Brachiopods, crustaceans, vertebrates, and charophytes from the Devonian Ly Hoa, Nam Can and Dong Tho formations of Central Vietnam

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ABSTRACT
New vertebrate remains are described from the Ly Hoa Formation (Quang Binh Province, Central Vietnam). They provide further information about the morphology and phylogenetic position of the antiarch *Vukhuclepis lyhoaensis* within the Yunnanolepididae, the first evidence for a Petalichthyida, a
suborbital plate tentatively referred to a Holonematidae, and evidence that a third arthrodire (in addition to the former and *Lyhoalepis duckhoai*), possibly a brachythoracid, is present in this fauna. Some new sarcopterygian remains referred to a Youngolepididae are also described. Some fragments are referred, with reservations, to a galeaspid. Associated fragments referred to an undetermined phyllocarid crustacean, as well as an undetermined arthropod are described, in association with this vertebrate fauna. The presence of Yunnanolepididae, Youngolepididae, and possibly galeasps clearly confirms the South Chinese affinity of the Ly Hoa vertebrate fauna. Its age remains debated, but its composition is rather suggestive of a late Early Devonian, probably Emsian, age. A new Chonetidina, *Corbicularia noongdensis* n. sp., is described from the brachiopod fauna of the Nam Can Formation (Nghe An Province, Central Vietnam) and suggests a Givetian-Frasnian age for this formation. A new Chonetidina, *?Holynetes caurongensis* n. sp., as well as *?Dagnachonetes* sp. are described from the Dong Tho Formation (Quang Binh Province, Central Vietnam), and also suggest a Frasnian age for the middle part of this formation. The basal part of the Dong Tho Formation has yielded remains of an antiarch referred to *Bothriolepis* sp., as well as utricles of Charophytes referred to *Sycidium haikouense*, a species known elsewhere in the Givetian of China.

RÉSUMÉ

Brachiopodes, crustacés, vertébrés et charophytes des formations de Ly Hoa, Nam Can et Dong Tho du Viêt Nam central.

De nouveaux restes de vertébrés sont décrits dans la Formation de Ly Hoa (Province de Quang Binh, Viêt Nam central). Ils fournissent des données complémentaires sur la morphologie et la position phylogénétique de l’antiarche *Vukhuclepis lyhoaensis* au sein des Yunnanolepididae et permettent de mettre en évidence la présence d’un petalichthyide et d’un second arthrodire, probablement un brachythoracid, dans cette faune. Une plaque sous-orbitaire isolée est attribuée avec doute à un Holonematidae. Quelques nouveaux restes de sarcopterygiens, attribués à un Youngolepididae, sont également décrits. Quelques fragments sont attribués, avec réserve, à un galéaspide. Des fragments de crustacés phyllocarides et d’arthropodes indéterminés sont décrits dans cette faune. Par la présence de Yunnanolepididae et de Youngolepididae et, peut-être, de galéaspides, la faune de vertébrés de la Formation de Ly Hoa présente clairement des affinités avec celle du Dévonien inférieur du bloc sud-chinois. Son âge reste cependant incertain, bien que l’ensemble de la faune de vertébrés suggère un âge dévonien inférieur tardif, probablement emsien. Un nouveau Chonetidina, *Corbicularia noongdensis* n. sp., est décrit dans la faune de brachiopodes de la Formation de Nam Can (Province de Nghe An, Viêt Nam central) et suggère un âge givetien-frasnien pour cette Formation. Un nouveau Chonetidina, *?Holynetes caurongensis* n. sp., ainsi que *?Dagnachonetes* sp. sont décrits dans la faune de brachiopodes de la Formation de Dong Tho (Province de Quang Binh, Viêt Nam central) et suggèrent également un âge frasnien pour la partie moyenne de cette formation. La partie basale de cette formation a livré des restes d’un antiarche attribués à *Bothriolepis* sp., ainsi que des utricules de charophytes attribuées à *Sycidium haikouense*, connu par ailleurs dans le Givétien de Chine.
INTRODUCTION

For historical reasons, the geology of Central Vietnam (or Trung Bo) has been comparatively less studied than that of northern Vietnam (or Bac Bo). During the last decade, palaeontological field campaigns have focused on the Middle Palaeozoic of this region, with the aim of testing the biogeographical implications of certain tectonic models, which assumed the existence of a separate Indochina Plate as early as mid-Palaeozoic times.

In this framework, the first discovery of Palaeozoic vertebrate remains in Central Vietnam has been recorded by Long (1993), on the basis of isolated micro-remains found alongside conodonts by Pham Kim Ngan (Institute of Geology and Mineral Resources, Hanoi), in residues derived from the marine, Givetian, Muc Bai (= Quy Dat) Formation. Long (1993) mentioned lungfish and actinopterygian scales, as well as possible plate fragments of indetermined placoderms. In addition, Long (1993) recorded chondrichthyan and actinopterygian scales from the marine, Famennian, Xom Nha Formation of the same area. Since then, this program of palaeontological research has focused on the proximal marine and terrigenous facies of the Silurian and Devonian, in hope of finding essentially continent-bound taxa, which could provide a better biogeographical signal. This expectation has been met with the discovery of vertebrate remains and plants in the Devonian terrigenous deposits formerly referred to as the “Ly Hoa Sandstones”, and now known as the Ly Hoa Formation (Pham Huy et al. 1999), which...
provided evidence for vertebrate taxa hitherto unknown outside the South China (Yangtse) Block (i.e. South China and northern Vietnam). This suggested close biogeographical relationships between Central Vietnam and South China in Devonian times (Tong-Dzuy et al. 1996; Janvier et al. 1997). This was also confirmed by the discovery of “wanglepidid” placoderms in the Late Silurian Dai Giang Formation at My Duc, Quang Binh Province (Tong-Dzuy et al. 1997; Janvier et al. 2003), yet in a more markedly marine facies, and in association with a rich brachiopod and trilobite fauna. The Devonian fish fauna of the Ly Hoa Formation is associated with crustacean remains referred to phyllocarids, which are also described herein, and some poorly preserved bivalves and lingulids.

This project was carried further between 1997 and 2000, with the study of the shallow water facies of other Devonian formations of Central Vietnam, namely the Middle to Late Devonian Nam Can and Dong Tho formations. In this framework, rich invertebrate faunas have been discovered, alongside some stratigraphically significant fish remains and charophyte utricles described herein. The invertebrate fauna of the Nam Can and Dong Tho formations includes abundant but poorly preserved brachiopods, in particular new chonetids, which are described in the present article, and provide additional data on the age of these two formations.

All the material described herein belongs to the collection of the Geological Museum (Bao Tang Dia Chat, thereafter abbreviated as BT) of the Geological Survey of Vietnam, 6 Pham Ngu Lao, Hanoi.

THE DEVONIAN VERTEBRATES AND CRUSTACEANS FROM THE LY HOA FORMATION

GEOGRAPHICAL AND GEOLOGICAL SETTINGS

The first, large vertebrate remains from Central Vietnam were discovered by Dr. Nguyen Duc Khoa (Hanoi) in a clayey and dolomitic lense of the Ly Hoa Formation (then regarded as a lateral facies of the Dong Tho Formation) at Cape Ly Hoa, about 10 m west of the famous Da Nhay (“dancing rock”) natural monument (1, Fig. 1B). Further excavations made in this particular locality have yielded a number of dermal plates, all belonging to an arthrodire, Lyhoalepis duckhoai Tong-Dzuy, Janvier & Doan Nhat, 1994, except for a possible acanthothoracid plate fragment (Janvier et al. 1997: fig. 4F) and some fragmentary sarcopterygian scales. Since 1994, several field campaigns have been carried out in the Ly Hoa Formation, which is represented in the Ly Hoa area by thick series of massive, generally white sandstones and quartzites, and where vertebrate remains occur sporadically in particular lenses. This formation extends around Cape Ly Hoa (Fig. 1A, B) over a relatively small area but is intensively quarried for grinding and building stones, and numerous bomb impact craters and roadcuts provide additional outcrops. The vertebrate remains are not abundant, but collections made during the last 10 years have increased to some extent their taxonomic diversity. Now, we know that the Ly Hoa Formation also yields antiarchs, namely the yunnanolepiform-like Vukhuclepis lyhoaensis Janvier, Tong-Dzuy, Ta Hoa & Doan Nhat, 1997, and youngolepidid sarcopterygians (Janvier et al. 1997), which both clearly indicate biogeographical affinities with the South China (Yangtse) Block (Tong-Dzuy et al. 1996; Young & Janvier 1999). The new material collected in 2000 and described herein confirms this conclusion and provides possible evidence for the occurrence of galeaspids, which are yet another taxon hitherto regarded as endemic to the South China Block. This vertebrate material from the Ly Hoa Formation often occurs in association with crustacean remains, namely phyllocarids, some of which are also described below.

