Truong Son Terrane which have been considered to have South China affinities)

commenced at least 55 million years after the early Rhuddanian and 45 million years after the early Telychian (based upon the latest ICS timescale), allowing time for significant plate movement (perhaps 2000–3000 km based upon current rates) between these two time intervals (Llandovery and Givetian). There is therefore no reason based

upon published fossil occurrence data as to why Llandovery graptolites from the Truong Son Terrane should be similar to those of South China (or other Silurian low latitude locations), unless of course the two continental blocks were indeed in close proximity at this time.



(caption on next page)

Fig. 4. (A) Generalized stratigraphical column for the Sepon Mine area shown on Fig. 2. Formation names were established by company geologists who used informal names for the ‘Highway’ and ‘Discovery’ formations. We therefore show these with a lower case initial f for formation. The formations in the area range from the Early Ordovician and possibly older, ‘Highway’ formation through to the Late Devonian to Tournaisian Phabing Formation. The siliciclastics of the Viséan or younger Boulapha Formation are regionally extensive and unconformable on the older succession and are overlain by Pennsylvanian to Permian carbonates (compiled from Cannell et al., 2015 and other sources). (B) Stratigraphy and lithologies of the 100 m of strata exposed in the Houay Yeng Pit. GPS reading on unconformity shown. The Vang Ngang Formation consists of three units, limestone, chert and graptolitic shale, which were assumed to be conformable. However, as they have thrust contacts and have different ages within the Silurian (with younger Silurian strata beneath older), this formation needs to be revised. Sample W261833 was collected from black shales of the upper Vang Ngang Formation in Houay Yeng Pit as shown. Sample HYG02 was collected from the upper volcanoclastics of the Namphuc Formation in the Houay Yeng Pit as shown. Samples W261834–261836 were collected in a small road-metal quarry 1.1 km from the Houay Yeng Pit and their approximate positions within the main Houay Yeng Pit stratigraphy are indicated in brackets.

4. Locality information

Graptolite specimens were collected from the upper Vang Ngang Formation and the uppermost Namphuc Formation of the Sepon Mine area in central Laos (Figs. 2–5). The geological setting and stratigraphy of the Sepon Mine area have been summarized by Cannell et al. (2015) and Thassanapak et al. (2018). Nine Palaeozoic formations have been mapped in the Sepon Mine area (Fig. 4) two of which are informally named (‘Highway’ and ‘Discovery’ formations). Because of the recent discovery of structural complexity (Figs. 4 and 5E), the Vang Ngang Formation is also in need of revision.

The oldest formation at the Sepon Mine is the approximately 1000 m thick, ‘Highway’ formation which consists of Lower to Upper Ordovician unfossiliferous siliciclastics with a few thin, peritidal limestone lenses and beds containing Lower and Upper Ordovician conodont faunas. The overlying Vang Ngang Formation consists of three unnamed members which were originally thought to be conformable. The 0–100 m thick lower member consists of limestones that from one drill-core have yielded the conodont *Pterospiriferus amorphognathoides* (S. Ekins, unpublished Honours thesis, University of Tasmania 2005) which ranges from the upper Telychian to lower Sheinwoodian. A micro-unfossiliferous correlate of this limestone member is faulted against red shales (10 m) and cherts and siliceous shales (4.5 m) of the second member. The cherts have yielded a Ludlow–Přídolí age radiolarian assemblage (Thassanapak et al., 2018). 24 m of pyritic, black shales are faulted against the radiolarian chert and yield the lower Silurian graptolites discussed herein. The chert and graptolitic shales are exposed in the main Houay Yeng Pit (Figs. 4 and 5A–D), incorrectly named the Hoi Yang pit in Thassanapak et al. (2018), and in a nearby road metal quarry (Fig. 5E). The thrust fault separating the chert and graptolitic shale is clearly seen in the small quarry (Fig. 5E). The overlying, mainly agglomeratic and tuffaceous, Namphuc Formation has a low angle (about 5°) unconformable contact with the graptolitic shale and contains deformed clasts of the graptolitic shale suggesting that the lower part of the Namphuc Formation was deposited rapidly and eroded the underlying graptolitic muds whilst they were still soft. The coarse volcanic clasts, pronounced lateral variations in thickness and sedimentology of the Namphuc Formation suggest deposition within a submarine fan close to an active volcanic arc. Andesite, diorite and dacite clasts are dated within a range from 439 ± 2 Ma to 433 ± 3.5 Ma (Smith, 2009), equating to the Aeronian–Telychian according to the latest ICS timescale. The percentage of volcanic material in the Namphuc Formation increases towards the east (Smith, 2009) where it merges with the Long Dai volcanic arc of eastern Laos and central Vietnam (Thassanapak et al., 2018). The grain size of the Namphuc Formation generally decreases upwards within the Houay Yeng Pit and thin tuffaceous beds are interbedded with graptolite-bearing siltstones and mudstones in the upper 5 m of the formation. In the Houay Yeng Pit, the conformably overlying, Kengkeuk Formation (30–200 m thick) consists of red to grey shales and siltstones (Fig. 5C) containing rare proetid trilobites. Elsewhere in the mine area monograptids are found, sometimes with *Aulacopleura* sp., other proetids and hyolithids. Succeeding formations (Fig. 4) are fossiliferous and range from the Middle Devonian to Viséan. They are summarized in Cannell et al. (2015) and Thassanapak et al. (2018). Sample W261838 was

collected from the upper Vang Ngang Formation in the Houay Yeng gold pit and samples W 261834–261836 from the same formation in the small road metal quarry 1.1 km to the east at 16° 55′ 43.63″ N, 105° 56′ 21.65″ E. Sample HYG 02 was collected from tuffaceous siltstones in the uppermost Nam Phuc Formation in the main Houay Yeng Pit.

5. Graptolites from the Sepon Mine area and their biostratigraphical significance

Graptolites were collected from the Vang Ngang and Namphuc formations. The species present and their biostratigraphical significance are discussed below. This is followed by a discussion of their biogeographical affinities. Figured specimens are housed in the Palaeontological Research Centre at Mahasarakham University, Thailand.

