A lungfish (Sarcopterygii, Dipnomorpha) tooth–plate from the Lower Devonian of Vietnam and the onset of modern dipnoan dental organization

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ABSTRACT

ABSTRACT–An isolated pterygoid tooth–plate of a lungfish from the Lower Devonian (Lochkovian–Pragian) of Vietnam is described. The material is negatively preserved and lacks associated jawbones to assign a reliable taxonomic status and phylogenetic position. The tooth–plate is composed of five main tooth–rows radially arranged, separated by several interrow denticles and flanked medially and laterally by smaller accessory rows and by a denticulated posterolateral field. The general structure of the tooth–plate displays predominantly primitive traits similar to those known in its contemporaneous *Diabolepis* from China. However, as opposed to *Diabolepis*, the tooth–plate possesses fewer and more organized rows of teeth, a condition typical of more derived dipnoans. Comparisons with other primitive forms indicate that the arrangement of teeth into distinct rows with a lack of interrow denticles is typical of juvenile specimens of *Diabolepis* which may imply that the presence of discrete tooth rows in more derived lungfish taxa is a product of paedomorphosis. Given its puzzling mix of primitive and derived features, this new pterygoid tooth–plate can be tentatively assigned to a previously known lungfish prearticular from Northern Vietnam, although with caution. Pending the finding of more complete remains, the condition showed by this new form might indicate that the establishment of the modern lungfish tooth–plate organization occurred no later than the Pragian.

INTRODUCTION

Devonian vertebrates have been known from Vietnam since the early 20th century (Mansuy 1915) and were initially represented by antiarchs (*Asterolepis* sp.), arthrodire

(*Homosteus* sp.) ‘placoderms’, and galeaspids (Tong–Dzuy Thanh and Janvier 1987) from the Yên Minh area, close to the Chinese frontier. Fieldwork in the 1950s and 1960s in Northern Vietnam retrieved further ‘placoderm’ and galeaspid remains from the Song Cau Group (comprising the Bac Bun and Si Ka Formations) dated as Lower Devonian. However, the richest and faunistically most diverse Devonian outcrops come from the Thai Nguyen and Lan Son Provinces, North–East of Hanoi, where galeaspids and ‘placoderms’ are associated with osteichthyan remains (rare actinopterygians and dipnomorph sarcopterygians).

The vertebrate localities from Northern Vietnam are Lower Devonian (Lochkovian and Pragian) in age, in particular from the Si Ka and Bac Bun Formations (Mansuy 1915; Tong–Dzuy Thanh and Janvier 1987, 1990; Tong–Dzuy Thanh et al. 1995; Janvier and Tong–Dzuy Thanh 1998; Janvier et al. 1993, 1996, 1997, 2003). These fish faunas present striking similarities with those from the Lower Devonian of Yunnan and Guangxi (South China block) and are characterized by the association of galeaspids, various endemic ‘placoderms’ (yunnanolepiform and procondylolepiform antiarchs and quasipetalichthyids) and the dipnomorph sarcopterygian *Youngolepis*. This vertebrate assemblage defines a Silurian to Lower Devonian biogeographic Province known as the “galeaspid–yunnanolepiform Province” (Young 1993) since it has been established that terranes extending north of the Red River (i.e., the Bac Bo area of Northern Vietnam) were merely the southern prolongation of the South China block (also known as Guangxi or Yangtze block) (Tong–Dzuy Thanh et al. 2011).

Sarcopterygian fossils are scarce in the Lower Devonian of Vietnam and are currently represented mainly by dipnomorphs. Numerous remains of *Youngolepis* (*Youngolepis* cf. *Y praecursor*) are known including an ethmoid portion of the skull, a complete lower jaw and several scales (Tong–Dzuy Thanh and Janvier 1990; Racheboeuf et al. 2005). Tong–Dzuy

Thanh and Janvier (1994) reported a new sarcopterygian form, *Langdenia campylognatha* (Janvier and Phuong 1999), an enigmatic, cosmine–covered putative dipnomorph, different from *Youngolepis* and dipnoans in that 1) the ethmoid portion of the skull is strikingly short, 2) the lower jaw bears several diagnostic features also known in *Psarolepis*, 3) Westoll–lines are absent, and 4) the cosmine pores are much smaller than those of *Youngolepis*. A third sarcopterygian form is represented by isolated scales reminiscent of those of early tetrapodomorphs like *Kenichthys* from the Middle Devonian of China (Chang and Zhu 1993) by the smooth covering of cosmine and the lack of striations on the anterior margin of the cosmine field. Furthermore, histological data illustrate the occurrence of enamel penetrating the pore–cavities, a condition solely known in dipnomorphs (e.g., *Youngolepis, Powichthys, Porolepis, Diabolepis*) (Mondéjar–Fernández 2018). Unfortunately, histological data is currently lacking from *Kenichthys* to grant a precise comparison.

