LOWER DEVONIAN BIOSTRATIGRAPHY AND VERTEBRATES OF THE TONG VAI VALLEY, VIETNAM

by TONG-DZUY THANH, P. JANVIER, TA HOA PHUONG *and* DOAN NHAT TRUONG

ABSTRACT. A new vertebrate assemblage is described from the base of the Khao Loc Formation at Tong Vai, Dong Van district, Ha Giang Province, Vietnam. It includes the galeaspid *Polybranchiaspis liaojaoshanensis*, two acanthothoracid placoderms, and the sarcopterygian *Youngolepis praecursor*. This assemblage is quite similar to that of the Xitun Formation of Yunnan (Late Lianhuashanian to Early Nagaolingian) and can also be correlated with the vertebrate faunas which occur at the base of the Bac Bun Formation of the Bac Bo in Vietnam. New data on the morphology of *P. liaojaoshanensis* are provided on the basis of this material, with special reference to the structure and ornamentation of the exoskeleton.

THE Tong Vai valley is situated near the Chinese–Vietnamese border, west of the Quan Ba hamlet, on the Ha Giang–Yen Minh main road in the Dong Van district (Text-fig. 1). From Quan Ba, the road to Tong Vai runs through a pass in a mountainous area of limestone and sericite-bearing shales. The distance between Quan Ba and the Tong Vai valley is directly about 10 km (18 km by road).

The Palaeozoic rocks of the Tong Vai valley and its surroundings were considered by Deprat (1915) to be Late Cambrian to Early Ordovician in age (see also the geological map of the Ma Li Po area in this work). Vassilevskaya (*in* Dovjikov 1965) regarded the 'Luong Kho Limestones' of the Tong Vai valley as Ordovician, on the basis of poorly preserved brachiopods and ostracodes of 'Ordovician-Silurian aspect'.

In 1973, Ta Thanh Trung and Hoang Anh Truong were the first to collect early Devonian fossils from this area. These included some brachiopods e.g. *Lingulella dussaulti* Patte) and a specimen of the galeaspid fish *Polybranchiaspis* sp. (Ta Thanh Trung 1978). Hoan Xuan Tinh (1976), chief engineer of the Geological Mapping Team for the Bao Lac sheet, correctly described, apart from a few inaccuracies, the stratigraphical sequence of the Early Devonian in the Tong Vai valley, and his description was later referred to in the 'Stratigraphy of Vietnam' (Vu Khuc and Bui Phu My 1990). Of the five members he described, the first two may not belong to the Devonian, but rather represent terrigenous beds that Vassilevskaya (*in* Dovjikov 1965) referred to the Late Cambrian, and Deprat (1915) to the Ordovician. The description of the *Polybranchiaspis*-bearing levels in Hoang Xuan Tinh's (1976) paper is quite different from the one made later by Ta Thanh Trung (1978), who collected the galeaspids from 'dark grey carbonate-bearing terrigenous deposits'. On the contrary, Hoang Xuan Tinh (1976) depicted his *Polybranchiaspis*-bearing third member of the Lower Devonian as a succession of opalescent, yellowish quartzitic sandstones, siltstones and mudstones, which he referred to as the 'Bac Bun Suite'. To this author, the 'Bac Bun Suite' comprised the Si Ka and Bac Bun formations first described by Dèprat (1915) and later reviewed by Tong Dzuy Thanh (1967, 1982) and Tong Dzuy Thanh *et al.* (1986). According to Hoang Xuan Thinh's description, his third member may be attributed to the Si Ka Formation, although, as will be mentioned below, such coarse terrigenous rocks do not seem to occur in the Lower Devonian of the Tong Vai valley.

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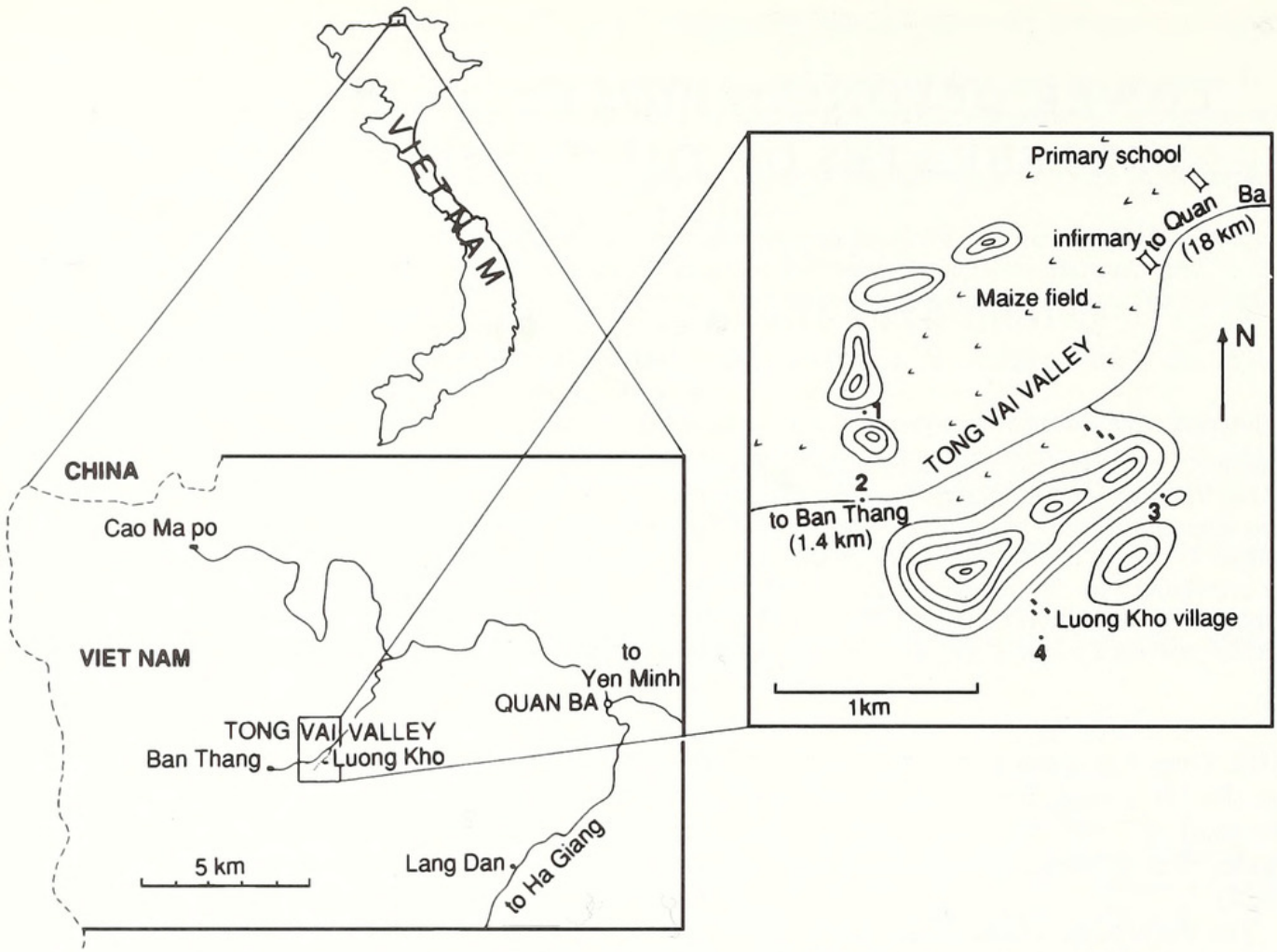


TEXT-FIG. 1. Locality Map; **1–4**, location of invertebrate and vertebrate-bearing exposures of member 3 of the Tong Vai section.