After the discovery of the first vertebrate-bearing lens near the Da Nhay, a number of other fossiliferous outcrops have been recorded from the Ly Hoa area. One of the richest outcrops is “locality 2” of Janvier et al. (1997), situated along the Ha Tinh-Dong Hoi highway, at the top of the Ly Hoa pass, and erroneously termed as a “small quarry” (2, Fig. 1C). Unfortunately, this outcrop has now practically disappeared, due to the enlargement of the highway. Conversely, this has resulted in a remarkable roadcut,
between the pass and the southern end of Ly Hoa beach, which has yielded a few fish remains, about 300 m north to the pass (3, Fig. 1C). At the level of locality 2, a road starts from the highway and leads to the numerous sandstone quarries situated further north and west (Fig. 1C). In 2000, a survey of all these quarries did not result in the discovery of much richer vertebrate-bearing outcrops. However, some of the quarries situated east of this road (4, Fig. 1C) have yielded a few antiarch remains and youngolepidid scales, a possible galeaspid fragment, and a petalichthyid plate has been found on an isolated block of fined-grained, clayey, white sandstone, a facies usually barren in this area. Three abandoned quarries that are situated at the point where the road curves to the west and passes to the other side of a small valley, turned out to be quite rich in vertebrate remains (5, Fig. 1C). Unfortunately, most of these remains are silicified and concentrated in extremely hard, ferruginous beds,
and their preparation is practically impossible. At the best, some specimens, generally seen in section on the surface of the blocks provide evidence for youngolepidid scales and bones, as well as relatively large antiarch plates (at any rate much larger than those referred below to \textit{Vukhuclepis}). In most outcrops of the Ly Hoa Formation, the vertebrate remains are silicified and this rules out hydrochloric acid preparation for obtaining a natural cast of the fossils. Conversely, when the vertebrate remains are not silicified, the bone is extremely fragile and breaks into minute prisms (see, e.g., Janvier et al. 1997: fig. 4H, I). The best type of preservation occurs in the more clayey and slightly dolomitic lenses, such as in locality 2, where the bones, albeit fragile, can be prepared with a needle.

**SYSTEMATICS**

\textbf{Phylum VERTEBRATA} Linnaeus, 1778  
\textbf{Class GALEASPIDA} Halstead Tarlo, 1967  
\textit{Galeaspida? gen. et sp. indet.}  
(Fig. 2)

Locality 4 has yielded an assemblage of strange, tuberculate fragments, which recall the lateral margin of a galeaspid head shield. Each of the tubercles seem to correspond to an individual unit and there is a clear suture line between adjacent units, as in some galeaspid. The tubercles are generally costulate, slightly spiniform near the natural margin of the fragments and some of them, which are
broken, seem to be hollow but crossed by scarce, thin fibres. In fact, thin sections reveal that the hard tissue itself is not preserved and that the fibres are probably internal casts of thin canals, filled with iron oxide. The aspect of this specimen recalls that of the tessellate exoskeleton fragment from the Lower Devonian of Qujing (Yunnan) referred to as an “asterosteid” rhenanid by Wang (1991), and which is more likely a fragment of a very large galeaspid. It is also strikingly similar to the exoskeleton of the unnamed Famennian galeaspid from Ningxia (China), figured by Pan (1987: pl. 2:2). However, the specimen from Ly Hoa differs from the latter two by its slightly costulate tubercles. At any rate, the structure and aspect of these fragments rule out any Palaeozoic arthropod known to date.

Class GNATHOSTOMATA Gegenbaur, 1874
Subclass PLACODERMI McCoy, 1848
Order ANTIARCHA Cope, 1885
Suborder YUNNANOLEPIDOIDEI Zhang, 1978
Family YUNNANOLEPIDIDAE Zhang, 1978
Genus Vukhuclepis Janvier, Tong-Dzuy, Ta Hoa & Doan Nhat, 1997

Vukhuclepis lyhoaensis Janvier, Tong-Dzuy, Ta Hoa & Doan Nhat, 1997 (Figs 3-9)

Antiarch remains are amongst the most abundant vertebrate remains in the Ly Hoa Formation, along with the youngolepidid sarcopterygian scales. To date, apart from the large plate fragments from locality 5 (Fig. 1C), there is no evidence for antiarchs other than Vukhuclepis lyhoaensis, which is quite distinctive due to its finely tuberculated ornamentation and very small size. It is not ruled out, however, that several species of this genus may occur in this fauna, yet currently available material does not indicate specific diversity. The material of V. lyhoaensis described by Janvier et al. (1997: figs 4A-D; 5-7) essentially consisted of plates of the thoracic armour, a poorly preserved paranuchal plate, and a presumed pectoral appendage. New collections add further information about the structure
Fig. 5. — Vukhuclepis lyhoaensis Janvier, Tong-Dzuy, Ta Hoa & Doan Nhat, 1997, Ly Hoa Formation, ?Lower Devonian, Ly Hoa, Quang Binh Province, Vietnam: A, left anterior ventrolateral plate in ventral (A1), dorsal (A2) and lateral (A3) aspects (BT 207e), associated with a left anterior dorsolateral plate (ADL) (BT 207f); B, right anterior ventrolateral plate, impression of the external surface (BT 207g); C, right anterior ventrolateral plate, impression of the ventral surface (BT 207h). Scale bars: 5 mm.
Fauna and flora from Devonian of Central Vietnam

Vukhuclepis lyhoaensis Janvier, Tong-Dzuy, Ta Hoa & Doan Nhât, 1997, Ly Hoa Formation, ?Lower Devonian, Ly Hoa, Quang Binh Province, Vietnam: A, camera lucida drawings of the anterior ventrolateral plate BT 207e (Fig. 5A), completed by information from the counterpart of the specimen and the contralateral AVL plate, in ventral (A1), dorsal (A2) and lateral (A3) views, and brachial recess in posterior view (A4); B, right anterior ventrolateral plate, impression of the lateral lamina of the specimen in Figure 5C (BT 207g); C, left anterior dorsolateral plate in lateral view (BT 207f; ADL, Fig. 5A2). Abbreviations: bra, brachial recess; cbr, possibly endoskeletal crest on the lateral wall of the brachial recess; grc, groove for the “Chang’s organ”; itca1, itca2, anterior and posterior branches of the anterior internal transverse crest; oaMV, overlap area of the median ventral plate; oaPL, overlap area for the postrolateral plate; oaPVL, overlap area for the posterior ventrolateral plate; ppc, prepectoral corner; rid, ridges on the anterior surface of the foremost branch of the anterior internal transverse crest; ?sut, possible suture between the spinal and AVL plate, or sensory-line groove. Scale bar: 1 mm.
of the thoracic armour and allow the description of two plates of the head armour, namely the nuchal and paranuchal plates.

DESCRIPTION

*Nuchal plate (Nu)*
The nuchal plate (Figs 3A; 4A) is roughly rectangular in shape and has the same general outline as that of the other, non-euantiarchan antiarchs; that is, relatively elongate in shape anteroposteriorly, and with a broad anterior embayment for the postpineal plate (oaPp, Fig. 4A2). Its dorsal surface is markedly vaulted and ornamented with evenly distributed, rounded tubercles (Figs 3A1; 4A1). Posteriorly, it shows a short portion of the supra-occipital cross-commissural sensory-line groove (scom, Fig. 4A1). The external openings for the endolymphatic ducts are situated about half-way between the midline and the posterolateral angle of the plate (ede, Fig. 4A1). The posterior margin of the plate is bordered with a broad and well marked obtected nuchal zone which is produced into a short median process (obt, Fig. 4A1). Its ventral surface shows a prominent, triangular supra-occipital thickening, posteriorly hollowed by a pair of pits for the supra-occipital neurocranial processes (poc, Fig. 4A2). The overlap areas for the paranuchal and lateral plates are approximately equal in size (oaPNu, oAL, Fig. 4A). As a whole it compares best with the Nu plate of *Yunnanolepis* (e.g., Zhang 1980: pl. 1:1; Tong-Dzuy & Janvier 1990: figs 11, 12), except for the position of the external openings of the endolymphatic duct, which are more medially placed in *Yunnanolepis*.