Dipnoans from Vietnam are solely known by small, fragmentary and disarticulated remains, including cosmine–covered dermal bones and scales showing Westoll–lines and a prearticular bone bearing an attached tooth–plate (Tong–Dzuy Thanh and Janvier 1987, fig. 8 A, B, pl. 1–3). This denticulated prearticular (TO5A) was recovered from the Trang Xa outcrops (base of the Bac Bun Formation, Lower Devonian), and is seemingly different from the contemporaneous *Diabolepis* from Yunnan. The prearticular is of small size, similar to that of *Diabolepis*, but probably belonged to an adult fish according to the large number of denticles. However, the denticles are less numerous and more regularly distributed in this indeterminate lungfish than in *Diabolepis*. Associated scales with a smooth cosmine–covering, fine pores and Westoll–lines from the same locality could also be attributed to this lungfish form.

Herein, we describe a new isolated pterygoid tooth–plate of a lungfish retrieved from the Bac Bun Formation (Pragian) of the Dông Mo Region of Northern Vietnam. It displays an interesting mix of primitive and derived features, some of them reminiscent of *Diabolepis*, while others are uncommon in an early dipnoan and bear more similarities with more derived lungfishes. Given its derived nature and proximity, it can be tentatively assigned to the previous indeterminate lungfish form from Trang Xa, although with caution.

GEOLOGICAL SETTING

The Devonian outcrops of Vietnam comprise mainly continental and shallow marine water deposits from the Lower and Middle Devonian, whereas the Upper Devonian might display several deep–water facies in some areas (Tong–Dzuy Thanh et al. 2011). The Bac Bo Region (or Northern Region) extends over the main Northern part of the country, limited by the Chinese border to the North, the Hanoi region to the South and the Song Ma and Dien Bien–Lai Chau faults to the West.

The Song Cau Group includes the Si Ka Formation (subcontinental facies consisting of conglomerate, greenish siltstone, clay shale, and marly shale) and the Bac Bun Formation (littoral to deltaic facies grading upwards into shallow marine facies consisting of grey, chocolate variegated weathering clay shale, marly shale and siltstone). The Si Ka Formation is mainly Lochkovian in age whereas the Bac Bun Formation includes to the upper portion of the Lochkovian and the base of the Pragian. These have been tentatively correlated with the Lianhuashan and Nakoaling Formations of Southern China respectively according to biostratigraphical and facies similarities (Tong–Dzuy Thanh and Janvier 1990). Vertebrate remains from the Si Ka and Bac Bun Formations include mainly galeaspids, ‘placoderms’ and

sarcopterygians. The lithological composition and fauna of the Si Ka and Bac Bun Formations suggest that the Song Cau Group probably represents a transitional environment, gradually ranging from lagoonal, coastal and deltaic facies to onshore shallow marine deposits (Tong–Dzuy Thanh et al. 2011).

The dipnoan remains described herein were retrieved in 2009 by a French–Vietnamese team. The fossils come from exposures of the Bac Bun Formation in the Tong Lot locality (20 min drive from Dông Mo) in the Dông Mo Region, Lang Son Province, Vietnam (coordinates: 21° 41.692' N 106° 33.280 E; altitude:1081 feet) (Fig. 1). This locality (DS 07, Fig. 1B) was already visited by a previous expedition (Tong–Dzuy Thanh and Janvier 1990), which retrieved vertebrate material of *Youngolepis* cf. *Y praecursor, Yunnanolepis* sp. and an indeterminate antiarch 'placoderm' from exposures of the slightly older Si Ka Formation. The fossil outcrops of the lower Member of the Bac Bun Formation of the nearby locality DS 04 (Fig. 1B) house a diverse and relatively well–preserved vertebrate fauna comprising galeaspids (*Polybranchiaspis* sp.), antiarch 'placoderms' (*Yunnanolepis bacboensis* and *Y.deprati*, *Chuchinolepis dongmoensis, Vanchienolepis langsonensis*), 'acanthodians' (*Nosteolepis*? sp.), and sarcopterygians (*Youngolepis* cf. *Y. praecursor*) (Tong–Dzuy Thanh and Janvier 1990). Further dipnoan remains have already been retrieved from exposures of the Bac Bun Formation at the Trang Xa fossil site (several scales and dermal bones covered with cosmine and displaying Westoll–lines and a prearticular dental plate) (Tong–Dzuy Thanh and Janvier 1987, fig. 8 A, B, pl. 1–3).