5.1. Vang Ngang Formation

The abundant and diverse graptolites in the assemblage from sample W261836 (small road metal quarry, Fig. 5E) are from rusty weathering, hard, dark grey to black mudstones. All graptolites are diagenetically flattened. The *ascensus-acuminatus* Biozone index species, *Akidograptus ascensus* Davies (Fig. 7L) and *Parakidograptus acuminatus* (Nicholson) (Fig. 7A) are both rare and represented by specimens lacking or with poorly preserved proximal ends. Other taxa present include the stratigraphically long-ranging *Normalograptus angustus* (Perner) (Fig. 7B and C), which is common, and *N. medius* (Törnquist) (Fig. 7N). *Normalograptus rhizinus* (Li and Yang) (Fig. 6A) with its distinctive, apparently spatulate virgella is represented by a single specimen as is *Neodiplograptus bifurcus* (NIGP) (Fig. 6B), the virgella of which bifurcates 4 mm from the sicular aperture. Obliquely preserved and scalariform specimens with virgellar bifurcation much closer to the sicular aperture (Fig. 6D) are assigned to *Neo. bicaudatus* (Chen and Lin). *Neodiplograptus lanceolatus* Štorch and Serpagli (Fig. 7I) is the only other identifiable *Neodiplograptus* species. There is one species of *Sudburigraptus* present, *S. cortoghianensis* (Štorch and Serpagli) (Fig. 7O), and two *Korenograptus* species: *K. illustris* (Koren’ and Mikhaylova) (Fig. 7H) and *K. sp.* (previously *Sudburigraptus sp.*) of Loydell (2007a) (Fig. 7E). *Glyptograptus dufkai* Štorch (Fig. 6C) is uncommon; also present are very narrow rhabdosomes, assigned here to *G. sp.* (Fig. 7M). The assemblage can be confidently assigned to the lower part of the *ascensus-acuminatus* Biozone as defined by Štorch et al. (in press).

The graptolites from sample W261835 (Fig. 4) are in rusty weathering medium grey to black mudstones. The low diversity assemblage of diagenetically flattened graptolites comprises *Cystograptus vesiculosus* (Nicholson) (Fig. 7K), *Normalograptus mirnyensis* (Obut and Sobolevskaya) (Fig. 7F), *N. rectangularis* (McCoy) (Fig. 7D) and *Parakidograptus acuminatus* (Fig. 7G and J), with specimens of this species on the same bedding surface as *Cy. vesiculosus*. The stratigraphical range of *Pa. acuminatus* extends no higher than the lowermost part of the *vesiculosus* Biozone (Štorch, 1983) thus providing a very precise age for this horizon. Štorch (1983) and Loydell (2007a) noted a reduction in sicular length in *Pa. acuminatus* in stratigraphically younger specimens. The Laotian material is consistent with this trend, with siculae 1.8–2.25 mm long in the four specimens with well-preserved proximal ends. An

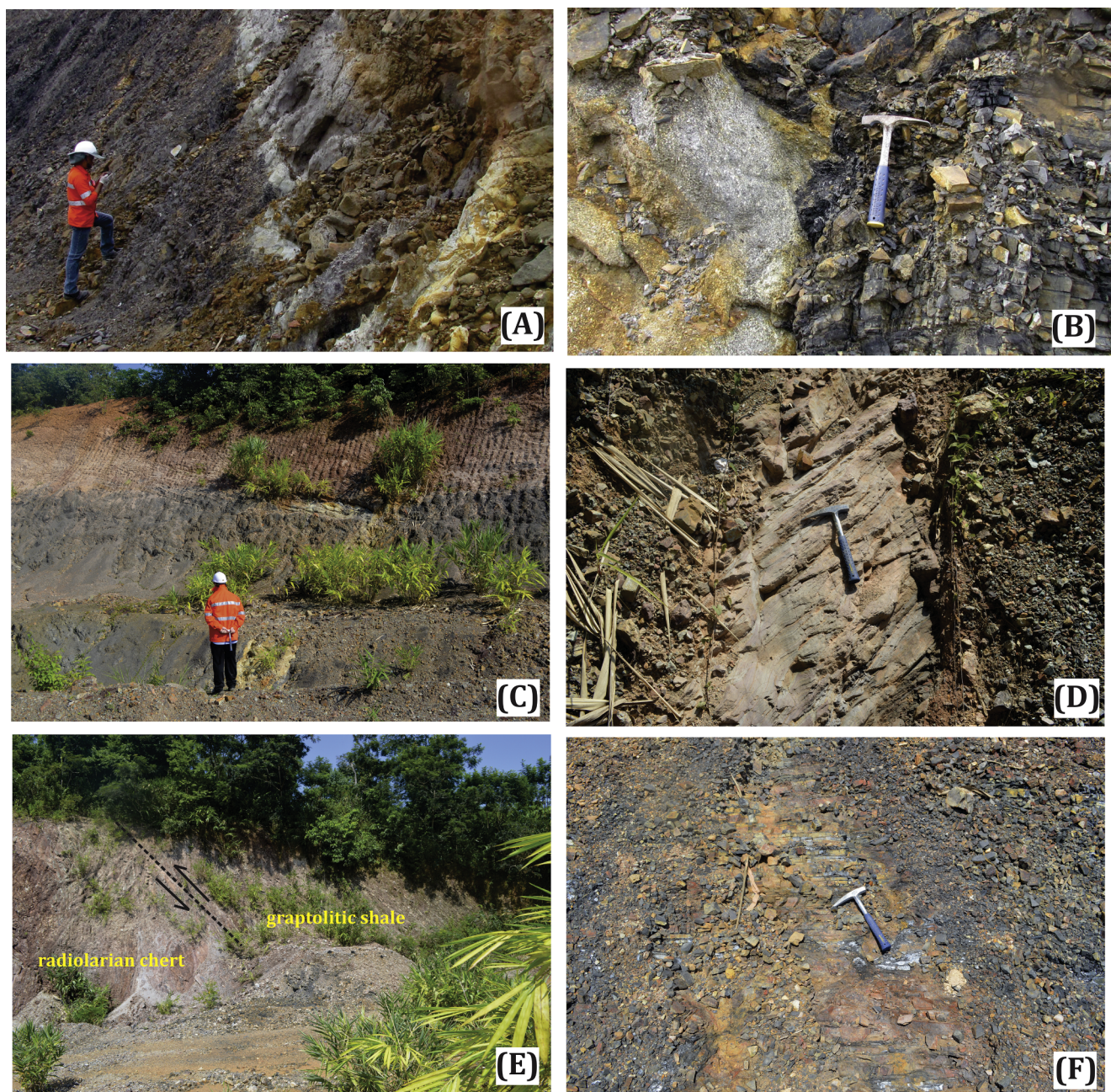


Fig. 5. Photographs of outcrops in The Houay Yeng Pit (A–D, F) and nearby, small road-metal quarry (E). A. Black graptolitic shale (lower Rhuddanian) of the Vang Ngang Formation overlain, with slight unconformity (on right), by the conglomeratic/agglomeratic/tuffaceous Namphuc Formation. (B) Contact between the lower Namphuc Formation (on left) and black shales of the Vang Ngang Formation. Houay Yeng Pit. (C) View of Houay Yeng showing weathered, light coloured, probably Permian, igneous dyke (just to right of figure) cutting gently dipping (about 6° to the right), black and red shales of the Kengkeuk Formation. (D) Upper part of Namphuc Formation, Houay Yeng Pit. Note cleavage in volcanoclastics at about 80° to bedding. (E) Lower Rhuddanian graptolitic shale of the upper Vang Ngang Formation thrust over upper Silurian radiolarian chert of the 'lower' Vang Ngang Formation in the small road-metal quarry at 16° 55' 43.63" N, 105° 56' 21.65" E, 1.1 km east of the Houay Yeng Pit (Thassanapak et al., 2018). Strike of strata is 160° and dip 60°. Thrust fault strikes 002° and dips 70°. Samples W261833, W261834 and W261836 were collected from this small quarry. Their approximate position on the main Houay Yeng Pit stratigraphy is shown in Fig. 4B. (F) Vang Ngang Formation in Houay Yeng Pit. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

unusual feature of the Laotian specimens is the narrowness of the rhabdosomes (they do not exceed 1 mm in width); the stratigraphically highest specimens illustrated by Štorch (1983) were much more robust.