*Paranuchal plate (PNu)*
A poorly preserved plate, showing only the basal bone lamella, is interpreted here as a possible PNu plate (Figs 3B; 4B). It is roughly trapezoidal, with at least two distinct overlap areas for the Nu and lateral (L) plates, respectively (oaNu, oAL, Fig. 4B). As far as can be seen, its overall shape would agree with that of the PNu plate of *Yunnanolepis*.

*Anterior median dorsal plate (AMD)*
A very small and poorly preserved AMD plate (Fig. 3C) shows much the same proportions as the larger specimen figured by Janvier et al. (1997: fig. 4B), with traces of the radiating ridges and tubercles of the dorsal surface. It confirms that the two overlap areas for the anterior dorsolateral plates did not meet anteriorly, as suggested by Janvier et al. (1997: fig. 6C) on the basis of another, incomplete AMD plate.

*Anterior ventrolateral (AVL) plate*
The AVL plate is known from several incomplete specimens, including the holotype (Janvier et al. 1997: fig. 4A). One of the characters mentioned in the diagnosis of *Vukhuclepis lyhoaensis* by Janvier et al. (1997) is the very short and almost square-shaped AVL plate. However, the lack of overlap areas for the median ventral (MV) plate now suggests that this specimen may not be complete and that part of its posterior margin was broken off. Yet the missing part of the plate may not be large, as there is a small remnant of the ventrolateral recess, which straddles the AVL-PVL suture (Janvier et al. 1997). In the new material collected in 1997, two AVL plates were found in association with an ADL plate and probably belong to the same, crushed thoracic armour (Fig. 5A, C). The outline of the AVL plate can be reconstructed by combining the part and counterparts of the plates of either sides (Fig. 6A2) and looks quite different from that of the holotype, with a very distinct, oblique, posteromedial overlap area for the MV plate (oaMV, Fig. 6A2). In this respect, it is thus quite similar to the AVL plate of all other antiarchs. In all AVL plates of *Vukhuclepis*, the brachial recess (bra, Fig. 6A3, A4) is very small and limited anterolaterally by a short prepectoral corner (ppc, Fig. 6A1, A2). In one of these plates, the ornamentation of the prepectoral corner and the area around the brachial recess is made up by much larger tubercles than on the remaining surface of the plate, and this area seems to be delimited by a row of tubercles, which suggest either a suture or a sensory-line groove (?sut, Fig. 6A1). The trace of a suture between the spinal plate and the AVL plate occurs in *Yunnanolepis porifera* Zhu, 1996 (Zhu 1996: fig. 7H, K), and a sensory-line groove is present in this area, yet closer to the brachial recess, in *Chuchinolepis dongmoensis* Tong-Dzuy & Janvier, 1990 (Tong-Dzuy & Janvier 1990:...
Fig. 7. — Vukhuclepis lyhoaensis Janvier, Tong-Dzuy, Ta Hoa & Doan Nhat, 1997, Ly Hoa Formation, ?Lower Devonian, Ly Hoa, Quang Binh Province, Vietnam: A, posterior dorsolateral plate (PDL) in dorsal view and posterior median dorsal (PMD) plates in ventral view (BT 207i and 207j, respectively); B, same specimens as in A, after preparation by transfer on resin, and with an associated posterolateral plate (PL); posterior dorsolateral plate (PDL) in ventral view and and posterior median dorsal (PMD) plates in dorsal view. Photographed in immersion in water. Scale bar: 5 mm.

fig. 21A). The anterior internal transverse crest is visible in one of the new specimens and appears similar in structure to that of the holotype. In fact, it is double and consists of one short and massive posterior crest (itca2, Fig. 6A2), and one, long and slender anterior crest (itca1, Fig. 6A2), separated by a shallow groove. The anterior surface of the anterior crest, which forms the postbranchial lamina proper, is ornamented with three or four transverse, parallel ridges (rid, Fig. 6A2), as in some
other non-euantiarchan antiarchs (e.g., *Chuchinolepis*; Tong-Dzuy & Janvier 1990: fig. 21B; Zhu 1996: figs 22, 23). The lateral lamina of the AVL plates displays at least two oblique ridges, which converge toward the brachial recess (Figs 5B; 6B) and, internally, a broad overlap area of the postero-lateral plate (oaPL, Fig. 6B). No detail could be observed inside the brachial recess (bra, Fig. 6A3, A4), except for a small, longitudinal, lateral ridge (cbr, Fig. 6A4), possibly made up by perichondral bone, and which is visible thanks to the broken extremity of the prepectoral corner.

**Anterior dorsolateral plate (ADL)**

A small anterior portion of ADL plate is associated with the two AVL plates mentioned above (ADL,
Fig. 5A2). Ventrally to its articular area, its anterior margin is developed into a massive knob, ornamented with large outgrowths. Further ventrally, a large, vertical groove extends along the anterior margin of the plate (grc, Fig. 6C). This groove occupies the position of the small recess referred to by Zhu (1996) as the “cavity for the Chang’s organ”, shared by Yunnanolepis and Phymolepis. However, Young & Zhang (1996: fig. 5B) showed that, at any rate in Phymolepis, this recess houses a very small, vestigial, anterolateral (AL) plate, possibly subdivided into two elements, and it was probably the same in Vukhuclepis.

**Posterior dorsolateral (PDL) and posterolateral (PL) plates**

In close association with the posterior median dorsal plate described below (PMD, Fig. 7) is an isolated PDL plate (PDL, Fig. 7). Both plates presumably belong to the same individual. The PDL plate is incomplete but shows most of its lateral lamina and patches of its dorsal lamina, which seems to have been relatively broad. The main lateral-line groove is broad and runs close to the dorsolateral ridge (mll, Fig. 8A2). The posterior part of the dorsal lamina is marked by a broad, posteromedially directed ridge (pdr, Fig. 8A2), which corresponds, on the internal surface, to the position of the thick internal posterior transverse crest (itcp, Fig. 8A1). This broad ridge probably met, medially, a short transverse elevation of the PMD plate (pdr, Fig. 8B2), that branched off posterolaterally from the anterior median dorsal process of this plate (pda, Fig. 8B2). The main lateral-line groove on the lateral lamina sends off a small dorsomedial branch that continues on the dorsal lamina along the anterior limit of this broad ridge (dslg, Fig. 8A2). The two patches that remain of the anteromedial part of the dorsal lamina also show a slight elevation and seem to correspond to two other, anteromedially directed ridges (Fig. 8A2), which were prolonged on the AMD plate, where similar ridges also occur (Fig. 9; Janvier et al. 1997: fig. 4B1). Such large dorsal ridges, mostly radiating from the centre of the AMD plate, but also from the anterodorsal corner of the ADL plate and the posterodorsal corner of the PDL plate, are a widespread character among early antiarchs. However they are best marked in the closely related genera Phymolepis and Mizia (Zhang 1978: pl. 6; Zhu 1996: pls 1, 2, figs 10, 11). In most of the trunk-armour plates of Vukhuclepis, the bone extending between these ridges is extremely thin, and almost unornamented externally, whereas the radiating ridges are thick and bear conspicuous tubercles. This, again, recalls Mizia longhuaensis Zhu, 1996 (Zhu 1996: fig. 10A, C, pl. 2:8, 10) from the Early Devonian (probably Pragian) Xujiachong Formation of Yunnan. Along the ventral margin of the lateral lamina of this PDL plate lies a narrow strand of dermal bone, ornamented with tubercles, and which is most probably a remnant of a slightly displaced PL plate (PL, Figs 7B; 8A2).

**Posterior median dorsal plate (PMD)**

An imperfect PMD plate (PMD, Fig. 7; Fig. 8B), which lies close to the PDL and PL described above, provides additional information to the first description by Janvier et al. (1997: figs 4C, 6B). Its posterior margin forms a blunt angle and...
Racheboeuf P. et al.