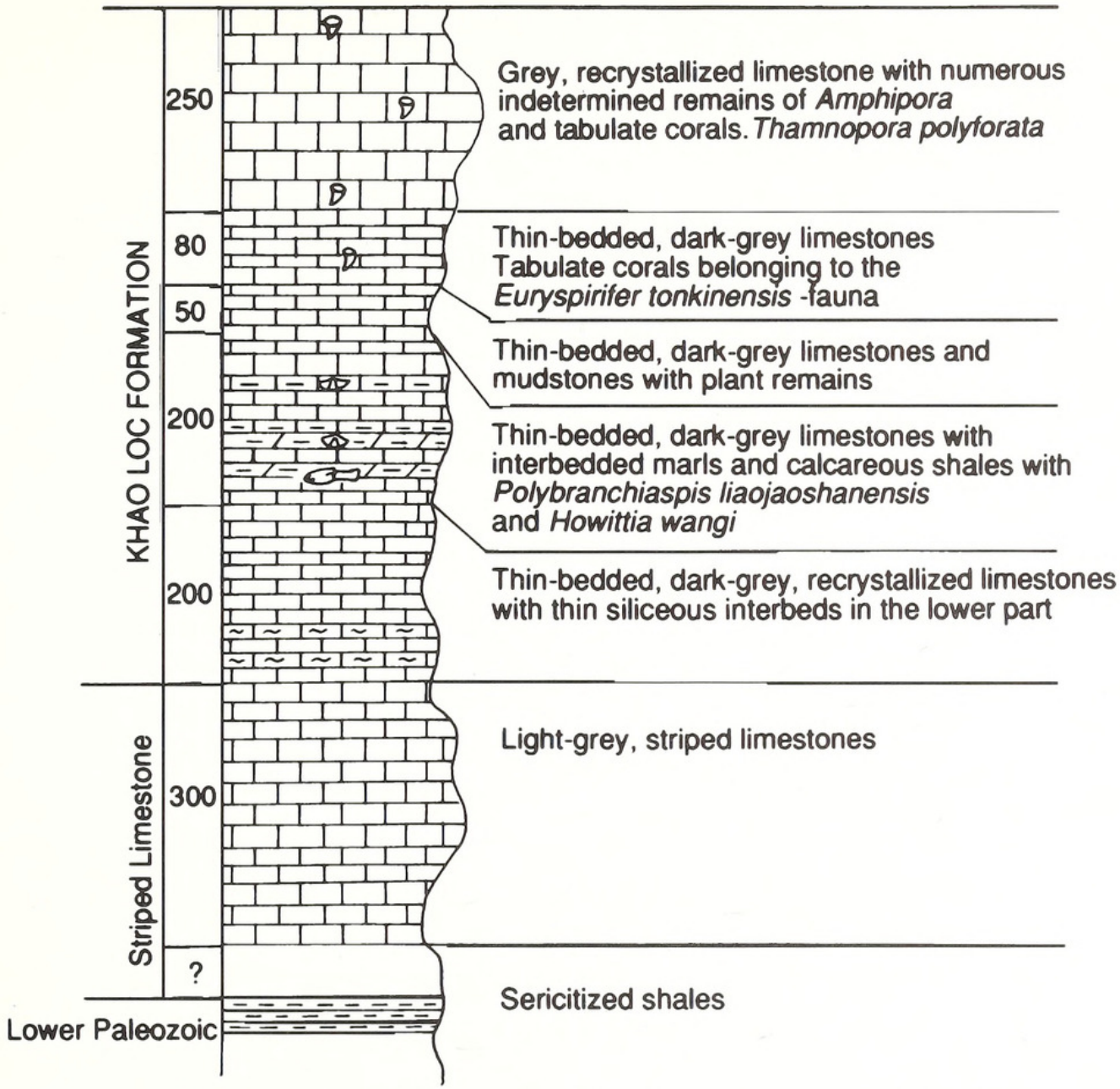
GEOLOGICAL SETTING

In summer 1991, one of us (T.H.P.) made a field trip to the Tong Vai valley and recorded several fossiliferous localities which have since been investigated, in spring 1993, by Tong-Dzuy Thanh, Ta Hoa Phuong and Doan Nhat Truong in the frame of the project KT 04.6.1.1. of the Vietnamese Fundamental Research Program in Natural Sciences.

Description

The eastern slope of the Tong Vai valley consists of sericitized shales and dark grey limestones, dated, with reservations, as Late Cambrian (Dovjikov 1965). The rest of the area consists mainly of limestones and interbedded marls. The complete stratigraphical column in Tong Vai, from the Upper Cambrian to the Devonian, is still unknown because of tectonic complications. However, six successive members can be distinguished in the Devonian, without any breaks (Text-fig. 2). These are, from base to top:

1. The basal member consists of light grey, relatively thin-bedded (200 mm) and sometimes opalescent, striped limestones. They resemble the Upper Palaeozoic limestones widespread in the north of Vietnam. Sometimes, they display a schistosity to various degrees. The contact between these limestones and the underlying Upper Cambrian is not clear and the thickness of this member cannot be estimated precisely. A thickness of only *c.* 300–350 m can be observed, but the sequence may be thicker. They have yielded only scolecodonts and small rounded masses or organic matter (F. Paris, pers. comm.).



TEXT-FIG. 2. Stratigraphical section of the Early Devonian of the Tong Vai valley.

2. The second member begins with cherts and dark-grey, recrystallized limestones and dolomites. Further up, the cherts disappear and the upper part of the member consists only of recrystallized limestones and dolomites. The thickness of this member is *c.* 200 m. It has yielded only scolecodonts (F. Paris, pers. comm.).

3. The third member consists of marls with interbedded dark grey limestone and mudstone layers. Locally, lenses of calcareous shales occur, in particular in the middle part of the member, and these weather to a pink colour. Abundant vertebrate remains occur about 50 m above the base of this member. They are associated with ostracodes and occur in dark grey calcareous siltstones (see below for faunal list).

40 m upwards, on the road from the Tong Vai valley to Ban Thang (**1**, **2**, Text-fig. 1), some brachiopods were collected in marls. They are referred by Duong Xuan Hao and Le Van De (1980) to *Howellella* ex. gr. *crispa* (Hisinger) and *Hysterolites wangiformis* Zuong. The latter species is *Howittia wangi* (*Orientospirifer wangi* Hou of Chinese authors). Other brachiopods occur near the top of this member, on a small hill on the roadside close to Luong Kho village (**3**, Text-fig. 1) and

were referred by Duong Xuan Hao to *Hysterolites wangiformis* (*Howittia wangi*) and *Tadschikia*? aff. *xuanbaoi* Zuong. The latter is similar to the type material from the lowermost Lower Devonian of the lower Da River basin (northwestern Vietnam). From Ta Thanh Trung's (1978) description, his *Polybranchiaspis* sp. and *Lingulella dussaulti* (Sample 2808/1) were certainly also collected in this member. The total thickness of this third member is *c.* 200 m.

4. The fourth member consists of thin-bedded black limestones intercalated with calcareous shales and mudstones, some of which are coal-bearing. It has yielded some undetermined plant remains which were collected from the mudstones. It is *c.* 50 m thick.

5. The fifth member consists of thin-bedded, dark grey limestones and marl lenses, which contain tabulate corals (in particular, abundant *Favosites kolimaensis* Rukhin) of the *Euryspirifer tonkinensis*-fauna. Its thickness is *c.* 80 m.

6. The uppermost member consists mainly of light grey recrystallized limestones with abundant traces of ramiform stromatoporoids. These limestones are very similar to the Middle Devonian *Amphipora* limestones formerly described by French geologists ('Calcaires à *Amphipora*'; Saurin 1956). The top of member 6 cannot be observed in the area of Tong Vai valley, because of faulting. Its observed thickness is *c.* 250 m.

Discussion

From Hoang Xuan Tinh's (1976) account, one of us (Tong-Dzuy Thanh 1982; Tong-Dzuy Thanh *et al.* 1986) referred the *Polybranchiaspis*-bearing beds of the Tong Vai valley to the Si Ka Formation. The new field observations presented in this paper suggests a reinterpretation of the Devonian of this area. The fauna of the third member unquestionably belongs to the *Howittia wangi* assemblage, which defines the Bacbunian regional stage in the Bac Bo (northern Vietnam, formerly called the Tonkin). Its major representatives are *Howittia wangi* and *Howellella* ex gr. *crispa*, and the vertebrates are quite similar to those in the corresponding stratigraphical level of Dong Mo and Trang Xa (Tong-Dzuy Thanh and Janvier 1990). The only, minor, difference is the presence of the brachiopod *Tadschikia*? aff. *xuanbaoi*, similar to the type material from northwestern Vietnam (Duong Xuan Hao and Le Van De 1980). There is some difference between the Tong Vai vertebrate fauna and that of more southernly localities, such as Trang Xa and Dong Mo (Tong-Dzuy Thanh and Janvier 1987, 1990). Although *Youngolepis* is present in both, no acanthothoracid material has been recorded from the latter two localities. Moreover, there is a marked difference in the structure and ornamentation of the exoskeleton of the galeaspid *Polybranchiaspis* from Tong Vai (see below) and those of the poorly preserved specimens from Dong Mo referred to by Tong-Dzuy Thanh and Janvier (1990, fig. 4) as '*Polybranchiaspis* sp.'. In the latter, the ornamentation consists of simple, rounded tubercles devoid of a basal recess, which are aligned into ridges along the shield margin. Therefore it is probable that the Dong Mo galeaspid, although a polybranchiaspidiform, does not belong to the genus *Polybranchiaspis*, but to a form which is closer to *Bannhuanaspis* (Janvier *et al.* 1993) in exoskeletal structure.