5.2. Namphuc Formation

Graptolites were generally not common in the interbedded mudstones and tuffs of sample HYG 02 (Figs. 4 and 5D), with the exception of a single bedding plane yielding numerous specimens (although no

proximal ends) of *Streptograptus pericoi* Štorch (Fig. 8A). Preservation is highly variable, including both diagenetically flattened and low relief specimens, presumably originally pyrite, but now weathered to iron oxides/hydroxides. Other graptolites present include a *Glyptograptus* proximal end, *Pristiograptus bjerringus* (Bjerreskov) (Fig. 8D), *P. variabilis* (Perner) (Fig. 8B), *Rastrites* fragments, a *Spirograptus* proximal fragment and a single specimen of *Torquigraptus obtusus* (Schauer) (Fig. 8C). This assemblage indicates a level in the upper *guerichi* Biozone (lower Telychian).

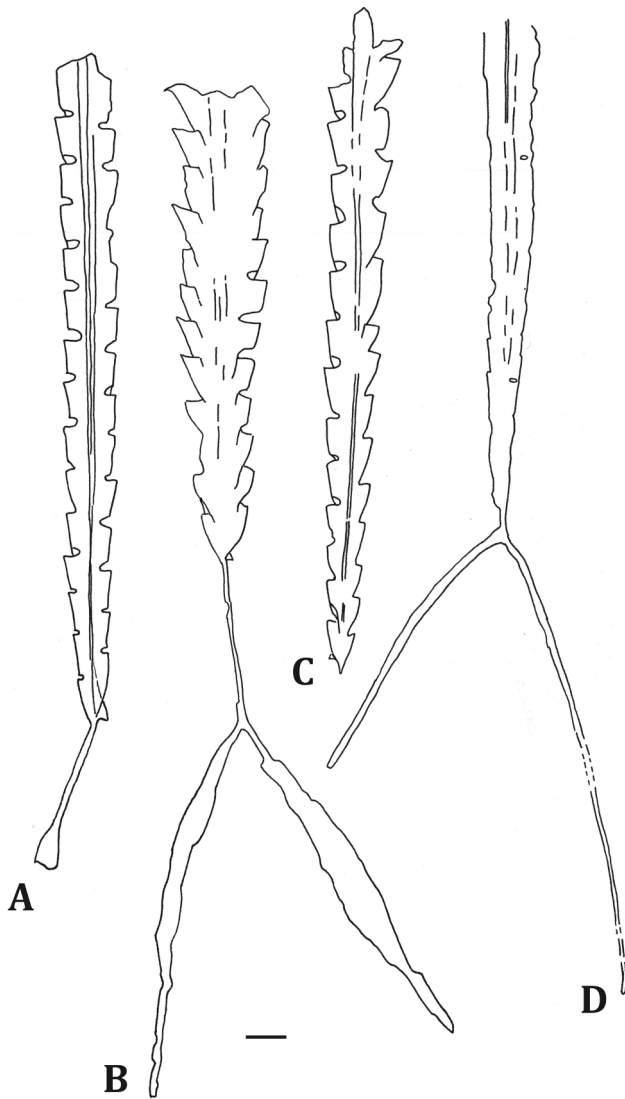


Fig. 6. Graptolites from the *ascensus-acuminatus* Biozone (Rhuddanian), Vang Ngang Formation, small road-metal quarry 1.1 km east of the Houay Yeng Pit (sample W261836, Fig. 4B). (A) *Normalograptus rhizinus* (Li and Yang), PRC530. (B) *Neodiplograptus bifurcus* (NIGP), PRC531. (C) *Glyptograptus dufkai* Štorch, PRC532; note that similarly geniculate mesial thecae, not apparent in the holotype, are illustrated by Štorch et al. (in press, Fig. 7s). (D) *Neodiplograptus bicaudatus* (Chen and Lin), PRC533. Scale bar represents 1 mm.

5.3. Palaeogeographical significance of the graptolites

During the Silurian the planktic graptolites exhibit varying degrees of faunal provincialism: at certain times (e.g. mid Sheinwoodian; Lenz et al., 2012) very different taxa characterized low latitude and higher latitude faunas, whereas at others (e.g. mid Homerian) provincialism appears to have been considerably less pronounced, perhaps reflecting a predominance of eurythermal taxa. For the Llandovery, Melchin (1989) recognised that certain taxa (e.g. *Paramonoclimacis*, *Agetograptus*, *Cyrtograptus sakmaricus* Koren') characterized low latitude assemblages, whilst Legrand (e.g. 2003) erected a new, local biozonation for the Rhuddanian of North Africa because of the endemism of most of the biserial graptolites of this age in the Algerian sections that he studied. Goldman et al. (2013) provide a brief review of other papers on Silurian graptolite provincialism, noting that distribution patterns indicate "faunal differentiation along roughly palaeolatitudinally

distributed belts." For the Late Ordovician Vandenbroucke et al. (2009) had similarly identified latitudinally distributed graptolite biotopes reflecting temperature-controlled climate zones. Thus, as emphasized by Vandenbroucke et al. (2009), the distribution of planktic graptolites was influenced by similar controls to those affecting modern planktic foraminifera, the most important being sea surface temperature (SST).

Inevitably, Silurian SSTs would have been affected by the disposition of the continents and deflections of warm currents polewards and cold currents equatorwards, thus extending locally the latitudinal ranges of stenothermic species. Melchin (2007 and pers. comm.), for example, noted that Llandovery graptolite assemblages from Arisaig, Nova Scotia had peri-Gondwanan affinities which he attributed to Arisaig being on the southern, Rheic margin of Avalonia, facing Gondwana, whereas Wales and England (also Avalonia) had more Iapetus-related faunas. It is of course possible that the composition of the Truong Son graptolite assemblage has a similar cause, with the area lying at a lower palaeolatitude than we show (Fig. 9) and being influenced by currents flowing northwards from Gondwana. It is also very important to recognise that the Silurian was an interval of major climatic fluctuations (reflected in global sea-level curves and the carbon isotope record; e.g. Loydell, 1998, 2007b; Cramer et al., 2011) and thus the latitudinal extent of any biogeographical provinces and presumably also the direction and strength of ocean currents will have varied through time.

Many of the species identified in the Laotian samples are very widely distributed and thus of limited palaeogeographical significance. These include the species with modified virgellae (*Normalograptus rhizinus*, *Neodiplograptus bifurcus* and *Neo. bicaudatus*) originally described from China and until recently appearing to be confined to Silurian low latitudes. Following the discovery of *Neo. bifurcus* in the Southern Alps of Austria (Štorch and Schönlaub, 2012), Štorch et al. (in press) have identified all three species listed above in the eastern Pyrenees of Spain, a locality that was on the northern margin of Gondwana during the Late Ordovician–early Silurian (Robardet and Gutiérrez-Marco, 2002; Margalef et al., 2016).