Fig. 10. — ?Holonematidae gen. et sp. indet., Ly Hoa Formation, ?Lower Devonian, Ly Hoa, Quang Binh Province, Vietnam, left suborbital plate in external (A) and internal (B) views (BT 207): A1, B1, photographs in immersion in water; A2, B2, camera lucida drawings. Abbreviations: ar, anterior vertical ridge; cusoa, anterior cutaneous sensory pit; ioc, infraorbital section of the postorbital sensory-line groove; orbn?, presumed orbital notch; sorg, supraoral groove; th, crescentiform dermal bone thickening supporting the palatoquadrate. Scale bar: 10 mm.

tapers posteriorly into a process (pdp, Fig. 8B), the ventral surface of which is ornamented with large pointed tubercles (Fig. 8B1). Ventrally, the anterior limit of this ornamented surface is bordered by a slight groove (gr, Fig. 8B1), which, in turn, is separated from the posterior ventral median process and pit (prmvp, Fig. 8B1) by a deep depression. Although slightly distorted, the dorsal surface of the PMD plate clearly shows a well developed anterior median dorsal process (pda, Fig. 8B2), separated from the posterior margin of the plate by a depressed area (dep, Fig. 8B2). This condition is strikingly similar to that in the genus Phymolepis, from the Cuifengshan Group of Yunnan (Zhang 1978: figs 10, 12, pl. 6:2, 3; Zhu 1996: figs 11B, C, 12, 14A-C).

REMARKS
A reconstruction of the thoracic armour of Vukhuclepis is attempted (Fig. 9), on the basis of various, isolated and associated plates described here and by Janvier et al. (1997). When the PMD and PDL plates described above, which are likely to belong to the same individual, are assembled so that their respective posterior limits are aligned, the massive, posterior internal transverse crest of the PDL plate is oriented in such a way that it most probably passed anteriorly to the posterior ventral median process of the PMD plate (prmvp, Fig. 8B1). At any rate, the part of the PMD plate that extends laterally to this process does not show any thickening that would indicate the presence of the medial part of the posterior internal transverse crest. This
character is unique to the Yunnanolepididae sensu Zhu (1996); that is, the clade including Yunnanolepis, Mizia and Phymolepis. Vukhuclepis is thus probably to be included in this clade. Although it is still incompletely known, in particular as to its skull roof, its overall morphology may have been quite similar to that of, e.g., Yunnanolepis porifera Zhu, 1996 (Zhu 1996: fig. 4).

Order ARTHRODIRA Woodward, 1891
Suborder PHLYCTAENIOIDEI Miles, 1973
Infraorder BRACHYTHORACI Gross, 1932
Family ?HOLONEMATIDAE Obruchev, 1932

?Holonematidae gen. et sp. indet.
(Fig. 10)

An isolated, incomplete suborbital plate from locality 4 (Fig. 1C) is tentatively referred to a holonematid. Although its ornamentation, which consists of more or less parallel, sinuous rows of tubercles (Fig. 10A), recalls that of the arthrodire Lyhoalepis duckhoai, previously described from the Da Nhay outcrop of Ly Hoa (locality 1, Fig. 1B; Tong-Dzuy et al. 1994; Janvier et al. 1997), it is unlikely that this suborbital plate belongs to Lyhoalepis. The latter displays essentially phlyctaenid-like characters that do not accord with the holonematid-like characters of this suborbital plate, such as, the large embayment (orbn?, Fig. 10A2) of its dorsal margin, which is suggestive of the posteriorly placed orbital emargination of the holonematid Holonema (Miles 1971: fig. 33A).

The external surface of the plate clearly shows three sensory-line grooves that meet anteriorly to its central area. The postorbital sensory-line groove enters the plate dorsally behind a dorsal process and runs anteroventrally (ioc, Fig. 10A2), but its connection to its ventral, infraorbital portion cannot be observed, owing to the poor preservation of the plate. The infraorbital portion of this groove then bends anteriorly, much in the same way as in eu-brachythoracid arthrodires. The supra-oral sensory-line groove is broad and posteroverventrally directed (sorg, Fig. 10A2). Immediately behind it, and close to the point of junction of the three grooves is a large, rounded sensory pit (cusoa, Fig. 10A2). There is evidence neither for a post-suborbital groove, nor for a distinct post-suborbital plate. Unfortunately, the anterodorsal part of the plate is missing, and this would have been crucial to rule out a more anterior position of the orbital margin.

The internal surface of the plate shows a well marked, vertical ridge (ar, Fig. 10B2), meeting the dorsal margin of the plate at the level of its anterodorsal process that bounds anteriorly the presumed orbital notch. Ventrally, it joins a crescentiform knob (th, Fig. 10B2), which is surrounded anteriorly by a spongiose area of the plate surface. This knob probably corresponds to the anterior palatoquadrate thickening of Holonema, for the attachment of the autopalatine.

Interestingly, this suborbital plate resembles somewhat that of Bimbianga burrinjuckensis Young, 2005, an Early Devonian (Emsian), supposedly primitive, holonematid with tuberculate ornamentation, from Burrinjuck, Australia.

Brachythoraci fam. indet.
(Fig. 11)

A few plate fragments also suggest the presence of a second arthrodire, and presumably yet another brachythoracid in the Ly Hoa fauna. In particular, a portion of a relatively large, gently curved plate,
ornamented with rounded tubercles and bearing a large overlap area (oa, Fig. 11), belongs to an arthrodire, which is certainly different from *Lyhoalepis* because all the thoracic plates and probably the skull-roof plates of the latter are fused and show no overlap surfaces (Tong-Dzuy *et al.* 1994). The shape of the overlap area and the curvature of this plate is somewhat suggestive of the dorsal part of the PDL plate of such a brachythoracid as *Coccosteus* (Miles & Westoll 1968: fig. 32).

**Order PETALICHTHYIDA Jaekel, 1911**

Petalichthyida indet.

(Fig. 12)

Petalichthyids (possibly macropetalichthyids) are now evidenced in the Ly Hoa fauna by an anterior ventrolateral plate associated with the proximal portion of a spinal plate (AVL, Sp, Fig. 12). In addition, it is probable that the spinal plate fragment figured by Janvier *et al.* (1997: fig. 4G) also belongs to this taxon. The AVL plate is exposed in internal aspect, but it is so thin that its external ornamentation of concentric ridges is clearly visible in immersion. The Sp plate is ornamented with parallel ridges and bears a lateral series of pointed tubercles. The overall shape of the specimen is almost point-for-point similar to the corresponding part of the thoracic armour in *Lunaspis broili* Gross, 1961, from the Emsian of Germany.

**Subclass OSTEICHTHYES Huxley, 1871**

**Infraclass SARCOPTERYGII Romer, 1955**

(Figs 13-15)

Apart from isolated scales, sarcopterygian remains are rare in the Ly Hoa fauna, but two new specimens are worth describing. Specimen BT 207n shows the internal impression of a large dermal plate (Fig. 13), whose margins still retain a very
Fauna and flora from Devonian of Central Vietnam

small strand of cosmine-covered bone. Owing to the lack of landmarks, such as the sensory-line canals or large sensory pores, the identity of this plate is quite difficult to determine. Considering its size and overall shape, it could be either an opercular, or a “cheek plate” (composed by the fused squamosal, quadratojugal and preopercular in certain basal dipnomorph and tetrapodomorph sarcopterygians, such as the Youngolepididae and Kenichthys). In the latter case, its outline would best agree with the cheek plate of Kenichthys (Chang & Zhu 1993: fig. 7F) and differs notably from those of Youngolepis described to date, whatever their wide range of individual variation (Tong-Dzuy & Janvier 1990: fig. 31A; Chang & Zhu 1993: fig. 13A). Only an isolated bone, presumably from the opercular series of Youngolepis and figured by Tong-Dzuy & Janvier (1990: pl. 7:7), bears some resemblance to this specimen.

The second sarcopterygian specimen is an isolated jaw bone (Fig. 14), interpreted here as either a dermopalatine or an ectopterygoid. It shows a large tusk insertion pit and one poorly preserved tusk (pt, t, Fig. 14B). The latter is sectioned near its base and displays a polyplocodont structure (pld, Fig. 14B). The lateral margin of this bone is covered with fields of denticles (dtc, Fig. 14B), as
in the dermopalatine, ectopterygoid and coronoids of *Youngolepis* (Chang 1991). In addition, many cosmine-covered scales occur in the Ly Hoa Formation. As a whole, they agree with those of *Youngolepis*, and generally show series of relatively large cosmine pores and dentine ridges in the anterior part of their external surface (Fig. 15).