MATERIAL AND METHODS

The dipnoan material is negatively preserved as a natural mould in highly weathered, fine–grained sandstone sediment. An elastomere cast of the mould has been made and whitened with ammonium chloride sublimate for photography, enabling the original features of the specimen to be highlighted. Line drawings were made from these photographs using Adobe Illustrator and finalised with Adobe Photoshop. The specimen is deposited in the Bao Tang Dia Chat collection of the Museum of Geology in Hanoï (Vietnam).

SYSTEMATIC PALAEONTOLOGY

OSTEICHTHYES Huxley, 1880

SARCOPTERYGII Romer, 1955

DIPNOMORPHA Ahlberg, 1991

DIPNOI Müller, 1845

Family undesignated

Dipnoi indet.

Material–BT521; isolated left pterygoid plate (Fig. 2)

Locality and Horizon–Tong Lot locality, Dông Mo Region, Lang Son Province, Vietnam. Base of the Bac Bun Formation, Lower Devonian (Lochkovian–Pragian).

DESCRIPTION

The pterygoid tooth–plate is 11 mm in maximum length and 4,5 mm in width (Fig. 2). It has a rhomboidal shape, with a well–developed postero–lateral extension (horizontal

postero–lateral lamina) (Fig. 2B, p.l.la). The horizontal plate is slightly convex in buccal view, with straight mesial and lateral margins, a wavy anterior margin, and a concave posterior portion. A lateral embayment of the posterolateral margin of the tooth–plate (Fig. 2B, emb) is poorly developed in comparison with more derived Devonian dipnoans such as *Dipterus*.

There are thirteen rows of teeth, including five main tooth–rows (Fig. 2B, 1–5r), and small denticle–formed rows, originating from the postero–medial portion of the tooth–plate and radiating anteriorly and antero–laterally. Each row has a variable number of rounded, slightly pointed to blunt teeth or denticles of variable sizes, decreasing in size and coalescing posteriorly. The larger and more pointed teeth are located anteriorly and laterally, while the smallest and more worn out ones are usually arranged around the centre of radiation of the tooth rows. The first row has six large teeth, flanked postero–medially by smaller denticles. The second and third rows are more clearly marked and wider than the others; the second row bears seven large teeth whereas the third row has eight teeth. The number of teeth then decreases from the fourth row, which has seven, to the fifth with only six. However, the anterior–most portion of the second row does not display the largest teeth as is usually found in other tooth–plated dipnoans, but a cluster of smaller denticles of variable sizes grouped in a rather disordered fashion at the anterior margin of the pterygoid plate. These smaller anterior denticles (Fig. 2B, a.de) are absent from the third, fourth and fifth rows.

The tooth rows are narrowly separated with small denticles occurring (Fig. 2B, int.de) between the first, second and third rows. Similar denticles occur medially to the first row, forming two smaller accessory rows (Fig. 2B, ac.r). Lateral to the fifth main row, smaller denticles also develop in pseudo–linear rows, radiating from the postero–medial origin point of the tooth–plate. In sum, a shagreen of small denticles covers the surfaces adjacent to the more organized regions across the tooth plate. The centre of radiation (Fig. 2B, ra.c) is

concave, and appears to lack any distinctive denticles. It is unclear if this is due to damage or a real structure.

In total, around thirteen rows of teeth, including the small denticle–formed rows and the five main teeth–rows, can be counted, arranged in a fan–like fashion from the radiation centre at an angle of approximately 140º. In the postero–lateral margin, several small denticles appear to be fused with each other, forming small dental plates (Fig. 2B, de.p), following the lateral and posterior contour of the bone, a condition similar to that of *Diabolepis* (Chang and Yu 1984). The mesial edge is straight and sharp, suggesting that the pterygoid tooth–plates might have met each other closely. Sharp "additive" mesial and posterior edges (Ahlberg et al. 2006) are absent. Because of the nature of the material as a negative imprint, it is not possible to histologically determine the nature of the teeth.