Those species in the Laotian graptolite assemblages that do have a restricted geographical distribution are known only from mid- to high-latitude peri-Gondwanan and/or Gondwanan localities. *Glyptograptus dufkai* has been recorded previously from the Czech Republic (Štorch, 1992) and Spain (Štorch et al., in press), and *Sudburigraptus cortoghianensis* from Sardinia (Štorch and Serpagli, 1993), Jordan (Loydell, 2007a), the Montagne Noire, France (Štorch and Feist, 2008) and Saudi Arabia (Williams et al., 2016a, 2016b). *Streptograptus pericoi*, from the Namphuc Formation is also a typical (peri-) Gondwanan species, recorded from localities in Spain (Štorch, 1998; Loydell et al., 2015).

Species that would be expected to occur in the diverse *ascensus-acuminatus* Biozone assemblage in sample W261836 if the Truong Son Terrane had been at a low palaeolatitude include *Hirsutograptus jidei-liensis* (Koren' and Mikhailova), *Korenograptus lacinosus* (Churkin and Carter) and *K. jerini* (Koren' and Melchin). All are recorded from the Tarim region, Xinjiang, China (Wang et al., 2015) and Zhejiang Province (Yangtze Platform), South China (Chen et al., 2007) with at least one of the three recorded in *ascensus-acuminatus* Biozone assemblages from Kazakhstan (Koren' et al., 1980), Uzbekistan (Koren' and Melchin, 2000), Alaska (Churkin and Carter, 1970) and Arctic Canada (Melchin et al., 2011). Thus, based upon the absence of these taxa and presence of typical (peri-) Gondwanan taxa in the Laotian assemblages an early Silurian location for the Truong Son Terrane close to Gondwana, but not to South China, and at a mid or high palaeolatitude seems most likely (Fig. 9).

6. Conclusions

Much remains to be done in terms of biostratigraphical,

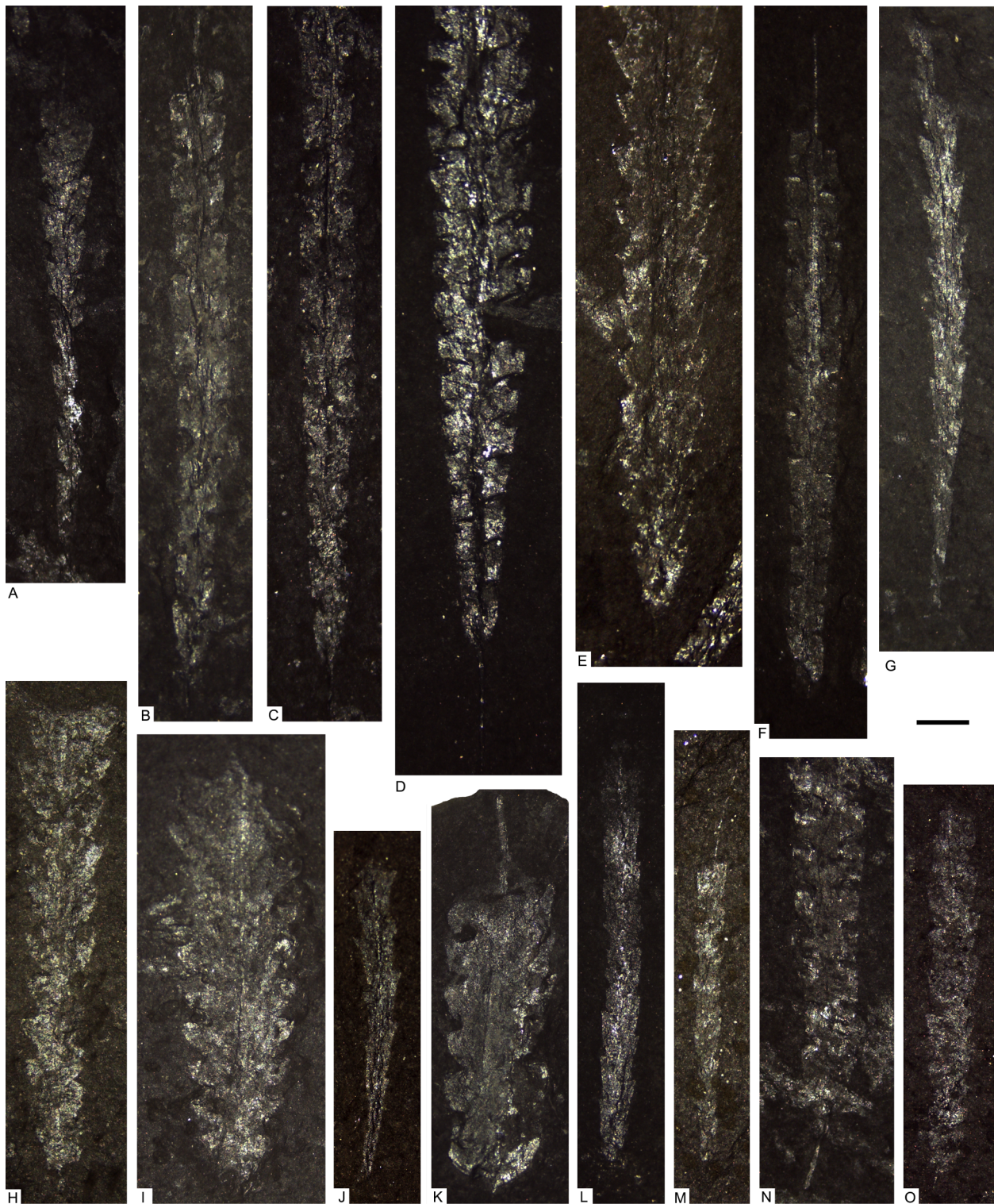


Fig. 7. Graptolites from the Rhuddanian *ascensus-acuminatus* and lowermost *vesiculosus* biozones (Rhuddanian), Vang Ngang Formation, small road-metal quarry 1.1 km east of the Houay Yeng Pit. (A, G, J) *Parakidograptus acuminatus* (Nicholson), PRC534, PRC535, PRC536. (B, C) *Normalograptus angustus* (Perner), PRC537, PRC538. (D) *Normalograptus rectangularis* (McCoy), PRC539. (E) *Korenograptus* sp. (= *Sudburigraptus* sp. of Loydell, 2007a), PRC540. (F) *Normalograptus mirmyensis* (Obut and Sobolevskaya), PRC541. (H) *Korenograptus illustris* (Koren' and Mikhaylova), PRC542. (I) *Neodiplograptus lanceolatus* Štorch and Serpagli, PRC543. (K) *Cystograptus vesiculosus* (Nicholson), PRC544; note the long sicula and slightly everted thecal apertures which distinguish proximal ends of this species from *Cy. ancestralis* Štorch which has horizontal to slightly introverted thecal apertures and a shorter sicula. (L) *Akidograptus ascensus* Davies, PRC545. (M) *Glyptograptus* sp., PRC546. (N) *Normalograptus medius* (Törnquist), PRC547; note the deep thecal apertural excavations. (O) *Sudburigraptus cortoghianensis* (Štorch and Serpagli), PRC548; no median septum is present, the nema distally showing an irregular course and no visible septum pressed through the rhabdosome (this is true of other specimens in our collection also), indicating assignment to *Sudburigraptus* rather than *Korenograptus* (which is septate and includes an undescribed species (M. Melchin pers. comm.) of similar dimensions to *S. cortoghianensis*, although this has wider thecal apertures and thus a more conspicuously serrated outline). A–C, E, H, I, L–O, from sample W261836 (Fig. 4), *ascensus-acuminatus* Biozone; D, F, G, J, K from sample W261835 (Fig. 4), *vesiculosus* Biozone. Scale bar represents 1 mm.