Phylum ARTHROPODA von Siebold, 1845
Subphylum PANCRUSTACEA
Zrzavý & Štys, 1997
Class MALACOSTRACA Linnaeus, 1778
Subclass PHYLLOCARIDA Packard, 1879

Phyllocarida gen. et sp. indet. (Fig. 16A)

A single probable phyllocarid representative has been collected at Ly Hoa, in an isolated block near locality 4 (Fig. 1C). Despite its questionable taxonomic assignment and its poor preservation, it is mentioned here in order to call the attention of future investigators. The specimen (Fig. 16A) was found on the bedding plane of a white, silty level, interbedded with sandstone beds. It was possibly complete initially, yet disarticulated, and its carapace, as well as its abdomen and appendages are strongly weathered. Its assignment to phyllocarid crustaceans rests on the ornament preserved on a small part of the carapace, which exhibits only narrow, undulating and anastomosing longitudinal ridges (a, Fig. 16A), of either ceratiocaridid or rhinocaridid type (Rolfe 1969; Racheboeuf 1994). Another carapace fragment of the same specimen, which may possibly belong to the posterior margin of the carapace, looks like a rounded margin and bears two short, laterally flattened spines, suggestive of the carapace margin of several representatives of the genus *Echinocaris*. Two, flattened fragments with a possibly spinose margin (b, Fig. 16A) may be abdominal segments.

Fig. 16. — Arthropoda, Ly Hoa Formation, ?Lower Devonian, Ly Hoa, Quang Binh Province, Vietnam: A, Phyllocarida gen. et sp. indet. (BT 207r); a, carapace fragment; b, possible abdominal segments; B, C, *Sinocaris*-like carapace; B, camera lucida drawing of BT 203q; C, camera lucida drawing of BT 203s (C1, part; C2, counterpart). Scale bars: 5 mm.

?Arthropoda incertae sedis
(Fig. 16B, C)

Janvier *et al.* (1997: figs 9, 10) briefly described a few arthropod remains from the Ly Hoa (“Dong Tho”) Formation. Some of them are large, peculiar carapaces ornamented with sharp, parallel and sometimes sinuous ridges, but these are not suggestive of any phyllocarid ornamentation known to date. Two of the specimens, one of which is almost complete, are illustrated here anew and more in detail (Fig. 16B). As pointed out by Janvier *et al.*
Fauna and flora from Devonian of Central Vietnam

(1997: 409) these specimens are quite similar to the presumed bivalved arthropod *Sinocaris asiatica* Mansuy, 1912 (Mansuy 1912: pl. 5:10, 11), from the Lower Devonian of eastern Yunnan. However, Rolfe (1969) wondered whether this taxon was an arthropod or a bivalve mollusc. At any rate, and assuming that the Ly Hoa specimens do belong to *Sinocaris* Mansuy, 1912, the remnants of their actual carapace are clearly made of calcium phosphate. Small carapace fragments have been sampled from the margin of specimen BT 203r (Janvier et al. 1997: fig. 9) and their structure in thin section shows a peculiar, spongiose layer, lined externally and internally by a lamellar layer. This certainly does vaguely recall the structure of bone, although its recrystallization precludes any further identification. However, the trabecules of calcified tissue of the spongiose layer are strangely folded, and thus unlike those of typical spongiose bone. This structure is, at any rate, entirely different from that of any bivalve mollusc. Although the wavy ornamentation of these carapaces somewhat recalls that of petalichthyids (which occur in this formation; see above) and phyllolepids, none of them would agree with the shape of any dermal plate of these placoderms. Provisionally, we would thus consider these specimens as possible arthropod carapaces and, if actually similar to *Sinocaris*, one more taxon shared by the Devonian of Central Vietnam and the South China Block.

**AGE OF THE LY HOA FAUNA**

The age of the Ly Hoa Formation remains a riddle. It was first regarded as a lateral facies of the Dong Tho Formation and dated as Givetian on the basis of its plant and spore assemblages, and of its presumed correlation with the Dong Tho Formation and the marine Muc Bai Formation (Tong Duy 1993; Tong- Lizuy et al. 1994; Tong-Dzuy & Cai 1995). However, owing to the uncertainty as to this correlation, Pham Huy et al. (1999) erected the name Ly Hoa Formation for the sandstone outcrops of the Cape Ly Hoa area and regarded this formation as a possible lateral facies of the Bao Giang and Rao Chan formations. All that is known at the moment is that it may be conformably overlain by the Givetian Minh Le Formation and, since its basal part is not known, it is provisionally regarded as Early to Middle Devonian in age (Tong-Dzuy in Vu Khuc et al. 2000). Apart from poorly informative bivalves, lingulids, crustaceans and plant debris, the only well preserved fossils from the Ly Hoa Formation are fishes, on which one has to rely for its dating. However, one remains faced with the problem of the presence of somewhat anachronistic taxa, already alluded to by Janvier et al. (1997).

Particularly problematic is the co-occurrence of a yunnanolepidid antiarch (*Vukhuclepis*), a possible acanthothoracid and presumed youngolepidid sarcopterygians on the one hand, and relatively advanced arthrodires (a holonematid and another possible brachythoracid) and a petalichthyid on the other hand (the presence of a galeaspid in the Ly Hoa Formation needs to be confirmed by the discovery of better preserved material). The first three are suggestive of a Lochkovian-Pragian age, whereas the latter are unknown before the late Emsian. All these taxa occur together, in the same beds, and one can rule out the possibility that they belong to two different parts of the formation. The Ly Hoa Formation has never yielded any euantiarch remains (a taxon that is now recognised in the lower part of the Dong Tho Formation [see below]), although its facies is exactly of the type where one could expect euantiarchs, such as bothriolepidids, if younger. This further confirms that the Ly Hoa Formation cannot be a lateral facies of the Dong Tho Formation.

There remains the question of the fossil flora of the Ly Hoa Formation, which consists of poorly preserved stems and leaves of lepidodendrales lycoptyes referred to as *Knorria* sp., *Protoplodendron* sp. and *Lepidodendropsis* sp. (determined by Dr. Cai Chongyang, Nanjing; see Tong-Dzuy & Cai 1995), and suggests a Middle Devonian (probably Givetian) age. Such a rather late age is inconsistent with the fish assemblage described above, in particular the presence of yunnanolepidid antiarchs, acanthothoracids and youngolepidid sarcopterygians which have hitherto never been recorded from the Middle Devonian. However, on account of the presumed Middle Devonian age of the Ly Hoa Formation,
Tong-Dzuy et al. (1994, 1996) and Janvier et al. (1997) suggested that this discrepancy could be explained by the endemism of these fish taxa on the so-called “Indochina Block”. This hypothesis now seems less and less likely, as no other more advanced fish taxa, such as euantiarchs, has ever turned up in association with the Ly Hoa fauna, apart from a Lunaspis-like petalichthyid and possible brachythoracid arthrodira, which would be consistent with an Emsian (or somewhat younger)
Fauna and flora from Devonian of Central Vietnam

However, it should be pointed out here that no fish has been found yet in clear association with the supposedly Middle Devonian lycophyte remains. The lycophyte stems all come from the quarry of Hoi Da, near the Minh Le railway station, northwest to Ly Hoa Pass, which yields no fish remains. Conversely, the only plant remains found to date at Ly Hoa are very elongate imprints, which may possibly be lycophyte leaves and occur essentially along the coast in cross-bedded and fine-grained sandstone, about 200-300 m south of the Da Nhay (Fig. 1B).

One possibility is thus that the fish remains are not of the same age as the plant remains, and that the Ly Hoa Formation is diachronous and ranges from the late Early Devonian to the Givetian. Another possibility is that the tectonics or the stratigraphy of the Ly Hoa sandstones is more complex than previously thought, and that we are dealing with two different sandstone formations (as in the case of the Do Son Formation of the Hai Phong area in northern Vietnam; Janvier & Tong-Dzuy 1998; Janvier et al. 2003). A thorough re-examination of all the outcrops referred to the Ly Hoa Formation is thus necessary.