DISCUSSION

Dipnoan Dentition

The lungfish dentition is unique among vertebrates and, aside from taxa bearing denticulated plates, it is composed of crushing plates specialized in grinding the food distributed on the upper (borne on the pterygoid) and lower jaws (prearticular, when present). The lungfish dental arrangement is not only remarkable but also highly variable in its morphology since the Devonian. Dipnoans display three different dentition organizations: tooth–plates, dentine plates, and denticulated plates, and sometimes combinations of these. Tooth plates comprising radiating rows of teeth are considered the primitive condition from which all the other morphotypes are derived (Ahlberg et al. 2006) and as such characterize many early dipnoans (e.g., *Diabolepis, Tarachomylax, Speonesydrion*) and more derived taxa,

including the extant lungfishes (*Lepidosiren*, *Protopterus*, *Neoceratodus*). Dentine plates are present in chirodipterids (e.g., *Chirodipterus*) as well as some primitive early Devonian forms (e.g. *Dipnorhynchus*) in which the dental surfaces are covered in thick sheets of dentine. Denticulated plates carry a widespread shagreen of small denticles (e.g., *Uranolophus, Melanognathus, Griphognathus, Conchopoma*) (Campbell and Barwick 1988; Schultze 2001; Smith and Krupina 2010).

The specialized lungfish dentition is likely to have been established very early on in their evolutionary history and its developmental pattern has been surprisingly conserved until Recent since the Lower Devonian (Reisz and Smith 2001). In the case of tooth–plated lungfishes, teeth are added labially to each row and rows form anterior to posterior, meaning that younger animals have fewer teeth and rows than adult animals. Moreover, teeth are consolidated into the tooth–plates and do not shed. This statodont condition implies that the ontogenetic history of the animal is preserved in the tooth–plates, revealing morphogenetic patterns of growth, wearing, and repair. The highly mineralized dentine (petrodentine) grows extensively and continuously, forming durable and commonly preserved hard dental plates, which are usually amongst the sole dipnoan elements found in fossil localities, especially after the Carboniferous due to an almost complete loss of endoskeletal ossification (Clack et al. 2011). Devonian taxa show a substantial amount of morphological diversity, particularly with respect to the dental plates. Dental morphology has formed the basis for previous attempts on lungfish phylogenies (e.g., Campbell and Barwick 1983, 1990, 2008), in which preference was given to functional feeding scenarios, dividing lungfish into tooth–plated, dentine–plated and denticulated lineages with each of the dental types evolving as separate radiations. This unparsimonious view has been challenged by numerous subsequent studies (e.g., Schultze and

Marshall 1993; Ahlberg et al. 2006) revealing that the different morphotypes have arisen multiple times in several different lineages.

Tooth–plate morphology can be diagnostic to genus or species, a useful condition in situations in which little or no skeletal material is available. Since the tooth–plates are permanent structures in lungfishes, forming in juveniles and continuing their growth into adulthood, their morphology can vary greatly during ontogeny, which can make identification of isolated tooth–plates difficult (Reed 1985). Kemp (1997, 2005) showed that these variations can be due to wear or to developmental changes in the basic structure of the tooth–plates and that anomalies affecting radial arrangement and shape of the teeth are common from the Devonian onwards. Growth series of fossil forms are known (Krupina and Reisz 1999) from which an understanding of the ontogenetic effects on tooth–plate morphology can be taken into account when diagnosing taxa based on tooth–plates alone. To this extent, detailed morphometrics of Carboniferous lungfish tooth–plates accounting for size have been able to identify several new taxa (Smithson et al. 2016). Tooth–plates are most useful in the identification of taxa if used in conjunction with further skeletal remains (Clack et al. 2018). It is thus unrealistic attempting to establish a reliable taxonomic position to BT521, solely based on a cast of an isolated tooth–plate. Nevertheless, it presents certain features that can be phylogenetically informative and allow comparison with other tooth–plated Devonian taxa.