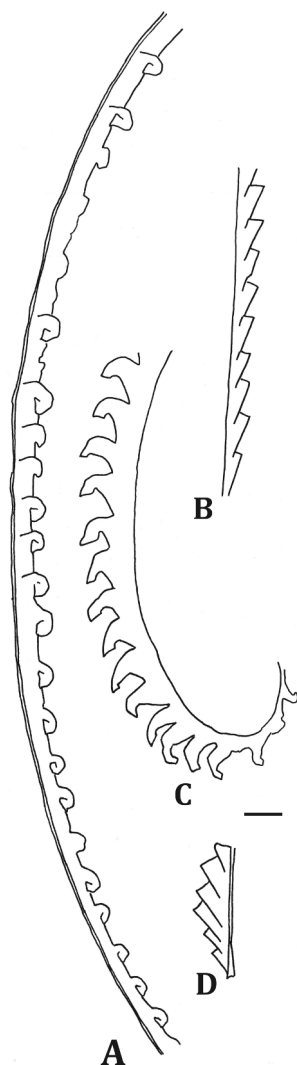


Fig. 8. Graptolites from the *guerichi* Biozone (Telychian), upper Namphuc Formation, Houay Yeng Pit (sample HYG 02, Fig. 4B). (A) *Streptograptus pericoi* Štorch, PRC549; the specimen is very similar to the holotype of this species (as are others in the Laotian material); the only similar *Streptograptus* species from the *guerichi* Biozone is *S. plumosus* (Baily), but this has more prominent metathecae. (B) *Pristiograptus variabilis* (Perner), PRC550; note the thin rhabdosome and limited thecal overlap that characterize this species. (C) *Torquigraptus obtusus* (Schauer), PRC608. (D) *Pristiograptus bjerringus* (Bjerrreskov), PRC551; note the rapid increase in dorso-ventral width, typical of this species. Scale bar represents 1 mm.

palaeoenvironmental and palaeobiogeographical studies of the fossils of the Indochina terranes and hopefully further studies will clarify the Palaeozoic palaeogeography of the region. Based upon published studies and examination herein of graptolites from the Sepon mine area (Truong Son Terrane), we conclude that the Truong Son Terrane during the Llandovery lay at a mid to high latitude and closer to peri-Gondwanan Europe and Arabia than it did to South China (Fig. 9). This position is supported by the independent studies of detrital zircons from the Truong Son Terrane by Uzuki et al., (2013) and Burrett et al. (2014). The graptolite assemblages from the Mojiang area, Yunnan, however, suggest that it was at a low palaeolatitude during the Silurian and thus this area (sometimes referred to as the Simao Terrane/block/subterrane; herein tentatively assigned to a northern extension of the Loei Terrane; Fig. 1) may well have been separate from the Truong Son Terrane at this time.

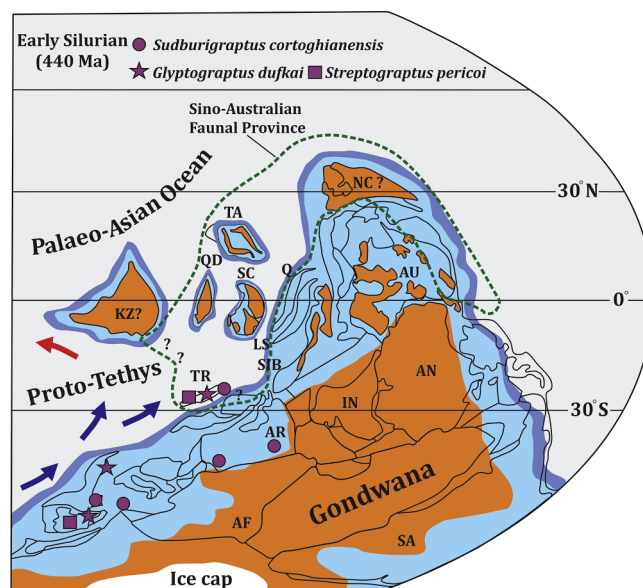


Fig. 9. Palaeogeographical reconstruction of the early Silurian (adapted from Huang et al., 2018) showing a suggested position of the Truong Son Terrane close to the Middle East sector of Gondwana in the Llandovery. Postulated cold to cool ocean currents (blue arrows) flowing northwards from the polar regions (Chen et al., 2017) would have transferred southern European - Middle eastern graptolite species along the margin of Gondwana. A warm equatorial current (red arrow) would have directed graptolites towards the west and towards northern European terranes. The palaeoequatorial position of South China for the Wenlock is controlled by palaeomagnetic data ($7^\circ \pm 6^\circ$) in either the northern or southern palaeohemispheres (Opdyke et al., 1987). The Silurian palaeoposition of North China has no reliable palaeomagnetic control. AF = Africa, AN = Antarctica, AR = Arabia, AU = Australia, I = India, KZ = Kazakhstan, LS = Lhasa Terrane, NC = North China, Q = Qiangtang Terrane, QD = Qaidam Terrane, SA = South America, SC = South China Terrane, SIB = Sibumasu (or Shan-Thai) Terrane, TA = Tarim, TR = Truong Son Terrane. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jseas.2018.11.013>.