NEW BRACHIOPODS FROM THE NAM CAN FORMATION

GEOLOGICAL SETTING

The Nam Can Formation is exposed along narrow bands in the Muong Xen area (Nghe An Province; locality MX 1, Fig. 17A) and rests conformably upon the Middle Devonian Huoi Loi Formation. It is conformably overlain by the Lower Carboniferous Huoi Poc Formation. In the section of the Noong De Pass (or Bactelemi [Barthelemy] Pass, Ky Son district, Nghe An province) section, the Nam Can Formation is regarded as being composed of four members, from base to top:

− 1: about 200 m thick, medium- to thick-bedded, dark-grey, bituminous limestone, which yields numerous remains of Amphipora Schulz, 1883, referred to Amphipora cf. A. pinguis Yavorsky, 1957 and A. ramosa minor Riabinin, 1932;
− 2: about 140 m thick, medium- to thin-bedded, dark-grey marls and marly limestone. The colour of the marls usually turns to a yellow-grey, green-grey and brown colour owing to weathering. Many corals, dacyroconarid and brachiopods occur in the marly limestone beds and are referred to Thamnopora polyforata (Schlotheim, 1820), Thamnophyllum sp., Homocenetus sp., Yunnanellidae gen. et sp. indet., Desquamatia sp. and a new species of the genus Corbicularia (see below);
− 3: about 60 m thick, medium- to thick-bedded, light-grey limestone. Some ramiform stromatopoids, such as Stachyodes costulata Lecompte, 1952, S. fasciculata Dong & Wang, 1989 and S. insignis Yavorsky, 1963, were collected in the lower part of this member;
− 4: about 30 m thick, thin-bedded, stripped, light-grey, brownish or redish lenticular and nodular limestones.

Based on these fossil assemblages the Nam Can Formation has been referered by Vu Khuc (1984) and Nguyen Huu et al. (1995) to the Givetian-Frasnian.

SYSTEMATICS

Phylum BRACHIOPODA Duméril, 1806
Order PRODUCTIDA
Sarytcheva & Sokolskaja, 1959
Suborder CHONETIDINA Muir-Wood, 1955
Family ANOPLIIDAE Muir-Wood, 1962
Subfamily CAENANOPLIINAE Archbold, 1980
Genus Corbicularia Lyaschenko, 1973


DISCUSSION

In the literature, four chonetoidean genera, namely Striatochonetes Mikrjukov, 1968, Rhyssochonetes Johnson, 1970, Corbicularia Lyaschenko, 1973, and Cedulia Racheboeuf, 1979, have been defined as including in their diagnosis concentric fila crossing the radial ornament. Cedulia has already been considered as a junior synonym of Rhyssochonetes (Racheboeuf 1981, 2000). The relationships between Striatochonetes, Rhyssochonetes, and Corbicularia have
also been discussed (Johnson 1978; Racheboeuf 1981), but the question remained unanswered, mainly because the preservation of the original specimens is different. The former of these three genera, *Striatochonetes*, was defined with *Strophomena setigera* Hall, 1843 as the type species. However *Strophomena setigera* exhibits no more than three to four concentric growth lines and lacks the typical concentric fila which are included in the original diagnosis, as established by Johnson (1978), and which are well developed in *S. krylovae* Mikrjukov, 1968 (Mikrjukov 1968: pl. 33, figs 3, 4). The genus name *Striatochonetes* has thus to be restricted to the type species *S. setigera* Hall, 1843, until the species is carefully revised.

The shell of *Corbicularia* Lyaschenko, 1973 is morphologically very close to that of *Rhyssochonetes* Johnson, 1970, and Johnson (1978: 125) considered that *Corbicularia* was a probable junior synonym of *Rhyssochonetes*. The main difference lies in: 1) a less transverse, more rounded, shell outline in *Corbicularia* than in *Rhyssochonetes*; 2) the orientation of the spines, which are at 45° in *Rhyssochonetes*, and high-angled to perpendicular in *Corbicularia*; and 3) the development of a pair of long but faint accessory septa in *Corbicularia*, at least in the species *C. cracoviensis* Balinski, 1979. Although the species assigned to *Corbicularia*, all from the Givetian and Frasnian of the Russian Platform, are poorly known internally, the two genera, *Rhyssochonetes* and *Corbicularia*, are here still provisionally regarded as distinct. The species *Striatochonetes? parisii* Racheboeuf, 1981, and *S.? goasquellouensis* Racheboeuf, 1981 are reassigned to *Corbicularia* according to their shell size and outline, and high-angled spines.

**Corbicularia noongdensis** n. sp.  
(Fig. 18A-I)

**Holotype.** — External mould of a ventral valve (BT 231b; Fig. 18B).

**Etymology.** — From the name of the type locality, the Noong De Pass.

**Locality and Age.** — Noong De (Bactelemi) Pass, Ky Son district, Nghe An Province, Central Vietnam. Middle part of the Nam Can Formation, Givetian-Frasnian (MX 1, Fig. 17A).

**Material examined.** — More than 50 decalcified isolated internal and external moulds of both valves, and external moulds of articulated shells, most of them tectonically distorted. Some specimens are illustrated in Figure 18A, C-I.

**Diagnosis.** — Small shell with a maximum of 32 ventral costellae, increasing by intercalation only, with 6-7 costellae per mm along anterior margin; two pairs of orthomorph, high-angled spines.

**Description**

Very small shell (maximum length: 2.4 mm; corresponding width: 3.2 mm), weakly transverse in outline, with moderately and regularly convex ventral valve, and weakly concave dorsal valve. Maximum width at hinge line. Ventral interarea flat, apsacline with small, prominent pseudodeltidium; dorsal interarea low and hypercline with small chilidium. Ornament of low, rounded costellae with a maximum of 32 costellae along the commissure; six to seven costellae per mm along anterior margin. Costellae increasing by intercalation only in ventral valve, and by bifurcation only in dorsal one. Radial ornament crossed by very thin concentric fila. Two orthomorph, high-angled, and symmetrically displayed spines on each side of beak, respectively at about 0.7 mm and 1.8 mm from beak.

Ventral valve interior with myophragm not extending anteriorly beyond one third the valve length. Diductor scars poorly impressed; adductor scars oval to semi-elliptical in outline, well limited. Teeth not observed. Periphery of the valve impressed by the outer ornament.

Dorsal valve interior with a very short brevisep- tum originating anteriorly to a narrow, elongate cardinal process pit. Cardinal process not observed. Two radial rows of stouter endospines, spinose accessory septa, on each side of the brevisep- tum, and reaching anterior margin of the valve. Inner socket ridges long and narrow, extending laterally parallel to hinge line. Anderidia very small but well defined, anteriorly divergent at about 90°. Muscle scars indistinct. Surface of the valve covered with relatively coarse, spaced and radially arranged endospines.
COMPARISON

By its external morphology, and its internal features as well, this new species from Vietnam is close to *Corbicularia parisi* (Racheboeuf, 1981) and *C. goasquellouensis* (Racheboeuf, 1981), both from the Frasnian of the Massif Armorican, France. However, *C. noongdensis* n. sp. exhibits a smaller shell, with thinner radial ribs (6 to 7 per mm). *C. parisi* has four costellae per mm along the anterior margin, and *Corbicularia goasquellouensis* five costellae in the same interval. *Corbicularia noongdensis* n. sp. has two spines on each side of the beak, like *C. parisi*, but the ventral costellae increase by intercalation only in *C. noongdensis* n. sp., instead of increasing by bifurcation, with rare intercalations towards the shell margin, in *C. parisi*. The ornament is quite similar to that of *C. goasquellouensis*, but the radial ribs are thinner, and the Armorican species has only one pair of spines instead of two.
DISTRIBUTION
To date, *Corbicularia noongdensis* n. sp. is only known from the Givetian-Frasnian of Central Vietnam. Other species of the genus *Corbicularia* are all late Givetian or Frasnian. In North Timan and the Volga-Ural region of Russia, *Corbicularia menneri* (Lyaschenko, 1958) occurs in the upper part of the lower Frasnian. *C. cracoviensis* Balinski, 1979 has been described from the lower Frasnian (Lower asymmetricus zone) of the Debnik Antiline, in southern Poland. In the western Massif Armorican, *C. parisii* is restricted to the upper part of the Kergarvan Formation (uppermost Givetian, hermanni-cristatus zone), while *C. goasquelloensis* ranges through the Traonliers Formation (lower Frasnian, asymmetricus zone).