According to the observations of one of us (T. D. T.), the fourth member of the Tong Vai section is quite similar in lithology to the base of the Khao Loc Formation in the Ban Hinh-Khao Loc section, which is situated not far South of Tong Vai. It can thus be suggested that the limestone of

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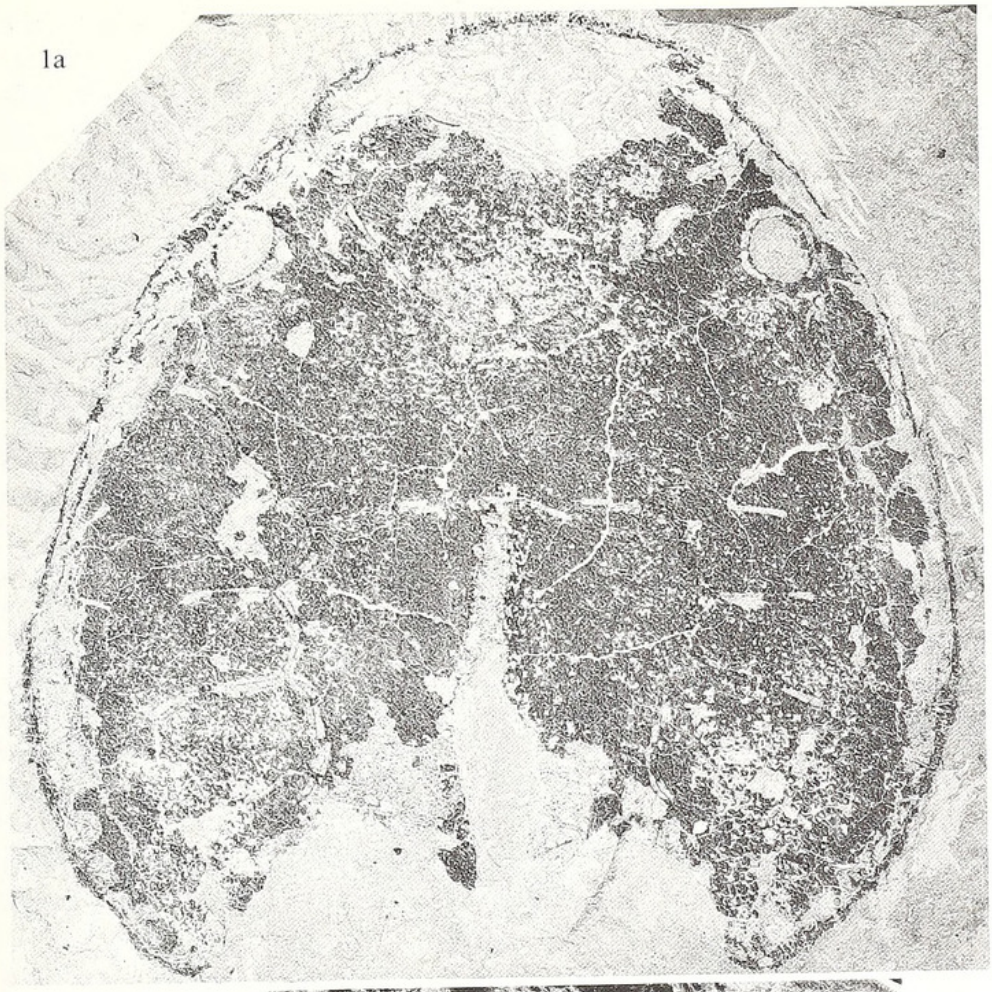
EXPLANATION OF PLATE 1

Figs 1–3. *Polybranchiaspis liaojaoshanensis* Liu, Pragian, Khao Loc Formation, Tong Vai, Ha Giang Province, Vietnam. 1, BT 170, head shield in dorsal view, photographed in immersion to show the pineal foramen (a) and elastomere cast of its incomplete counterpart (b); note the ostracodes surrounding the specimens. 2, BT 171, right side of a headshield in dorsal view, elastomere cast of natural impression. 3, BT 172, left side of a headshield in internal view, elastomere cast of the internal surface of the exoskeleton and the ornamentation of the posterior wall of the median dorsal duct. All × 2.

1a



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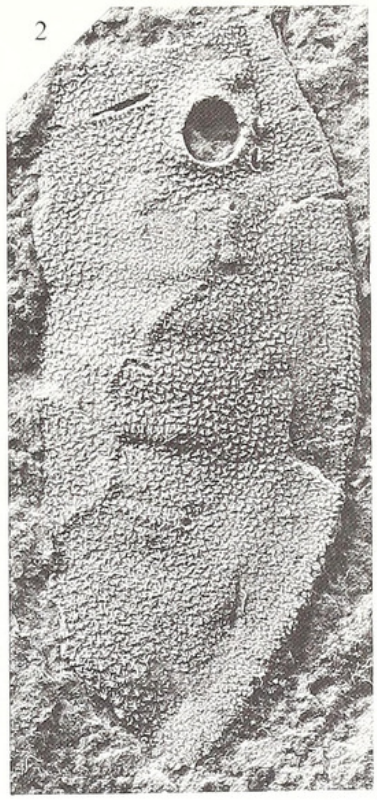

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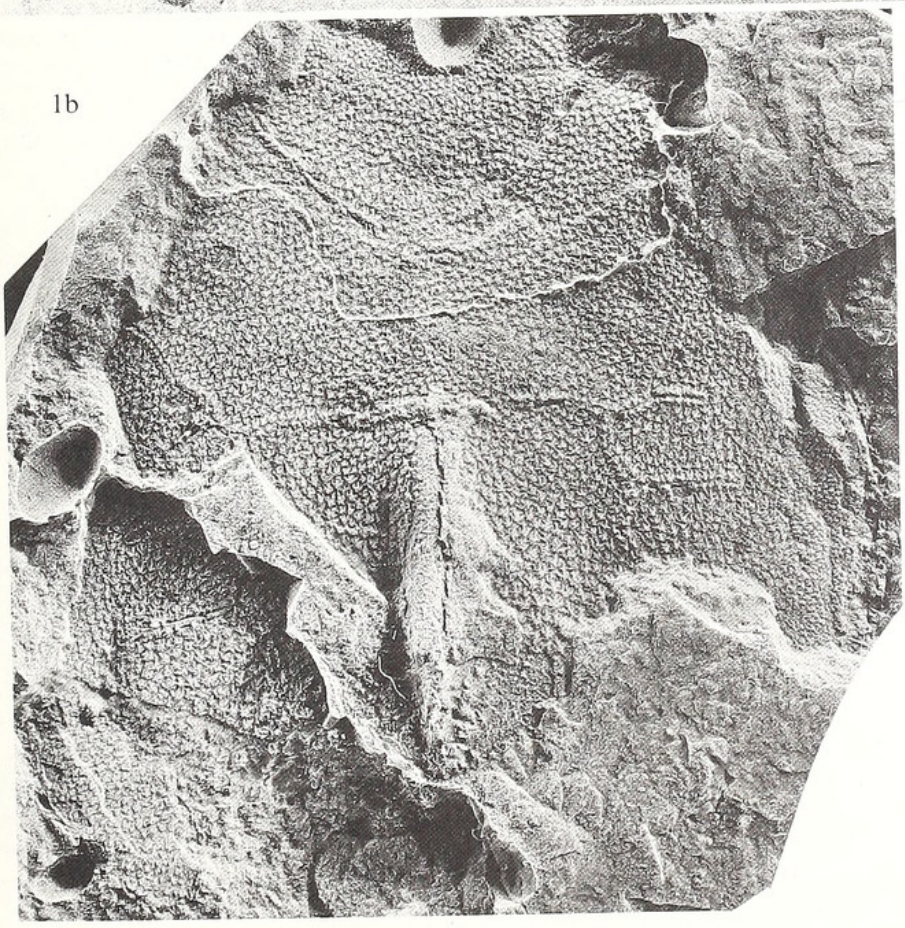

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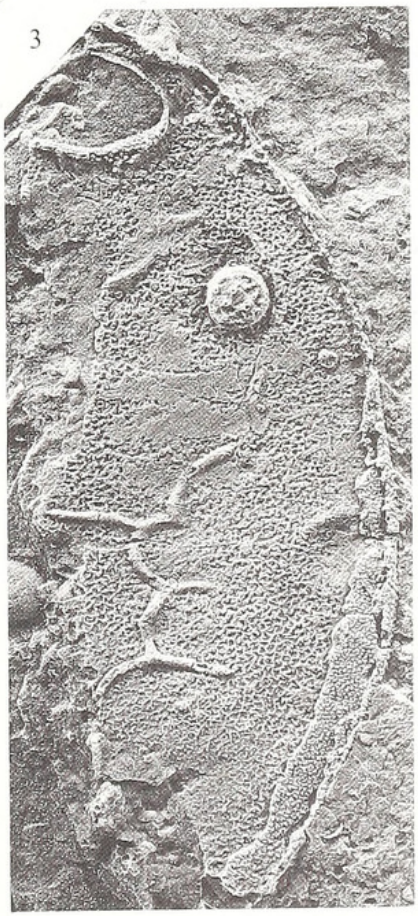

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member 4 and upwards can be attributed to the Khao Loc Formation (Pragian-Givetian), which is widespread in the Northwest of Ha Giang Province (Text-fig. 2). The limestones of the uppermost member of Tong Vai (member 6) can be correlated with the upper part of the Khao Loc Formation and the Ban Pap Formation. The latter formation is widely distributed in the North of Vietnam. This correlation is supported by the abundance of *Amphipora*, a guide fossil for the Middle Devonian limestone in the North of Vietnam.