Devonian Tooth–plated Dipnoans and Comparison

The primitive state of the lungfish dentition, as displayed in *Diabolepis* from the Lochkovian of China include: 1) paired dental plates consisting of radial rows of teeth that converge on the posteromedial corner, 2) radial tooth rows in which the teeth gradually increase in size from posteromedial to labial, 3) tooth patches of graded size teeth on the

shortened premaxilla and dentary, and 4) a complete cover of denticles and teeth on the palate and the inner bones of the lower jaw (Smith and Chang 1990). BT521 displays a radial disposition of teeth in rows that agrees with the plesiomorphic condition of the palatal plates of *Diabolepis* (Fig. 3 A–E). Tooth plates with a similar organization of teeth in rows are found in numerous other Devonian dipnoans such as *Dipterus* from the Middle–Late Devonian of Europe and North America (White 1965), *Stomiahykus* from the Eifelian of Canada (Bernacsek 1977), *Eoctenodus* from the Frasnian of Australia (Long 1987), *Howidipterus* from the Givetian of Australia (Long 1992), *Erikia* from the Emsian of China (Chang and Wang 1995), *Scaumenacia* from the Frasnian of Québec (Cloutier 1996), *Tarachomylax* from the Emsian of Russia (Barwick et al. 1997), *Speonesydrion* from the Emsian of Australia (Campbell and Barwick 1983, 1984), *Andreyevichthys* from the Famennian of Russia (Krupina and Reisz 1999), *Adelargo* from the Famennian of Australia (Johanson and Ritchie 2000), *Orlovichthys* from the Famennian of Russia (Krupina et al. 2001), *Sinodipterus* from the Eifelian of China (Qiao and Zhu 2009), *Harajicadipterus* from the Givetian of Australia (Clement 2009) and *Rhinodipterus* from the Frasnian of Australia (Clement 2012).

The occurrence of small interrow denticles in BT521 is also similar to the condition of *Diabolepis* (Chang and Yu 1984) and other tooth–plated Devonian forms like *Andreyevichthys* (Smith and Krupina 2001), *Sinodipterus* (Qiao and Zhu 2009) and *Harajicadipterus* (Clement 2009), contrasting with the condition seen in *Dipterus* (White 1965; Jarvik 1980) and *Tarachomylax* (Barwick et al, 1997). Interrow denticles appear to be absent from many Middle Devonian lungfishes but they occur in *Harajicadipterus* (Givetian; Clement 2009), *Sinodipterus* (Eifelian; Qiao and Zhu 2009), and several Late Devonian indeterminate forms from the USA (Reed 1985). However, BT521 deviates from the primitive pattern seen in *Diabolepis* in that the tooth–plate displays fewer rows and those present appear more

organized than in *Diabolepis,* a condition typical of more derived forms (e.g., *Tarachomylax, Andreyevichthys, Dipterus*) (Fig. 3). The posterior lamina of the pterygoid plate displays an array of denticles spreading over the lateral margin. In *Diabolepis* (Chang and Yu 1984), part of the incompletely preserved posterolateral field is covered by denticles with several of them fused resulting in a somewhat broad plate. In our material, numerous small denticles also occur in the posterior lamina with some evidences of fusion in its most lateral margin, a condition also known in *Andreyevichthys* (Smith and Krupina 2001) though lacking in *Tarachomylax* (Barwick et al. 1997) (Fig. 3 G, I). Finally, and unlike *Diabolepis,* the denticles in BT521, as well as the fused plates, are relatively small.

BT521 certainly represents an adult form as evidenced by the numerous rows of teeth. Radial arrangement of the teeth in rows in the pterygoid tooth–plate has been described in the juvenile specimens of *Diabolepis* (Chang 1995) but in the adult this radial organization is less clear, resulting in a more irregularly–distributed denticle field (Fig. 3 A, C). This apparent loss of order was critically considered by Campbell and Barwick (2001) to refute the dipnoan nature of *Diabolepis* since primitive dipnoans such as *Tarachomylax* display regular radial teeth throughout their ontogeny (Barwick et al. 1997). The retention of a radial arrangement of the teeth in tooth–plated forms more derived than *Diabolepis* might represent a further argument for the role of paedomorphosis in lungfish evolution (Bemis 1984). However, the occurrence of interrow denticles in Lower Devonian adult forms like *Diabolepis* and BT521 can blur the regular and radial arrangement of denticles occurring in juveniles.