NEW BRACHIOPODS, FISHES AND CHAROPHYTES FROM THE DONG THO FORMATION

**GEOLOGICAL SETTING**
The Dong Tho Formation is exposed in narrow bands in the western part of the Quang Binh and Ha Tinh provinces. In the Cau Rong section (localities CR1, CR2, Fig. 17B), it is probable that only the lower and middle parts of this formation are exposed. This section, from base to top, is as follows:

1. About 100 m thick, light-grey, medium-grained quartz sandstone, with interbeds of thin-bedded siltstone and shale. The sandstone yielded the fish remains and charophytes described below (CR1, Fig. 17B);

2. About 140 m thick marls, siltstones and black shales interbedded with siltstone, which turns to a yellow-grey, brown or pink colour, by weathering. The siltstone and shale yield many brachiopods, namely *Calvinaria cracoviensis* (Gurich, 1903), *Leiorhynchus levis* Gurich, 1903, *Camarotoechia polita* Ljashenko, 1960, and *Dagnachonetes* sp. (see description below). Locally occur some specimens of the dacryoconarid *Homocetus* sp., but their poor preservation does not allow any more precise identification. Nevertheless, the few characters they display are consistent with a Late Devonian, probably Frasnian age (Nguyen Huu 1983).

The boundary between the Ba Nuong beds and the overlying Frasnian-Famennian Xom Nha Formation has not been observed, but, in the Quy Dat area, the Dong Tho Formation is clearly overlain conformably by the Xom Nha Formation.

**SYSTEMATICS**

Phylum BRACHIOPODA Duméril, 1806
Order PRODUCTIDA

Sarytcheva & Sokolskaja, 1959

Suborder CHONETIDINA Muir-Wood, 1955

Family ANOPLIIDAE Muir-Wood, 1962

Subfamily HOLYNETINAE Racheboeuf, 1981

Genus *Holynetes* Havliček & Racheboeuf, 1979

**Type species.** — *Holynetes holynensis* Havliček & Racheboeuf, 1979. Eifelian, Czech Republic.

*Holynetes caurongensis* n. sp. (Fig. 18J-O)

**Holotype.** — External mould of a ventral valve (BT 231j; Fig. 18J).

**Etymology.** — From the type locality, Cau Rong.
LOCALITY AND AGE. — Cau Rong, Minh Hoa district, Quang Binh Province, Central Vietnam. Outcrop along the road between Qui Dat and Ly Hoa. Lower part of the Dong Tho Formation, Givetian (Fig. 17B).

MATERIAL EXAMINED. — 48 decalcified isolated internal and external moulds of both valves, and external moulds of articulated shells, most of them tectonically distorted (some specimens are illustrated in Figure 18J-O)

DIAGNOSIS. — Three orthomorph perpendicular spines on the right side of the shell only; costellae originating by bifurcation on ventral valve, and by intercalation on dorsal valve; costellae number 11-14 per 2 mm; dorsal valve interior with stout isolated endospines, deep and large cardinal process pit, and poorly developed (or absent?) accessory septa.

DESCRIPTION
Shell small and transverse in outline (maximum width: 8.0 mm; corresponding length: 5.6 mm), with maximum width at hinge line. Shell concavoconvex with longitudinal profile of ventral valve regularly, and markedly arched. Posterolateral branches of commissures at about 90° to hinge line. Length/width ratio decreasing with growth from 0.83 (ventral valve 1.7 mm long) to about 0.65 for ventral valves more than 4.5 mm long. Ventral interarea apsacline and dorsal one hypercline; both interareas flat and lying in the same plane. Small but prominent pseudodeltidium and chilidium. Ornament of narrow, rounded and relatively high radial ribs with intervals of the same width. Costellae originating by bifurcation on ventral valve, and by intercalation on dorsal valve. A ventral valve (4.8 mm long) exhibits a total of 55 costellae along the commissure, eight of them originating by bifurcation; costellae number 11-14 per 2 mm at anterior margin. Spines orthomorph, high-angled (about 90°), on the right side of the shell only, respectively at 0.2 mm, 0.7 mm and 2.5 mm from beak.

Ventral valve interior with a short and thin myophragm, not overpassing one-fourth the valve length. Teeth and muscle field not observed. Visceral cavity with scarce, isolated, relatively strong endospines in its posterolateral parts. Periphery of the valve impressed by the external ornament.

Dorsal valve interior with deep cardinal process pit and relatively stout, elongated and rounded inner socket ridges. Other characters are not observed.

DISCUSSION
Because of the poor development, or of the possible absence of accessory septa, this new species is only tentatively assigned to the genus Holynetes. However, among Eifelian representatives of the genus, H. holynensis Havlíček & Racheboeuf, 1979 from the Czech Republic, and H. cf. holynensis from Spain, exhibit variably developed, often hardly perceptible accessory septa (Havlíček & Racheboeuf 1979; Racheboeuf 1981). The lack of complete, well preserved dorsal interiors of the specimens from Vietnam precludes definite statement about the real lack of accessory septa in the new species.

?Holynetes caurongensis n. sp. closely resembles H. stephaniae Racheboeuf, 1981 (Givetian, Ker-sadiou Formation, western Massif Armoricain, France) in size, shape, outline, and ornament. However H. stephaniae bears a unique spine on the right side of the shell, and it exhibits a pair of well developed, long and blade-like accessory septa. The new species can be distinguished from H. holynensis by the presence of three spines instead of two in the latter, as well as by its ornament; in H. holynensis ventral radial ribs increase both by intercalation and bifurcation on the ventral valve, and mostly by bifurcation on the dorsal valve.

ENVIRONMENT
In its type locality, ?Holynetes caurongensis n. sp. is only associated with locally abundant dacryoco-narids (homoctenids), bivalves (aviculopectinids) and rare, small, smooth ostracods. The pink colour of the sediment is due to weathering. Originally, it probably consisted of dark to black shale and silty shale. The faunal assemblage is suggestive of a relatively deep benthic assemblage position, corresponding to the benthic assemblages BA3 or BA4 in an outer shelf position.

DISTRIBUTION
To date, ?Holynetes caurongensis n. sp. is only known from the Givetian of Central Vietnam. The genus Holynetes is currently known from the Eifelian of the Czech Republic (H. holynensis; Choteč limestone, Pinacites jugleri Horizon) and the Eifelian-Givetian of the Massif Armorican,
France (*H. musculosus*; Saint-Fiacre Formation, Eifelian, Costatus costatus conodont Zone, and *H. stephaniae*; Kersadiou Formation, Givetian, Varcus conodont zone; Lethiers & Racheboeuf 1999). In Spain, *H. cf. holynensis* was reported from the Gustalapiedra Formation of Palencia and from the Moyuela and Barreras formations of the Iberian Chains, i.e. in upper Eifelian to lower Givetian beds (Garcia-Alcalde et al. 2000). Outside Europe, the genus was reported from the Lower Devonian of Guangxi, South China (*H. abnormis*, Zlichovian) by Vogel et al. (1989), but this generic assignment, although probable, remains questionable.

**Family CHONETIDAE Bronn, 1862**

**Subfamily DAGNACHONETINAE**

Racheboeuf, 1981

**Genus Dagnachonetes** Afanasyeva, 1978

?Dagnachonetes** sp.

**LOCALITY AND AGE.** — Ba Nuong (Fig. 17B), Minh Hoa district, Quang Binh Province, Central Vietnam. Upper part of the Dong Tho Formation, Frasnian.

**MATERIAL EXAMINED.** — Some 30 isolated valves, all variably mineralized and distorted, but strongly weathered, have been collected from the Ba Nuong locality.

**DISCUSSION**

Due to the poor preservation of the available specimens, none of the internal features could be studied and described. The shell is transverse in outline, with its maximum width (about 15 mm) at mid-length. The longitudinal profile is weakly to moderately arched. Spines are not observed. Only the external ornament could be observed on some incomplete external moulds. It is composed of low, rounded, sinuous costellae, increasing mainly by bifurcation on the ventral valve; the costellae are crossed by very thin, undulating concentric fila. Such a kind of ornament strongly recalls that of the genus *Dagnachonetes* which is mainly known from Poland, Russia, France, Spain, and South China in Eifelian to lower Frasnian beds.