The red beds of the Si Ka Formation do not occur in the Tong Vai area. Instead, below the Bacbunian faunal assemblage (fishes and *Howittia wangi*), there is a thick series of limestones (members 1 and 2), which are devoid of stratigraphically significant fossils (only scolecodonts are found). They may be a lateral equivalent of the Si Ka Formation.

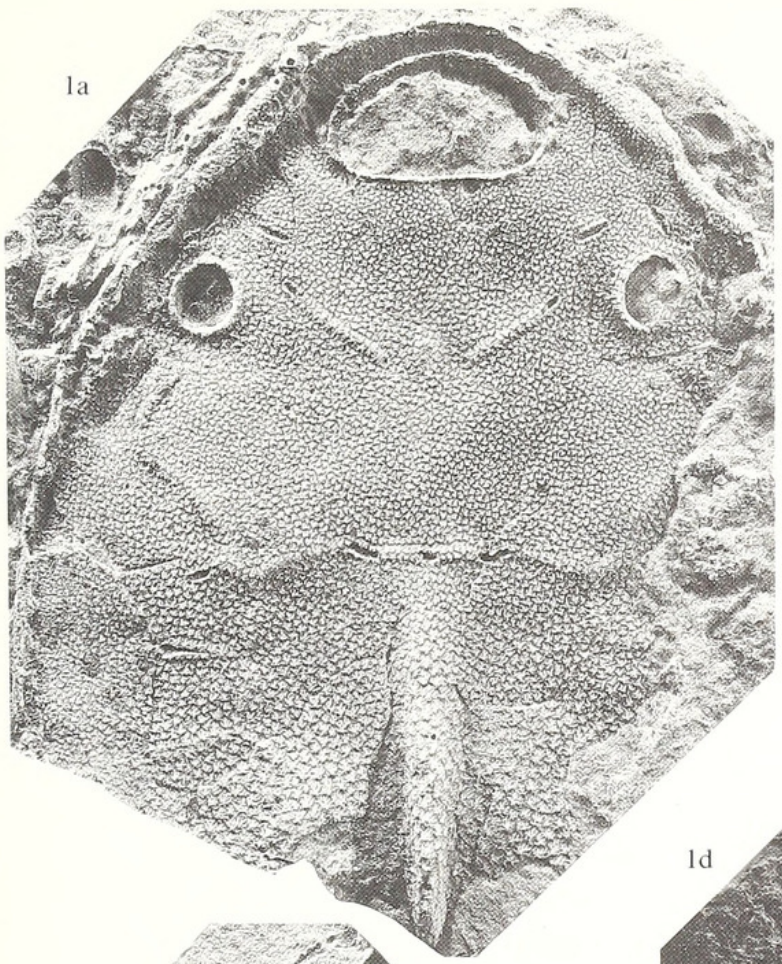
The correlation of the Bac Bun and overlying Mia Le formations of the Bac Bo with the Nakaoling (Nagaoling) and Yukiang formations (or stages) or southern China have been proposed in our former papers (Tong-Dzuy Thanh 1982; Tong-Dzuy Thanh *et al.* 1986, 1988*a*, *b*; Tong-Dzuy Thanh and Janvier 1987, 1990) on the basis of both vertebrate and invertebrate faunas. It is further supported by the new material described herein.

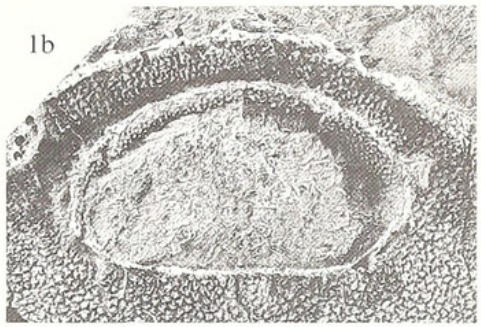
The Bacbunian vertebrates in northeastern Vietnam are frequently found in association with invertebrates of the *Howittia wangi* assemblage or in beds which immediately underlie this assemblage. By comparison with the data provided by S. T. Wang (1991), the Bacbunian vertebrate assemblage (in Dong Mo, Trang Xa, Tong Vai and other Vietnamese localities) is very similar to that of the Xitun Formation of the Cuifengshan Group in eastern Yunnan (China). Moreover, the Lower Devonian succession in the northeastern Bac Bo, from the Sika to Bac Bun and Mia Le formations is closely similar to that from the Lianhuashan to Nakaoling and Yukiang formations of Guangxi, China (Yang *et al.* 1981). This striking resemblance is seen in both the lithology and the faunal assemblages. As a result of the greater faunal diversity in northern Vietnam, these formations can be precisely dated, in particular the Mia Le Formation, which is clearly Pragian in age (Tong-Dzuy Thanh 1982; Tong-Dzuy Thanh *et al.* 1988*a*). This has been recently confirmed by the discovery of dacryoconarids of the *Nowakia zlichovensis* and *N. barrandei* zones, and a rich conodont assemblage of the *Perbonus*-zone (determined by Pham Kim Ngan, Hanoi), in the base of the limestones which overlie the Mia Le Formation in the Dong Van – Ma Lu section (Ha Giang Province, near the Chinese–Vietnamese border). Here, in the uppermost beds of the Mia Le Formation, one of us (T.H.P.) discovered new dacryoconarids among which is the well-known Pragian species *Nowakia arcuaria* (H. Lardeux, pers. comm.).

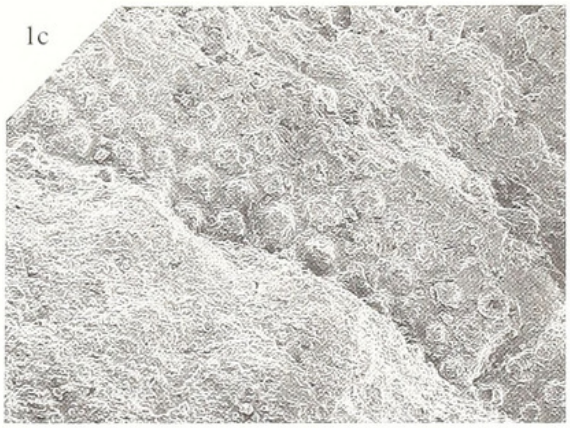
In conclusion, these data suggest that: (1) the Bac Bun Formation, which underlies the Mia Le Formation and contains the vertebrates described below, may be Late Lochkovian to Early Pragian in age; (2) the Bac Bo area of northern Vietnam and the Yunnan–Guangxi areas of southern China belong to the same palaeobasin, characterized by endemic fish faunas; (3) the Bacbunian vertebrate and invertebrate faunas of northern Vietnam display mixed features of the Yunnan and Guangxi assemblages; and (4) they correspond to a foreshore to near-shore palaeoenvironment. Further south, in the Phu Luong and Trang Xa area, the larger amount of detritic sediments in the Sika and Bac Bun Formations suggests an even more near-shore to deltaic type of environment.