References

- Agematsu, S., Sashida, K., Ibrahim, A.B., 2008. Biostratigraphy and paleobiogeography of Middle and Late Ordovician conodonts from the Langkawi Islands, northwestern peninsular Malaysia. *J. Paleontol.* 82, 957–973.
- Bouček, B., Münch, A., 1943. Die Retioliten des mittel-europäischen Llandovery und unteren Wenlock. *Mitteilungen der Tschechischen Akademie der Wissenschaft* 53 (41), 1–58.
- Bouttathep, B., 2013. Geology of the Sepon copper and gold deposits, Laos. In:

- Senebottalath, C., Roibang, P. (Eds.), Proceedings of 2nd Lao–Thai Technical Conference on Geology and Mineral Resources. Department of Geology and Minerals, Vientiane, Lao PDR, pp. 164–187.
- Brett, C.E., Boucot, A.J., Jones, B., 1993. Absolute depths of Silurian benthic assemblages. *Lethaia* 26, 25–40.
- Burrett, C., Khin Zaw, Meffre, S., Lai, C.K., Khositanont, S., Chaodumrong, P., Udchachon, M., Ekins, S., Halpin, J., 2014. The configuration of Greater Gondwana – evidence from LA ICPMS, U–Pb geochronology of detrital zircons from the Palaeozoic and Mesozoic of Southeast Asia and China. *Gondwana Res.* 26, 31–51.
- Cannell, J., Stewart, J., Williams, P., Wallace, M., Burrett, C., Davis, B., 2015. The Sepon copper deposits (Laos) and their relation to Carlin-like gold mineralisation. In: Proceedings of the PACRIM Congress 2015. Australian Institute of Mining and Metallurgy, Hong Kong, pp. 1–10.
- Chen, X., Zhang, Y., Yu, G., Liu, X., 2007. Latest Ordovician and earliest Silurian graptolites from northwestern Zhejiang, China. *Acta Palaeontol. Sin.* 46 (Suppl.), 77–82.
- Chen, Z., Männik, P., Fan, J., 2017. Llandovery (Silurian) conodont provincialism: an update based on quantitative analysis. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 485, 661–672.
- Churkin, M., Carter, C., 1970. Early Silurian graptolites from southeastern Alaska and their correlation with graptolitic sequences in North America and the Arctic. United States Geological Survey Professional Paper 653, pp. 1–51.
- Cocks, L.R.M., Torsvik, T.H., 2013. The dynamic evolution of the Palaeozoic geography of eastern Asia. *Earth-Science Rev.* 117, 40–79.
- Cramer, B.D., Brett, C.E., Melchin, M.J., Männik, P., Kleffner, M.A., McLaughlin, P.I., Loydell, D.K., Munnecke, A., Jeppsson, L., Corradini, C., Brunton, F.R., Saltzman, M.R., 2011. Revised correlation of Silurian provincial series of North America with global and regional chronostratigraphic units and $\delta^{13}\text{C}_{\text{carb}}$ chemostratigraphy. *Lethaia* 44, 185–202.
- Dzhailov, M., 1991. Atlas iskopaemoi fauni i flori Tadshikistana, Ordovik. Silur. Devon. Akademiya Nauk Tadshikskoi SSR, Institut Geologii, Dunshabe, 272 pp. (in Russian).
- Goldman, D., Maletz, J., Melchin, M.J., Fan, J., 2013. Graptolite palaeobiogeography. In: Harper, D.A.T., Servais, T. (Eds.), Early Palaeozoic Biogeography and Palaeogeography. Geological Society, London, Memoirs 38, pp. 415–428.
- Huang, H., He, D., Li, Y., Li, J., Zhang, L., 2018. Silurian tectonic-sedimentary setting and basin evolution in the Sichuan area, southwest China: implications for palaeogeographic reconstructions. *Mar. Petrol. Geol.* 92, 403–423.
- Janvier, P., Thanh, Tong-Dzuy, 1998. The Silurian and Devonian vertebrates of Việt Nam: a review. *J. Geol. (Geol. Survey of Vietnam), Series B* 11 (12), 18–28.
- Janvier, P., Thanh, Tong-Dzuy, Phuong, Ta Hoa, Truong, Doan Nhat, 1997. The Devonian vertebrates (Placodermi, Sarcopterygii) from Central Vietnam and their bearing on the Devonian palaeogeography of Southeast Asia. *J. Asian Earth Sci.* 15, 393–406.
- Khin Zaw, Meffre, S., Lai, C.K., Burrett, C., Santosh, M., Graham, I., Manaka, T., Salam, A., Kamvong, T., Cromie, P., 2014. Tectonics and metallogeny of mainland Southeast Asia – a review and contribution. *Gondwana Res.* 26, 5–30.
- Koren, T.N., Melchin, M.J., 2000. Lowermost Silurian graptolites from the Kurama Range, eastern Uzbekistan. *J. Paleontol.* 74, 1093–1113.
- Koren, T.N., Mikhaylova, N.F., Tzai, D.T., 1980. Class Graptolithina (graptolites). In: Apollonov, M.K., Nikitin, I.F., Bandaletov, S.M. (Eds.), The Ordovician–Silurian Boundary in Kazakhstan. Nauka Kazakh SSR, Alma-Ata, pp. 121–170.
- Lai, C., Meffre, S., Crawford, A.J., Zaw, Khin, Xue, C., Halpin, J.A., 2014. The Western Ailaoshan Volcanic Belts and their SE Asia connection: a new tectonic model for the Eastern Indochina block. *Gondwana Res.* 26, 52–74.
- Legrand, P., 2003. Silurian stratigraphy and paleogeography of the northern African margin of Gondwana. *New York State Museum Bull.* 493, 59–104.
- Lenz, A., 1988. Upper Llandovery and Wenlock graptolites from Prairie Creek, southern Mackenzie Mountains, Northwest Territories. *Canadian J. Earth Sci.* 25, 1955–1971.
- Lenz, A., Kozłowska, A., 2007. New and unusual upper Llandovery graptolites from Arctic Canada. *Acta Palaeontol. Polon.* 52, 489–502.
- Lenz, A., Kozłowska-Dawidziuk, A., 2004. Ludlow and Pridoli (Upper Silurian) graptolites from the Arctic Islands. NRC Research Press, Ottawa Canada, 141 pp.
- Lenz, A.C., Melchin, M.J., 1987. Silurian retiolites from the Cape Phillips Formation, Arctic Islands, Canada. *Bull. Geol. Soc. Denmark* 35, 161–170.
- Lenz, A., Senior, S., Kozłowska, A., Melchin, M.J., 2012. Graptolites from the mid Wenlock (Silurian), middle and upper Sheinwoodian, Arctic Canada. *Palaeontograph. Canadiana* 32, 1–93.
- Loydell, D.K., 1998. Early Silurian sea-level changes. *Geol. Mag.* 135, 447–471.
- Loydell, D.K., 2003. Late Telychian graptolites of the Rauckkofel Bodentörl section (central Carnic Alps, Austria). *Jahrbuch der Geologischen Bundesanstalt* 143, 57–61.
- Loydell, D.K., 2007a. Graptolites from the Upper Ordovician and lower Silurian of Jordan. *Special Papers Palaeontol.* 78, 1–66.
- Loydell, D.K., 2007b. Early Silurian positive $\delta^{13}\text{C}$ excursions and their relationship to glaciations, sea-level changes and extinction events. *Geol. J.* 42, 531–546.
- Loydell, D.K., Cave, R., 1993. The Telychian (upper Llandovery) stratigraphy of Buttington Brick Pit, Wales. *Newslett. Stratigr.* 29, 91–103.
- Loydell, D.K., Frýda, J., Gutiérrez-Marco, J.C., 2015. The Aeronian/Telychian (Llandovery, Silurian) boundary, with particular reference to sections around the El Pintado reservoir, Seville Province, Spain. *Bull. Geosci.* 90, 743–794.
- Loydell, D.K., Kleffner, M., Mullins, G.L., Butcher, A., Matteson, D.K., Ebert, J.R., 2007. The Williamson Shale (Silurian) of New York: a biostratigraphical enigma. *Geol. Mag.* 144, 225–234.
- Loydell, D.K., Männik, P., Nestor, V., 2003. Integrated biostratigraphy of the lower Silurian of the Aizpute-41 core, Latvia. *Geol. Mag.* 140, 205–229.