The occurrence of denticle fusion on the labial margins is also considered an adult feature, as seen in the adult tooth–plates of *Diabolepis, Tarachomylax* and *Andreyevichthys* (Fig. 3B, G, I). BT521 also lacks large fused dentine fields in the postero–medial portion of the tooth–plate, as opposed to *Diabolepis* (Fig. 3C). Large specimens of *Diabolepis* typically

display regions where individual teeth and denticles fuse to form dentine patches (Smith and Chang, 1990) more similar to the Lower Devonian dentine–plated taxa such as *Dipnorhynchus*. However, the condition seen in *Diabolepis* differs from that of *Dipnorhynchus* and similar taxa in being due to wear and, in some cases, the formation of reparative dentine. The development of dentine plates in lungfish cannot therefore easily be regarded as being due to heterochrony.

Further dental or skeletal remains from Lower Devonian lungfishes from Vietnam are difficult to associate with BT521. A left prearticular carrying its tooth–plate (TO5A, Fig. 3F) from an indeterminate lungfish was retrieved from the Trang Xa fossil site and was described by Tong–Dzuy Thanh and Janvier (1987) as belonging to an adult animal, despite its small size that is comparable to the prearticular of *Diabolepis* (Chang and Yu 1984, fig. 5A; Smith and Krupina 2001, fig. 3C). In the posteromedial corner, several denticles have fused into a shining crushing plate, similar to the one present in *Diabolepis* (Fig. 3D). However, as opposed to *Diabolepis*, the prearticular plate carries fewer tooth rows (four), a condition more similar to that of more derived forms such as *Tarachomylax* (five) (Fig. 3H), *Dipterus* (variable) (Fig. 3L), or *Rhinodipterus* (variable). The posterior portion of the prearticular plate is elongate, forming a postero–lateral process, unlike in *Diabolepis* and similar to more derived forms. This structure may therefore represent a derived condition for the prearticular tooth plate in dipnoans indicating that the Trang Xa lungfish might be a more derived form than its contemporary *Diabolepis*. This prearticular plate could belong to the same taxon as BT521 due to the mix of primitive and derived features, but it is currently impossible to ascertain.

Paleobiogeographical Implications

It is now well established that the earliest–known dipnoans are Lower Devonian (Lochkovian–Pragian) in age. From the beginning of the Devonian, numerous forms are found widespread across continental Euramerica (e.g., *Uranolophus, Tarachomylax, Jessenia*) (Denison 1968; Barwick et al. 1997; Otto and Bardenheuer 1996) and Gondwana (e.g., *Dipnorhynchus , Speonesydrion*) (Campbell and Barwick 1982, 1983 1984, 2000) as well as the China block of northern Gondwana (e.g., *Diabolepis, Erikia*) (Chang and Wang 1995; Chang 1995). Indeterminate dipnoan remains have also been described from the Lochkovian to Pragian of Vietnam, the United States and Spitsbergen (Clément et al. 2006). Lower Devonian dipnoan remains are rare and usually represented by disarticulated and poorly preserved material, but where present are commonly found associated with a diverse array of 'placoderms' and other osteichthyans (Janvier 1996).

The Bac Bun Formation paleoenvironment has been reconstructed as part of a shallow marine realm from the northern margin of Gondwana, covering most of Northern Vietnam during the Lower Devonian (Tong–Dzuy Thanh et al. 2011) (Fig. 1C). The occurrence of lungfishes in these Lower Devonian deposits (e.g., Tong–Dzuy Thanh and Janvier 1990) is consistent with the assumption that the earliest dipnoans like the Lochkovian *Diabolepis* (Chang 1995), Emsian *Cathlorhynchus* (Qiao and Zhu, 2015), Emsian *Erikia* (Chang and Wang, 1995) and the Pragian–Emsian *Dipnorhynchus* and *Speonesydrion* (Campbell and Barwick 1982, 1983, 1984, 2000) were essentially marine animals.