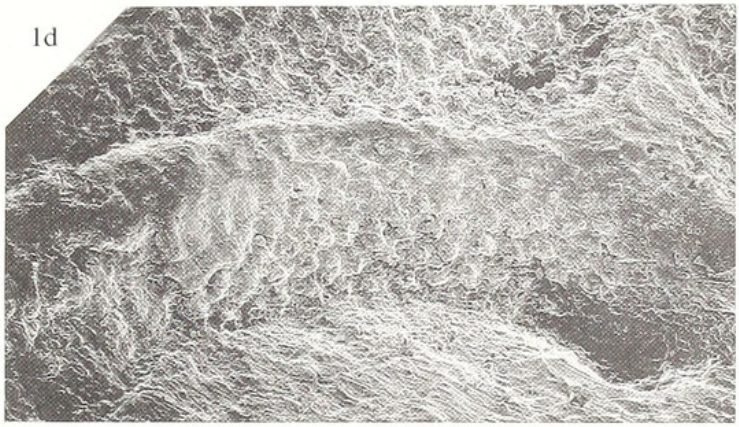
EXPLANATION OF PLATE 2

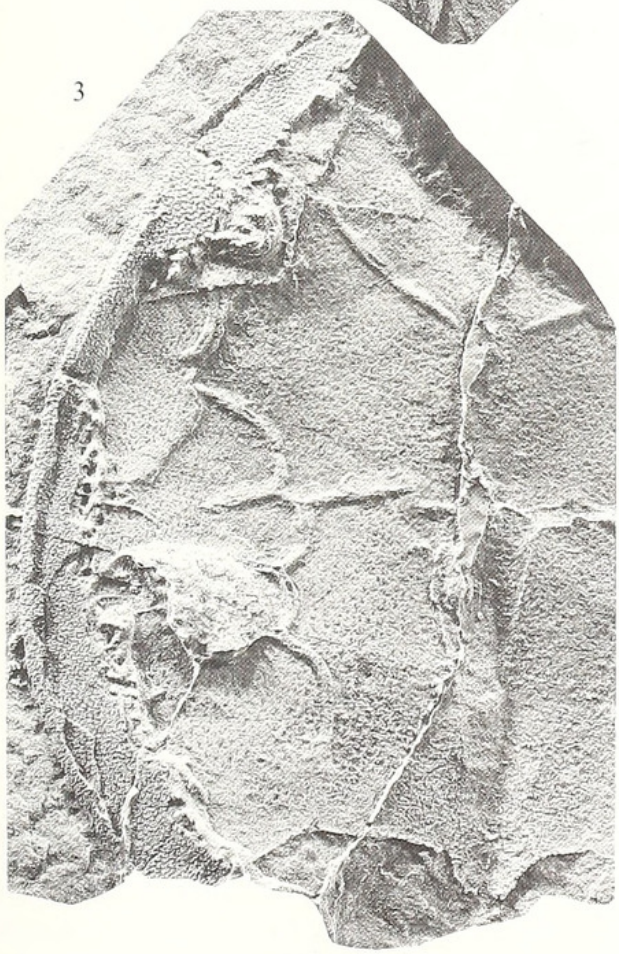
Figs 1–3. *Polybranchiaspis liaojaoshanensis* Liu, Pragian, Khao Loc Formation, Tong Vai, Ha Giang Province, Vietnam. 1, BT 173, incomplete headshield in dorsal view, elastomere cast of the specimen (a, × 2), close-up view of the median dorsal opening, lit from the left (b, × 3), and S.E.M. photograph of the elastomere cast of the anterior wall of the median dorsal opening (c, × 20; d, × 15), to show the denticles on the anterior wall of the duct. 2, BT 172 (same specimen as Pl. 1, fig. 3), S.E.M. photograph of an elastomere cast of the ornamentation on the posterior wall of the median duct, partly folded against the internal surface of the exoskeleton, × 15. 3, BT 174, incomplete headshield in ventral view, elastomere cast showing the ventral rim of the dermal headshield and the internal surface of the dorsal exoskeleton, × 2.

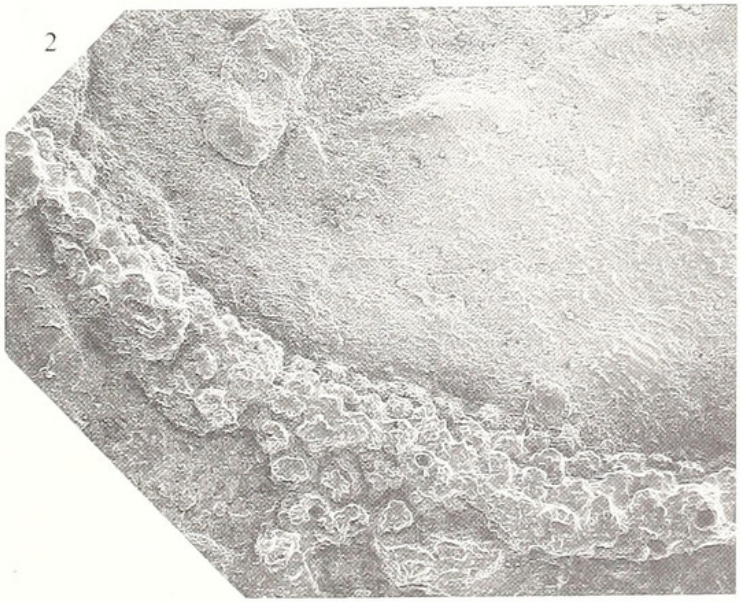












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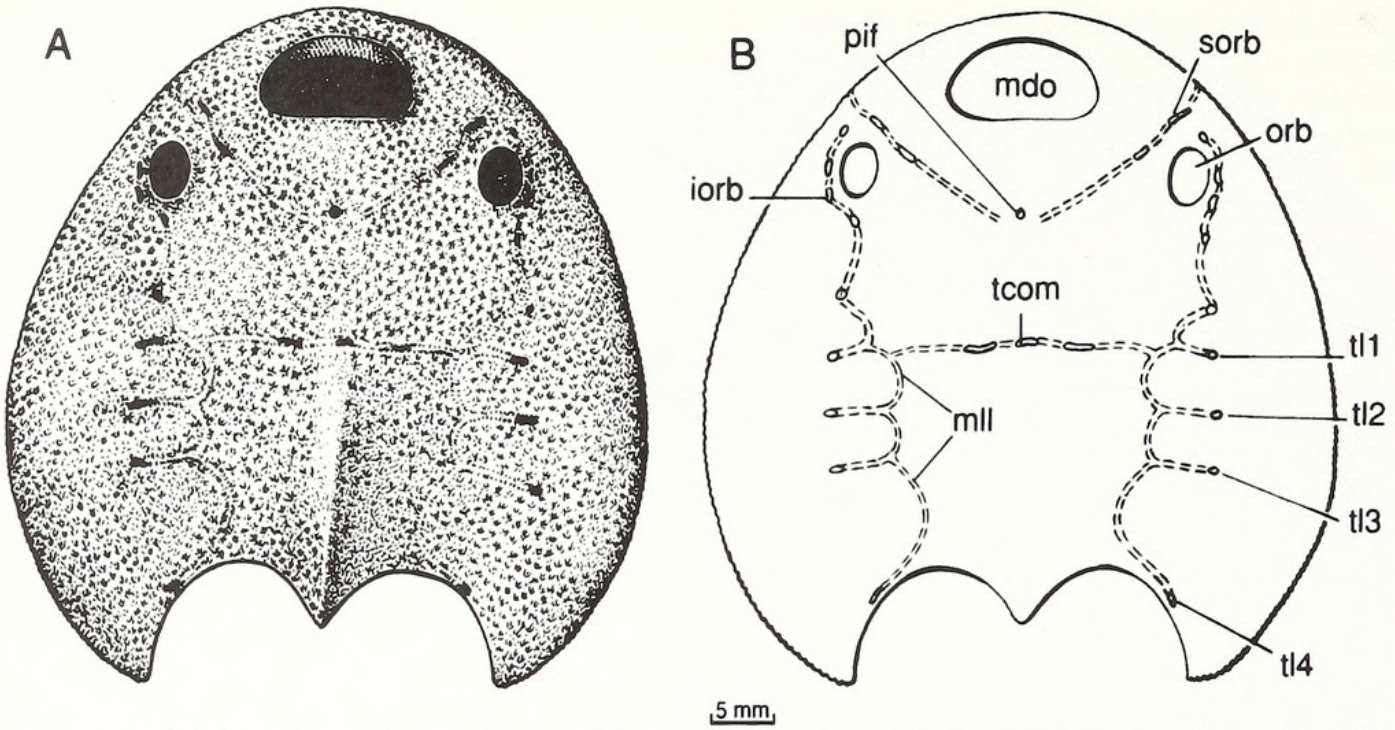
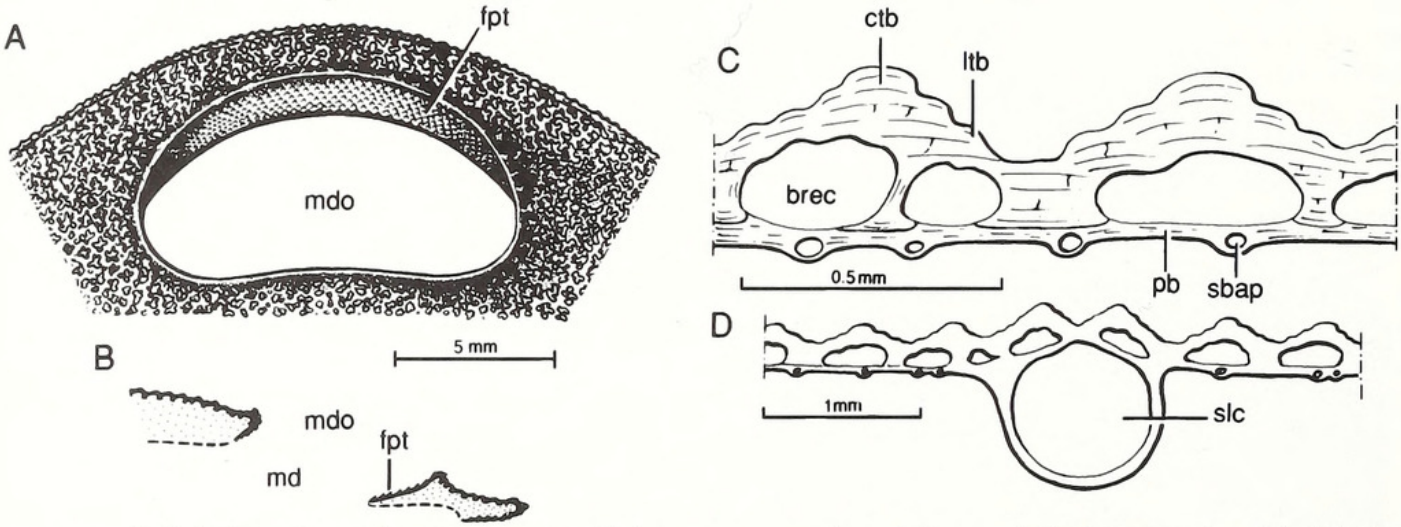