- Loydell, D.K., Sarmiento, G.N., Štorch, P., Gutiérrez-Marco, J.C., 2009. Graptolite and conodont biostratigraphy of the upper Telychian–lower Sheinwoodian (Llandovery–Wenlock) strata, Jabalón River section, Corral de Calatrava, central Spain. *Geol. Mag.* 146, 187–198.
- Loydell, D.K., Walasek, N., Schovsbo, N.H., Nielsen, A.T., 2017. Graptolite biostratigraphy of the lower Silurian of the Sommerodde-1 core, Bornholm, Denmark. *Bull. Geol. Soc. Denmark* 65, 135–160.
- Margalef, A., Castiñeiras, P., Casas, J.M., Naveda, M., Liesa, M., Linnemann, U., Hofmann, M., Gärtner, A., 2016. Detrital zircons from the Ordovician rocks of the Pyrenees: geochronological constraints and provenance. *Tectonophysics* 681, 124–134.
- Melchin, M.J., 1989. Llandovery graptolite biostratigraphy and paleobiogeography, Cape Phillips Formation, Canadian Arctic Islands. *Canadian J. Earth Sci.* 26, 1726–1746.
- Melchin, M.J., 2007. Biostratigraphic and paleobiogeographic significance of some Aeronian (lower Silurian) graptolites from the Arisaig Group, Nova Scotia, Canada. *Acta Palaeontol. Sin.* 46 (Suppl.), 311–319.
- Melchin, M.J., Mitchell, C.E., Naczk-Cameron, A., Fan, J., Loxton, J., 2011. Phylogeny and adaptive radiation of the Neograptina (Graptoloida) during the Hirnantian mass extinction and Silurian recovery. *Proc. Yorkshire Geol. Soc.* 58, 281–309.
- Metcalfe, I., 1998. Palaeozoic and Mesozoic geological evolution of the SE Asian region: multidisciplinary constraints and implications for biogeography. In: Hall, R., Holloway, J.D. (Eds.), Biogeography and Geological Evolution of SE Asia. Backhuys, Leiden, pp. 25–41.
- Metcalfe, I., 2005. Asia/South-East. In: Selley, R.C., Cocks, L.R.M., Plimer, I.R. (Eds.), *Encyclopaedia of Geology*. Elsevier, Oxford, pp. 169–196.
- Nguyen Van Phuc, 1981. Graptolite faunas in Vietnam. In: Proceedings of the Fourth Regional Conference on the Geology of Southeast Asia. Geological Society of the Philippines, Manila, pp. 347–354.
- Nguyen Van Phuc, 2002. Ordovician – Silurian and Lower Devonian graptolite bearing beds from Vietnam. *VNU J. Sci., Nat. Sci. Technol.* 18, 38–50.
- Opdyke, N., Huang, K., Xu, G., Zhang, W., Kent, D., 1987. Paleomagnetic results from the Silurian of the Yangtze paraplatform. *Tectonophysics* 139, 123–132.
- Racheboeuf, P., Phuong, To Hoa, Hung, Nguyen Huu, Feist, M., Janvier, P., 2006. Brachiopods, crustaceans, vertebrates, and charophytes from the Devonian Ly Hoa, Nam Cam and Dong Tho formations of Central Vietnam. *Geodiversitas* 28, 5–36.
- Rickards, R.B., Parkes, R.A., Wright, A.J., 2005. Llandovery (Early Silurian) graptolites from the Quidong Basin, NSW. *Proc. Linn. Soc. New South Wales* 126, 143–152.
- Robardet, M., Gutiérrez-Marco, J.C., 2002. Silurian. In: Gibbons, W., Moreno, T. (Eds.), *The Geology of Spain*. The Geological Society, London, pp. 51–66.
- Rong, J., Boucot, A.J., Su, Y., Strusz, D.L., 1995. Biogeographical analysis of Late Silurian brachiopod faunas, chiefly from Asia and Australia. *Lethaia* 28, 39–60.
- Rong, J., Cocks, L.R.M., 2014. Global diversity and endemism in Early Silurian (Aeronian) brachiopods. *Lethaia* 47, 77–106.
- Rong, J., Chen, X., Su, Y., Ni, Y., Zhan, R., Chen, T., Fu, L., Li, R., Fan, J., 2003. Silurian palaeogeography of China. *New York State Museum Bull.* 493, 243–298.
- Rossignol, C., Bourquin, S., Hallot, E., Poujol, M., Dabard, M.-P., Martini, R., Villeneuve, M., Cornée, J.-J., Brayard, A., Roger, F., 2018. The Indosinian orogeny: a perspective from sedimentary archives of North Vietnam. *J. Asian Earth Sci.* 158, 352–380.
- Smith, S., 2009. A discussion of the volcanic and conglomerate facies of the Sepon district. Lane Xane Minerals Laos (LXML), unpublished company report, 26 pp.
- Sone, M., Metcalfe, I., 2008. Parallel Tethyan sutures in mainland Southeast Asia: new insights for Palaeo-Tethys closure and implications for the Indosinian orogeny. *Comptes Rendus Geosci.* 340, 166–179.
- Steevens, P., Pereira, E., 2002. Llandovery miospore biostratigraphy and stratigraphic evolution of the Parana Basin, Paraguay – palaeogeographic implications. *Bulletin de la Société Géologique de France* 173, 407–414.
- Štorch, P., 1983. Subfamily Akidograptinae (Graptolithina) from the lowermost Silurian of Bohemia. *Věstník Ústředního Ústavu Geologického* 58, 295–299.
- Štorch, P., 1992. Some new or little known graptolites from the lower Silurian of Bohemia (Prague Basin, Barrandian area). *Časopis pro mineralogii a geologii* 37, 193–202.
- Štorch, P., 1998. New data on Telychian (upper Llandovery, Silurian) graptolites from Spain. *J. Czech Geol. Soc.* 43, 113–141.
- Štorch, P., Bernal, J.R., Gutiérrez-Marco, J.C., in press. A graptolite-rich Ordovician–Silurian boundary section in the south-central Pyrenees, Spain: stratigraphical and palaeobiogeographical significance. *Geol. Mag.*
- Štorch, P., Feist, R., 2008. Lowermost Silurian graptolites of Montagne Noire, France. *J. Paleontol.* 82, 938–956.
- Štorch, P., Manda, Š., Loydell, D.K., 2014. The early Ludfordian *leintwardinensis* graptolite Event and the Gorstian-Ludfordian boundary in Bohemia (Silurian, Czech Republic). *Palaeontology* 57, 1003–1043.
- Štorch, P., Schönlaub, H.-P., 2012. Ordovician–Silurian boundary graptolites of the Southern Alps, Austria. *Bull. Geosci.* 87, 755–766.
- Štorch, P., Serpagli, E., 1993. Lower Silurian graptolites from southwestern Sardinia. *Bollettino della Società Paleontologica Italiana* 32, 3–57.
- Thanh, Tong-Dzuy, Boucot, A.J., Rong, J., Fang, Z., 2001. Late Silurian marine shelly fauna of central and northern Vietnam. *Geobios* 34, 315–338.
- Thanh, Tong-Dzuy, Janvier, P., Phuong, Ta Hoa, 1996a. Fish suggests continental connections between the Indochina and South China blocks in Middle Devonian time. *Geology* 24, 571–574.
- Thanh, Tong-Dzuy, Hong-fei, Hou, Phuong, Ta Hoa, Hung, Nguyen Huu, Truong, Doan Nhat, 1996b. Outlines on stratigraphy and remarks on paleobiogeography of Devonian in Southeast Asia. *J. Geol. Series B* 7–8, 10–34.
- Thanh, Tong-Dzuy, Phuong, Ta Hoa, Boucot, A.J., Goujet, D., Janvier, P., 1997. Silurian vertebrates from Central Vietnam. *Comptes Rendus de l'Académie des Sciences, Série II* 324, 1023–1030.
- Thanh, Tong-Dzuy, Phuong, Ta Hoa, Janvier, P., Hung, Nguyen Huu, Cuc, Nguyen Thi Thu, Duong, Nguyen Thuy, 2013. Silurian and Devonian in Vietnam – stratigraphy and facies. *J. Geodynamics* 69, 165–185.
- Thassanapak, H., Udchachon, M., Burrett, C., 2012. Devonian radiolarians and tentaculitids from central Laos. *J. Asian Earth Sci.* 60, 104–113.