The so–called Indochina block, to which northern Vietnam belonged during the Palaeozoic, was a mere southwestern prolongation of the South China block from the Late Silurian to the Lower Devonian (Tong–Dzuy Thanh and Phuong 1994; Wang et al. 2010) (Fig. 1C). Outcrops of Lochkovian and Pragian age of Northern Vietnam bear faunal as well as floral assemblages similar to those of Southern China (Racheboeuf et al. 2005, 2006; Gonez

et al. 2011) and in the case of vertebrates display the same endemic faunas (Janvier et al. 1993, 1996, 1997). Particularly, the Dông Mo fauna is similar to that of the Xitun Formation of Yunnan, China (Wang et al. 2010). The close proximity and faunal similarities between Northern Vietnam and Southern China during the Lower Devonian allow referring the Vietnamese vertebrates to the coeval Xitun fauna from China (Wang et al. 2010) resulting in a putative paleoecological co–occurrence of the primitive *Diabolepis* with the likely more derived tooth–plated indeterminate forms from the Si Ka and Bac Bun Formations of Trang Xa and Dông Mo localities. The connection between the Chinese and Vietnamese terranes was maintained until the end of the Lower Devonian when a moderately broad rift isolated the vertebrate faunas from Vietnam, resulting in a survival of several 'placoderm' and sarcopterygian taxa, previously known exclusively from China, until the early Carboniferous when the barrier disappeared at the level of Northern Vietnam (Tong–Dzuy Thanh et al. 2011).

CONCLUSION

A new tooth–plated lungfish from the Lower Devonian (Lochkovian–Pragian) of Vietnam displays predominantly primitive traits in the general structure of the pterygoid tooth–plate similar to the contemporary taxon *Diabolepis,* in particular a denticulated posterolateral field. Unfortunately, the material is negatively preserved and too incomplete, lacking associated jawbones, to assign a reliable taxonomic status and phylogenetic position. The peculiar arrangement of the teeth rows and the occurrence of interrow denticles in the pterygoid tooth–plate is typical of the Lower Devonian dipnoans that possess tooth ridges (e.g. *Diabolepis, Tarachomylax*) rather than dentine plates. The ordering of the individual

teeth into distinct rows with a lack of interrow denticles is typical of smaller, and presumably younger, specimens of *Diabolepis* which may imply that the presence of discrete tooth rows is a product of paedomorphosis in many of the more–derived taxa from the Devonian to Recent. Pending the finding of more complete remains, this condition might indicate the onset of the modern lungfish tooth plate organization no later than the Pragian (Lower Devonian).

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FIGURES

FIGURE 1. Geographic and palaeogeographic setting of the fossil locality. **A.** Map of Vietnam. **B.** Detailed inset of the Dông Mo area (modified after Tong–Dzuy Thanh and Janvier 1990). **C.** Paleogeographical reconstruction of the latest Silurian – early Devonian (middle Pridolian – middle Pragian, 418–402 Mya) (after Golonka 2000). Stars in B indicate localities previously surveyed (Tong–Dzuy Thanh and Janvier 1990). The large white–filled star (in B and C) indicates the locality from which the dipnoan material was retrieved. [planned for 2/3 page width]

FIGURE 2. Indeterminate dipnoan pterygoid tooth–plate (BT521). Lower Devonian, Bac Bun formation, Dông Mo, Vietnam. **A**. Photograph of the specimen. **B**. Interpretative drawing. **Abbreviations**:**1–5r**, tooth–rows; **a.de**, anterior denticles; **ac.r,** accessory tooth–rows; **de.p,** dental plates, **emb**, lateral embayment; **int.de,** interow denticles; **p.l.la,** horizontal postero–lateral lamina; **ra.c,** centre of radiation. [planned for page width]

FIGURE 3. Tooth–plates comparison in Devonian dipnoans. All drawings represent tooth–plates from the left side. **A–D.** *Diabolepis*, **A–B,** juvenile; **C–D,** adult (**A,C,** pterygoid tooth–plate, **B,D,** prearticular tooth–plate) (after Chang and Yu 1984, Smith and Chang 1990; Chang 1995). **E.** BT521, pterygoid tooth–plate. **F.** TO 5A, prearticular tooth–plate (after Tong–Dzuy Thanh and Janvier 1987; reversed from original). **G–H.** *Tarachomylax* (Barwick et al. 1997; reversed from original) (**G,** pterygoid tooth–plate; **H,** prearticular tooth–plate); **I–J.** *Andreyevichthys* (**I,** pterygoid tooth–plate; **J,** prearticular tooth–plate) (after Smith and

Krupina 2001). **K–L.** *Dipterus* (**K,** pterygoid tooth–plate, **L,** prearticular tooth–plate) (after Jarvik 1967). [planned for page width]