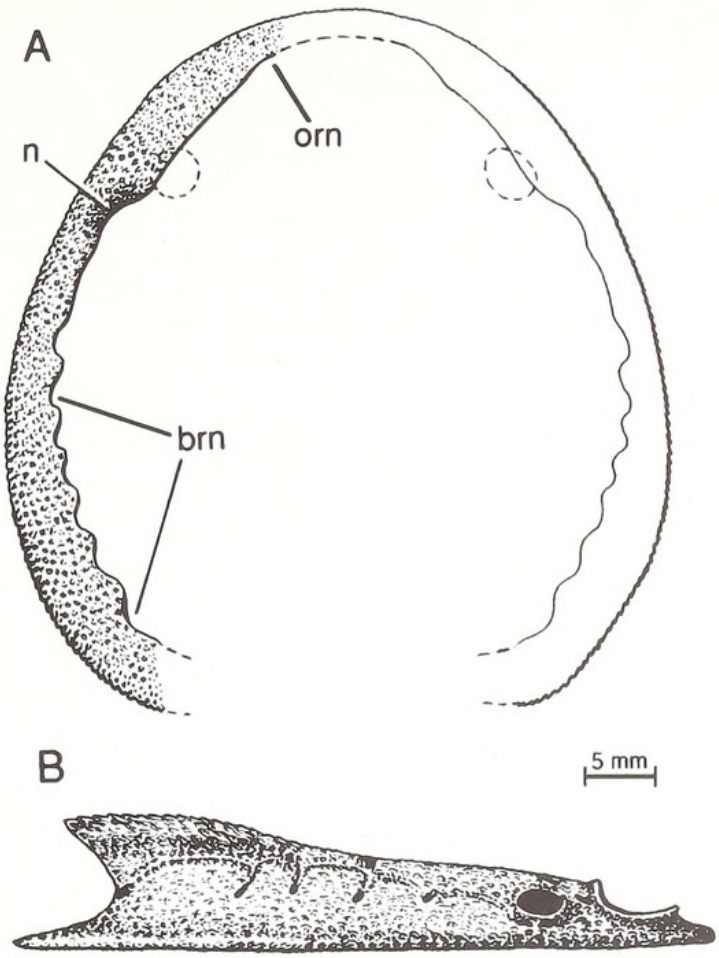
TEXT-FIG. 3. *Polybranchiaspis liaojaoshanensis* Liu. A, reconstruction of the headshield in dorsal view (based on several specimens from Tong Vai); B, distribution of the sensory-line canals. Abbreviations: *iorb*, infraorbital canal; *mdo*, median dorsal opening; *mll*, main lateral-line; *orb*, orbit; *pif*, pineal foramen; *sorb*, supraorbital canal; *tcom*, transverse commissural canal; *tl1–4*, transverse lateral canals.



TEXT-FIG. 4. *Polybranchiaspis liaojaoshanensis* Liu. A, reconstruction of the exoskeleton around and inside the median dorsal opening; B, reconstructed sagittal section through the median dorsal opening and duct; C, vertical section through two tubercles of the exoskeleton (combined from several thin sections); D, vertical section through the exoskeleton and a sensory-line canal (combined from several thin sections). Abbreviations: *brec*, basal recess of exoskeleton; *ctb*, central tubercle; *fpt*, forward pointing tubercle of median dorsal duct; *ltb*, lateral, or secondary tubercle; *md*, median dorsal duct; *mdo*, median dorsal opening; *pb*, perichondral bone; *sbap*, subaponeurotic vascular canals; *slc*, sensory-line canal.

SYSTEMATIC PALAEONTOLOGY

The vertebrate material from the Tong Vai valley consists mainly of well preserved galeaspid headshields, as well as isolated placoderm plates and the cosmine-covered dermal bones and scales of a sarcopterygian. All the specimens come from the marls and shales of member 3, and are associated with smooth-shelled ostracodes. The material described herein is registered in the



TEXT-FIG. 5. *Polybranchiaspis liaojaoshanensis* Liu, reconstruction of the exoskeletal headshield. A, ventral view; B, lateral view. Abbreviations: *brn*, branchial notch; *n*, notch; *orn*, oral notch.

collection of the Geological Museum (Bao Tang Dia Chat, here abbreviated BT), 6 Pham Ngu Lao Str., Hanoi. Casts are deposited in the collection of the Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris).

Class GALEASPIDA Halstead Tarlo, 1967
Order POLYBRANCHIASPIDIFORMES Liu, 1965
Family POLYBRANCHIASPIDIDAE Liu, 1965

Genus POLYBRANCHIASPIS Liu, 1965

The genus *Polybranchiaspis* was erected by Liu (1965) for the species *P. liaojaoshanensis* Liu, 1965 (erroneously spelled as *P. liaojiaoshanensis* by Liu 1975 and several subsequent authors) from the Cuifengshan and Xitun formations of Yunnan (China). *Polybranchiaspis* now comprises nine species (including the type species), all from Yunnan.

Polybranchiaspis liaojaoshanensis Liu, 1965

Plates 1–2, Plate 3, figures 1, 2; Text-figures 3–5

Type specimen. An almost complete headshield (Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, No. V.3027; Liu 1965, pl. 3, fig. 1), from the Cuifengshan Group at Qujing, Yunnan. A relatively large hypodigm is now also known from this locality. Some other *Polybranchiaspis* species, e.g. *P. gracilis* Cao, 1985, *P. yunnanensis* Cao, 1985, *P. rhombicus* Cao, 1985 and *P. sinensis* Cao, 1985, described from the same locality and formation, are probably reflections of intraspecific variation within *P. liaojaoshanensis*.

Material. The material from Tong Vai consists of five more or less complete headshields (BT 170–175) and numerous exoskeleton fragments (not numbered).

Locality and horizon. All the specimens described are derived from the four fish-bearing exposures of the Tong Vai valley (**1–4**, Text-fig. 1), which correspond to the same shaly horizon in the basal part of the third member of the Tong Vai section (second member of the Khao Loc Formation proper; Text-fig. 2).

Description. The headshield of the *Polybranchiaspis* species from Tong Vai is indistinguishable from that of *P. liaojaoshanensis* Liu from the Cuifengshan Formation of Yunnan (Liu 1965, 1975). On the basis of the photographs of the incomplete headshields discovered by Ta Thanh Trung (now deposited in the Geological Institute, Beijing), Tong-Dzuy Thanh and Janvier (1987) referred the Vietnamese specimens to *P.* cf. *gracilis* Cao, recorded from the same formation by Cao (1985). The latter was said to be characterized by posterolateral orientation of the foremost lateral transverse sensory-line canal (*tl1*, Text-fig. 3B). However, examination of large populations of *P. liaojaoshanensis* from Yunnan now suggests that *P. gracilis* lies within the range of variation of *P. liaojaoshanensis*.

The exoskeleton of the *Polybranchiaspis* specimens from Tong Vai is well preserved (in contrast to previously described Chinese material) and has yielded new information about its structure and ornamentation. Most of the specimens have been prepared as impressions, by removing the exoskeleton with hydrochloric acid, and making elastomere casts (Pl. 1, figs 1b, 2–3; Pl. 2, fig. 1; Pl. 3, fig. 1).