- Thassanapak, H., Udchachon, M., Burrett, C., 2018. Silurian radiolarians from the Sepon Mine, Truong Son Terrane, central Laos and their palaeogeographic and tectonic significance. *Geol. Mag.* 155 (8), 1621–1640.
- Torsvik, T.H., Cocks, L.R.M., 2009. The Lower Palaeozoic palaeogeographical evolution of the northeastern and eastern peri-Gondwanan margin from Turkey to New Zealand. In: Bassett, M.G. (Ed.), *Early Palaeozoic peri-Gondwana terranes: new insights from tectonics and biogeography*. Geological Society, London, Special Publication 325, pp. 3–21.
- Torsvik, T.H., Cocks, L.R.M., 2013. New global palaeogeographical reconstructions for the Early Palaeozoic and their generation. In: Harper, D.A.T., Servais, T. (Eds.), *Early Palaeozoic Biogeography and Palaeogeography*. Geological Society, London, Memoirs 38, pp. 5–24.
- Torsvik, T.H., Cocks, L.R.M., 2016. *Earth History and Palaeogeography*. Cambridge University Press 317 pp.
- Udchachon, M., Thassanapak, H., Feng, Q., Burrett, C., 2017a. Palaeoenvironmental implications of geochemistry and radiolarians from Upper Devonian chert/shale sequences of the Truong Son fold belt, Laos. *Geol. J.* 52, 154–173.
- Udchachon, M., Thassanapak, H., Burrett, C., 2017b. Palaeoenvironment and palaeogeography of Middle and Upper Devonian strata from the Loei fold belt, Indochina terrane (northeast Thailand). *Palaeobiodiv. Palaeoenvir.* 97, 497–516.
- Usuki, T., Lan, C., Wang, K., Chiu, H., 2013. Linking the Indochina block and Gondwana during the Early Palaeozoic: evidence from U-Pb ages and Hf isotopes of detrital zircons. *Tectonophysics* 586, 145–159.
- Vandenbroucke, T.R.A., Armstrong, H.A., Williams, M., Zalasiewicz, J.A., Sabbe, K., 2009. Ground-truthing Late Ordovician climate models using the paleobiogeography of graptolites. *Paleoceanography* 24, PA4202. <https://doi.org/10.1029/2008PA001720>.
- Wang, Q., Deng, J., Li, C., Li, G., Yu, L., Qiao, L., 2014. The boundary between the Simao and Yangtze blocks and their locations in Gondwana and Rodinia: constraints from detrital and inherited zircons. *Gondwana Res.* 26, 438–448.
- Wang, W., Muir, L.A., Chen, X., Tang, P., 2015. Earliest Silurian graptolites from Kalpin, western Tarim, Xinjiang, China. *Bull. Geosci.* 90, 519–542.
- Wang, W., Qu, Q., Zhu, M., 2010. A brief review of the Middle Palaeozoic vertebrates from Southeast Asia. *Palaeoworld* 19, 27–36.
- Wang, Y., Zhang, Y., 2010. Llandovery sporomorphs and graptolites from the Manbo Formation, the Mojiang County, Yunnan, China. *Proc. R. Soc. B* 277, 267–275.
- Williams, M., Komatsu, T., Tanaka, G., Hung, Nguyen Huu, Zalasiewicz, J., Vandenbroucke, T.R.A., Wallis, S., Perrier, V., 2016a. Upper Llandovery (Telychian) graptolites of the *Oktavites spiralis* Biozone from the Long Dai Formation, at Lam Thuy village, Quang Binh Province, central Vietnam. *Canadian J. Earth Sci.* 53, 719–724.
- Williams, M., Zalasiewicz, J., Boukhamsin, H., Cesari, C., 2016b. Early Silurian (Llandovery) graptolite assemblages of Saudi Arabia: biozonation, palaeoenvironmental significance and biogeography. *Geol. Quart.* 60, 3–25.
- Young, G., 2010. Placoderms (armored fish): dominant vertebrates of the Devonian Period. *Annu. Rev. Earth Planet. Sci.* 38, 523–550.
- Young, G., Janvier, P., 1999. Early-middle Palaeozoic vertebrate faunas in relation to Gondwana dispersion and Asian accretion. In: Metcalfe, I. (Ed.), *Gondwana dispersion and Asian accretion*. IGCP 321 final results volume. Balkema, Rotterdam, pp. 115–140.
- Zhang, Y., Fan, J., Wang, Y., Song, Y., Cheng, J., 2013. A mid-Telychian (Llandovery) graptolite fauna from Mojiang, Yunnan Province, southwestern China. *Memoirs of the Association of Australasian Palaeontologists* 44, 123–142.
- Zhang, Y., Wang, Y., Zhan, R., Fan, J., Zhou, Z., Fang, X., 2014. Ordovician and Silurian Stratigraphy and Palaeontology of Yunnan, southwest China. Science Press, Beijing 138 pp.
- Zhang, Y., Lenz, A.C., 1997. Uppermost Wenlock and Ludlow graptolites from southern Yunnan, China. *Canadian J. Earth Sci.* 34, 1220–1238.