Phylum VERTEBRATA Linnaeus, 1778

Class GNATHOSTOMATA Gegenbaur, 1874

Subclass PLACODERMI McCoy, 1848

Order ANTIARCHA Cope, 1885

Suborder EUANTIARCHA

Janvier & Pan, 1982

Family BOTHRIOLEPIDIDAE Cope, 1886

**Genus Bothriolepis** Eichwald, 1840

**Bothriolepis** sp. (Fig. 19)

Fish remain is derived from the basalmost member of the Dong Tho Formation at Cau Rong (CR1, Fig. 17B). They consist of poorly preserved antiarch plates, the vermiculate ornamentation of which is strongly suggestive of the genus *Bothriolepis* (Fig. 19). One of these plates can be readily identified as an incomplete posterior ventrolateral plate (PVL), as it shows overlap areas for the anterior ventrolateral and median ventral plates, respectively (oaAVL, oaMV, Fig. 19A2, B2). Its lateral lamina gently increases in height posteriorly and its overall shape agrees with that of most generalized *Bothriolepis* species, such as *B. canadensis* (Whiteaves, 1880), from the lower Frasnian Escuminac Formation of Canada (Stensiö 1948). Although poorly informative, this material is nevertheless interesting as it suggests that the antiarchs of the Dong Tho Formation are quite different from those of the Ly Hoa Formation, described above. Despite a somewhat similar, siliciclastic lithology, no evidence for either *Bothriolepis*, or euantiarchs in general, occurs in the Ly Hoa Formation. Although bothriolepidids seem to occur somewhat earlier in eastern Asia and Australia than in Euramerica, their earliest occurrence being in the late Emsian in China (Zhu 2000), they become fairly abundant only in the early Eifelian (Wang S. T. 1993). This, again, suggests that the Ly Hoa Formation is significantly older, most probably Early Devonian in age, than the Dong Tho Formation, and is not a lateral facies of the latter.

Phylum CHAROPHYTA Migula, 1897

Class CHAROPHYCEAE Smith, 1938

**Phylum VERTEBRATA Linnaeus, 1778**

Class GNATHOSTOMATA Gegenbaur, 1874

Subclass PLACODERMI McCoy, 1848

Order ANTIARCHA Cope, 1885

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Janvier & Pan, 1982

Family BOTHRIOLEPIDIDAE Cope, 1886

**Genus Bothriolepis** Eichwald, 1840

**Bothriolepis** sp. (Fig. 19)
Fauna and flora from Devonian of Central Vietnam

Order SYCIDIALES Mädler, 1952, emend. Feist & Grambast-Fessard, 2005
Family SYCIDIACEAE Karpinsky, 1906
Genus Sycidium Sandberger, 1849

*Sycidium haikouense* Z. Wang, 1976
(Fig. 20)

The charophytes come from about 25 g of the matrix of the fish remains just described. It was impossible to extract well preserved specimens, because the fossils are extremely fragile and completely pyritized, but rubber cast of their external, natural mould allows a reconstruction of their shape (Fig. 20). The form represented in this sample can be referred to *Sycidium haikouense* Z. Wang (Sycidiaceae). This species is known from the Donggangling Formation of South China, which is correlated to the Givetian of Europe (Z. Wang 1976). The size range and overall morphology of the fructification of *S. haikouense* (Table 1), which is ovoid in shape and slightly thinner in its upper part, as well as the number of its vertical elements (ribs) and of polygonal cells per rib, are also shared by the form described here from Cau Rong. Only the length/width ratio is higher by one tenth of units in the only specimen
Racheboeuf P. et al.


<table>
<thead>
<tr>
<th>Character</th>
<th>China</th>
<th>Vietnam</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length</td>
<td>1670-2200 µm</td>
<td>1875 µm</td>
</tr>
<tr>
<td>Width</td>
<td>1490-2300 µm</td>
<td>1550-1750 µm</td>
</tr>
<tr>
<td>Length/width</td>
<td>0.97-1.12</td>
<td>1.21</td>
</tr>
<tr>
<td>Number of ribs</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td>Number of polygons</td>
<td>16-18</td>
<td>16-17</td>
</tr>
</tbody>
</table>

from Vietnam on which it could be measured, and this suggests for the latter a slightly more elongated overall shape of the fructification, yet this does not preclude its attribution to *S. haikouense*.

The presence of *S. haikouense* in the Dong Tho Formation increases the fossil record of Devonian charophytes along the northern margin of the Gondwana, which already included the floras from Queensland (Australia; Feist *et al.* 2000), South China (S. Wang & Chang 1956; Z. Wang 1976; Zhang *et al.* 1978; Z. Wang & Lu 1980; Z. Wang *et al.* 1980; Hu & Zeng 1982; Li & Zhou 1982), Iran (Feist & Grambast-Fessard 1985; Mistiaen *et al.* 2000, and southern France (Feist & Feist 1997). In addition, this is the first record of fossil charophytes from Vietnam, at any rate in the Palaeozoic.

CONCLUSIONS

New vertebrate material from the Ly Hoa Formation of Central Vietnam provides additional data on the morphology of *Vukhuclepis*, which probably belongs to the Yunnanolepididae, as defined by Zhu (1996), or is most closely related to this family. A peculiar shield fragment from the Ly Hoa Formation is referred here to a galeaspid, but this needs to be confirmed by better preserved and unambiguous material. This, alongside the confirmation of the presence of youngolepidid sarcopterygian remains, clearly indicates biogeographical affinities with the Early Devonian (Lochkovian-Pragian) vertebrate faunas of the Yangtse Platform (South China Block). There remains, however, an uncertainty as to the precise age of the Ly Hoa Formation. The presence of a possible macropetalichthyid and possible primitive brachythoracid arthrodires (notably a ho-
Fauna and flora from Devonian of Central Vietnam

lonematid) suggest a relatively late Early Devonian, possibly Emsian, age, but makes very unlikely the Givetian age which has been proposed for the Ly Hoa Formation on the basis of plant assemblages found at Minh Le. It is suggested here that the Ly Hoa Formation is either diachronous, or composed of two different sandstone units, Lower Devonian and Givetian in age, respectively.

The phyllocarid remains from the Ly Hoa Formation are unfortunately too poorly preserved to provide any valuable stratigraphic or palaeobiogeographic information. Nevertheless, they clearly confirm the proximal, marine environment of the Ly Hoa Formation, previously suggested by evidence for small lingulids. The still enigmatic Sinocaris-like carapaces are proved to be made up by calcium phosphate and display a three-layered structure, with a spongiose middle layer. They are thus unlikely to be large bivalves.

The biogeographical affinities of the vertebrate fauna of the Ly Hoa Formation has bearings on the question of the age of the Song Ma suture. Although this fauna includes widespread taxa, such as the Lunaspis-like petalichthyid, it is mainly composed of taxa which are hitherto unrecorded outside the Yangtse Platform (or South China Block), except for galeaspids (still questionable), which are also known from North China (Pan 1986). Although certain geophysical models suggest that the Indochina Block is derived from the Australian margin of the Gondwana, none of these endemic taxa has even been found in the Lower Devonian of Australia, with the possible exception of the primitive holonematid described herein, which bears some resemblance to Bimbianga burrinjuckensis, from the Emsian of Australia. Assuming that a Gondwanan origin of the Indochina Block is likely, and that its accretion with South China occurred at the level of the Song Ma suture, the South Chinese affinities of the Ly Hoa vertebrate fauna, as well as that of the Late Silurian My Duc vertebrate fauna (Tong-Dzuy et al. 1997), suggest that it occurred before the Late Silurian. The age of the collision between the Indochina and South China blocks (thus the Song Ma suture) has been the subject of vivid debates and, according to various authors, was regarded as ranging from the Cambrian to the Late Triassic (e.g., Sengör & Hsü 1984; Gatinsky & Hutchison 1987; Metcalfe 1988, 1990, 1993, 1995, 1996; Hutchison 1989; Mouret 1994; Phan Van 1995). However, recent field investigations by Findlay (1997) on the Song Ma terrane provide a very strong support for an Ordovician to Early Silurian age for this collision.

New chonetidid brachiopods are described from the Nam Can and Dong Tho formations, respectively. They confirm the Givetian-Frasnian age of the Nam Can and Dong Tho formations. Fish remains referred to Bothriolepis sp. and associated with the charophyte Sycidium haikouense in the basalmost part of the Dong Tho Formation also suggest a late Givetian age for the base of this formation.

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