Ornamentation. In external aspect, the ornamentation of the exoskeleton of *P. liaojaoshanensis* shows relatively large but low, star-shaped tubercles (Pl. 1, figs 1b, 2–3; Pl. 2, fig. 1a; Pl. 3, fig. 1a; Text-figs 3A, 4C–D, 5). These are smaller in the anterior part than in the posterior part of the dorsal surface of the shield. Also, in the posterior part of the shield, particularly on the median dorsal crest and along the lateral margins, they tend to become elongated, and even spine-shaped (Text-figs 3A, 5B). The tubercles on the ventral rim of the shield are very small (Pl. 1, fig. 3; Pl. 2, fig. 3; Text-fig. 5A). They are irregular in shape, with a large median elevation, or central tubercle (*ctb*, Text-fig. 4C), and four or five 'branches', each of which is made up by two or three smaller, lateral tubercles (Pl. 3, fig. 1a; *ltb*, Text-fig. 4C). These 'branches' may unite one tubercle with neighbouring ones. Although the sensory-line canals are closed over most of their course, their pattern can be traced as a result of the presence of double rows of smaller tubercles (Pl. 1, figs 1b, 2; Pl. 2, fig. 1a; Text-fig. 3A). In internal view, each of these tubercles is hollowed by a shallow depression, or basal recess (Pl. 1, fig. 3; Pl. 3, fig. 1b; *brec*, Text-fig. 4C), which often leaves a more or less polygonal impression on the surface of the internal natural mould of the exoskeleton. The perichondral layer of the endoskeleton, when still present, closes these polygonal recesses basally (Pl. 1, fig. 3; *pb*, Text-fig. 4C posteriorly to the orbit). This pattern has, for a long time, given the impression that the galeaspid exoskeleton was made up of small tesserae, like that of osteostracans (Halstead *et al.* 1979). Janvier (1981) also regarded this polygonal pattern as evidence for a honeycomb-like structure to the galeaspid exoskeleton, and compared it with the similar structure of the heterostracan exoskeleton. Both interpretations appear now to be incorrect. A vertical thin section through the exoskeleton of *Polybranchiaspis* (Text-fig. 4C–D) displays basically the same histological structure as in the Dong Mo '*Polybranchiaspis* sp.', *Bannhuanaspis* (Tong-Dzuy Thanh and Janvier 1990, pl. 1; Janvier 1990; Janvier *et al.* 1993) and *Xiushuiaspis* (*Changxingaspis*, N. Z. Wang 1991), that is, an acellular, aspidine-like structure with horizontal incremental lines. There is no evidence for any type of dentinous tissue and one cannot distinguish any histological discontinuity between the tubercles. The walls of the basal recesses are made up of the same kind of laminar hard tissue as the tubercles.

The relation of the structure in *Polybranchiaspis* to that in *Bannhuanaspis* (where there is no basal recess and where each tubercle seems to correspond to one exoskeletal unit, in particular in the posterior part of the shield) is unclear. If each of the star-shaped tubercles of *Polybranchiaspis*, with its basal recess, is regarded as a single dermal unit, then it may be regarded primitive, and comparable to, for example, a thelodont scale with its pulp cavity. Conversely, one may consider that the star-shaped tubercles of *Polybranchiaspis* are in fact compounds of much smaller units, represented by the central tubercle and the adjacent cusps on the radiating ridges. Then, each of these 'primary' tubercles would correspond to one single unit of *Bannhuanaspis*. The former hypothesis could be supported by the fact that a similar pattern (stellate or costulated tubercles with a large basal recess) occurs also in the Silurian galeaspid *Hanyangaspis* (N. Z. Wang 1986), which was regarded by Janvier (1981) and N. Z. Wang (1991) as the most generalized galeaspid on the basis of several other characters. The latter hypothesis could be supported by the fact that the structure of the exoskeleton of *Bannhuanaspis* is remarkably simple and passes progressively to the body squamation. Also the latter structure (small units, each corresponding to a single, simple tubercle) seems to be that seen in most other galeaspids, in particular the Eugaleaspidiformes. No major conclusions concerning the polarity of the character states in the galeaspid exoskeleton can reasonably be drawn from such sparse data, and a review of the exoskeletal structure in all other galeaspids is urgently needed.

Sensory-line canals. The sensory-line canals of *P. liaojaoshanensis* are remarkably large and form prominent ridges on the internal surface of the exoskeleton, well beyond the base of the walls of the basal recesses (Pl. 1, fig. 3; Pl. 2, fig. 3; *slc*, Text-fig. 4D). The fact that their basal part is often 'unfinished' suggests that they are partly lined by the perichondral bone lamella of the endoskeleton. The cast of the natural impression of the external surface shows that the sensory-line canals were closed over most of their length (Pl. 1, figs 1b, 2; Pl. 2, fig. 1a). The supraorbital and lateral transverse canals were open only distally (Pl. 1, fig. 2; Pl. 2, fig. 1a; *sorb*, *tl1–4*, Text-fig. 3B), and the infraorbital canal opened by only a few broad slits, lateral to the orbits (Pl. 1, fig. 2; Pl. 2, fig. 1a; *iorb*, Text-fig. 3B). In some specimens, the transverse commissural line opens in a few short slits (Pl. 1, fig. 1b; Pl. 2, fig. 1a; *tcom*, Text-fig. 3B). There is no evidence of small sensory-line pores along the canals. This condition differs from that in all other vertebrates, and the function of such, almost entirely closed sensory-line canals remains unexplained.

Subaponeurotic vascular plexus. The presence of a dense subaponeurotic vascular plexus below the exoskeleton of galeaspids has been recorded by Halstead *et al.* (1979) and described by N. Z. Wang (1991) in the Silurian genus *Xiushuiaspis*. It is here shown to be present also in *P. liaojaoshanensis* (Pl. 1, fig. 3; Pl. 3, fig. 2). This network of vascular canals lies between the exoskeleton and the underlying endoskeletal shield, but is lined with perichondral bone (*sbap*, Text-fig. 4C). It is thus situated within or just below the perichondral lamella which closes basally the basal recesses. Its structure is closely similar to that of osteostracans and gnathostomes.

Median dorsal opening. The main defining characteristic of galeaspids is a large median dorsal opening (*mdo*, Text-figs 3B, 4A–B) in the anterior part of the headshield, which is currently interpreted as the external opening of an inhalent duct (*md*, Text-fig. 4B), comparable in function, and perhaps homologous to the nasopharyngeal duct of extant hagfishes (Janvier 1984). The paired olfactory organs open into this duct immediately below its external opening. The duct communicates basally with the gill chamber. This median dorsal opening and its duct are known to be partly lined by a thin layer of exoskeleton (Wang and Wang 1982; Janvier 1984; Liu 1985). Some of the *Polybranchiaspis* specimens from Tong Vai display delicate details of the dermal ornamentation of the duct. In the anterior wall it consists of minute, tilted pyramid-shaped tubercles which point toward the exterior (Pl. 2, fig. 1b–d; *fpt*, Text-fig. 4A–B). The latter are arranged in rows which are parallel to the margin of the median dorsal opening. In contrast, in the posterior wall of the duct, the ornamentation consists of irregularly arranged tubercles which are more similar to those of the external surface of the headshield, and pass posteriorly to small, independent platelets (Pl. 1, fig. 3; Pl. 2, fig. 2). However, even in this part of the duct, the tubercles are tilted toward the exterior.

This new information is of great importance to the understanding of the functional interpretation of the median dorsal opening in galeaspids. It is well known that, in fishes in general, the apertures through which water passes from the exterior to the interior (margin of nasal opening, spiracle, etc.) are lined with minute tubercles or denticles which point toward the exterior, the role of which essentially is to repel ectoparasites (Patterson 1977). The presence of such externally pointing tubercles in galeaspids is thus evidence for an inhalent (and not exhalent, as suggested by Belles-Isles 1985) function of the median dorsal opening, and accords with the position of the olfactory cavities observed in other galeaspids (N. Z. Wang 1991). This condition can be directly compared with the forward-pointing denticles recently discovered inside the snout of some thelodonts, and which have been regarded by Brugghen and Janvier (1993) as evidence for an inhalent nasopharyngeal opening (but in a terminal position) in thelodonts.

In *Polybranchiaspis*, the external margin of the median dorsal opening is lined by a prominent ridge, somewhat accentuated in our specimens by a slight dorsoventral flattening of the rest of the shield (Pl. 2, fig. 1a–b).

Pineal foramen. The pineal foramen seems to be a variable character in galeaspids. Liu (1965) described the pineal opening of *P. liaojaoshanensis* as very small, but Halstead *et al.* (1979) considered that there was no pineal opening, as in heterostracans. The Tong Vai specimens show a very clear, rounded pineal opening, which is variable in size but fairly large (Pl. 1, fig. 1a; Pl. 2, fig. 1a; *pif*, Text-fig. 3B), and surrounded by a crown of small tubercles.

Orbit and orbital cavity. In one specimen from Tong Vai (Pl. 1, fig. 3), the perichondral lining of the orbital cavity is partly preserved and appears almost hemispherical in shape, yet the posterior ventral myodome (or trigeminal chamber) cannot be observed. The orbits are almost circular in shape and protrude slightly above the level of the surrounding exoskeleton (Pl. 1, fig. 2; Pl. 2, fig. 1a). Although the exoskeleton is certainly thicker

around the orbits, there is no major change in the aspect of the ornamentation along the orbital margin, contrary to what is commonly observed in osteostracans.

Absence of endolymphatic opening. In spite of the excellent state of preservation of the exoskeleton and ornamentation in our specimens, we have been unable to see any trace of the endolymphatic opening. To date, the latter has been observed only in the Silurian galeaspid *Xiushuiaspis* (N. Z. Wang 1991), where it lies in front of the posterior transverse commissural sensory-line canal (probably homologous to the unique commissural canal of *Polybranchiaspis*). We can thus conclude that there is no endolymphatic opening in *P. liaojaoshanensis*.

Ventral rim. The ventral rim of the headshield is covered with minute stellate tubercles. Along the margin of the oralobranchial fenestra, at least seven branchial notches are visible in one of our specimens (Pl. 2, fig. 3; *brn*, Text-fig. 5A), which is incomplete. Here again, no change in the aspect of the ornamentation is noticeable along the notch margin, and the exoskeleton passes to the smooth surface of the perichondral bone which lines the branchial fossae. Liu (1975) recorded twelve branchial notches in *P. liaojaoshanensis* from Yunnan, where the actual branchial fossae can be observed. It is probable that three or four of the branchial notches in our specimen are less marked, because they lie in the narrowest part of the rim, just behind the level of the orbit. At this level, the rim is recurved dorsally (i.e. toward the oralobranchial cavity), and this does not seem to be due to distortion. This branchial division of the rim ends, immediately behind the level of the orbits, in a well-marked notch (*n*, Text-fig. 5A). Anteriorly, it is much broader, until it reaches the oral region. Only the lateral part of the oral notch is visible in our material (*orn*, Text-fig. 5A). In one specimen (Pl. 1, fig. 2), the external surface of the part of the exoskeleton which extends behind the orbits shows a series of seven or eight 'waves', corresponding to the position of the underlying branchial fossae.

Remarks on galeaspid taphonomy. Owing to their extremely thin exoskeleton (*c*. 0·1–0·4 mm) and often weakly ossified endoskeleton, complete galeaspid headshields are preserved only in very low energy environments, such as in the third member of the Tong Vai section and at a few Chinese localities. Nevertheless, even in such quiet deposits, some headshields are broken, and seem to have broken always in the same way: the anterior rim of the median dorsal duct, or the lateral parts of the shield are detached from the central part (Pl. 1, figs 2–3; Pl. 2, fig. 1a). This suggests that there are areas of weakness in the headshield, in particular in the epibranchial region, where the roof of the oralobranchial chamber meets the dorsal exoskeleton. This is probably the reason why, in many galeaspids (*Asiaspis*, *Lungmenshanaspis*, *Pentathyraspis*), large fenestrations occur in this particular area, and have been interpreted as either dorsal 'fields' (by reference to those in osteostracans) or dorsal branchial openings (N. Z. Wang 1991; Pan 1992). In some well preserved specimens from Tong Vai, there are often small patches of exoskeleton which are missing in the epibranchial region, and this is presumably due to pre-preservational damage. These fenestrations are thus most probably artefacts of preservation.

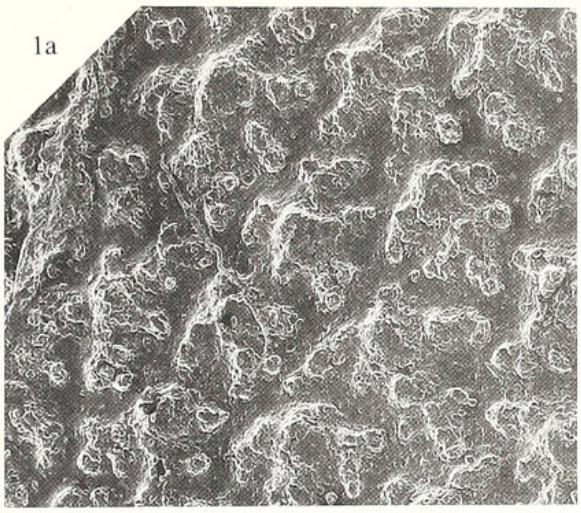
EXPLANATION OF PLATE 3

Figs 1–2. *Polybranchiaspis liaojaoshanensis* Liu, Pragian, Khao Loc Formation, Tong Vai, Ha Giang Province, Vietnam. 1, S.E.M. photograph of an elastomere cast of the external (a), BT 171, and internal (b), BT 172, surface of the exoskeleton, ×45. 2, BT 175, headshield with exoskeleton removed and photographed in immersion, to show the subaponeurotic vascular plexus (sensory-line canals darker), ×5.

Fig. 3. Acanthothoraci gen. et sp. indet. 1, BT 167, Pragian, Khao Loc Formation, Tong Vai, Ha Giang Province, Vietnam. Natural cast of the right anterolateral and spinal plates (a, ×4), and S.E.M. photographs of an elastomere cast of the impression, showing a lateral stellate tubercle of the anterolateral plate (b, ×150) and some crescentiform tubercles of the postbranchial lamina (c, ×100).

Figs 4–5. Acanthothoraci gen. et sp. indet. 2, same locality and horizon as Pl. 3, fig. 3. 4, BT 165, natural impression of the right anterior ventrolateral and spinal plates in ventral view (a) and elastomere cast of the latter (b), ×4. 5, BT 168, left anterolateral and anterior ventrolateral plates in lateral view, most of the bone missing, ×4.

Fig. 6. *Youngolepis praecursor* Zhang and Yu, BT 169, Pragian, Khao Loc Formation, Tong Vai, Ha Giang Province, Vietnam. Right lower jaw in lateral view, ×3.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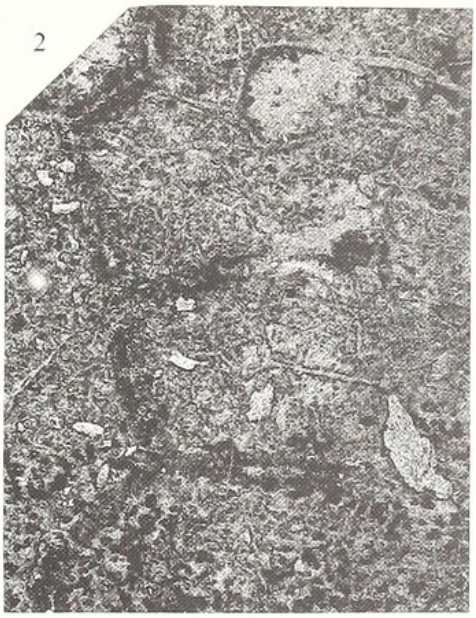
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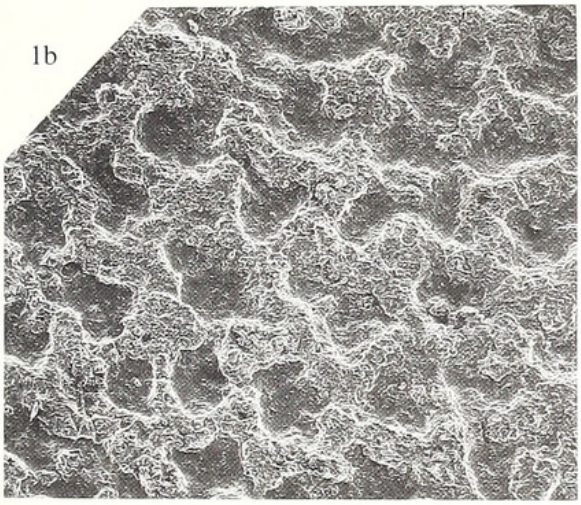
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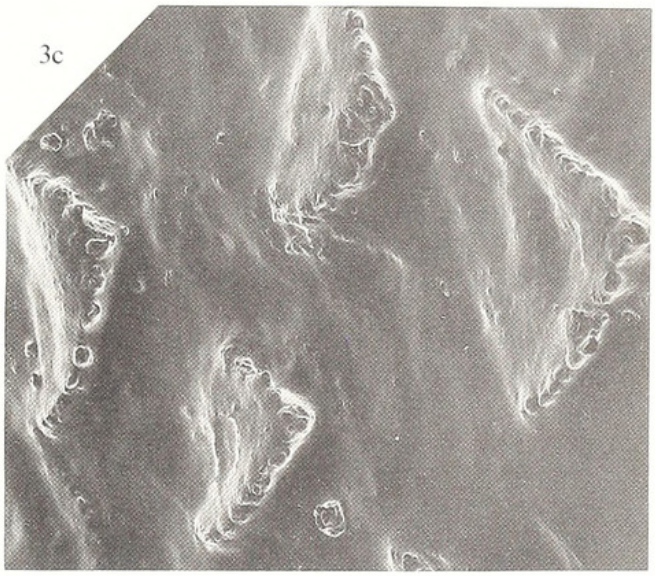
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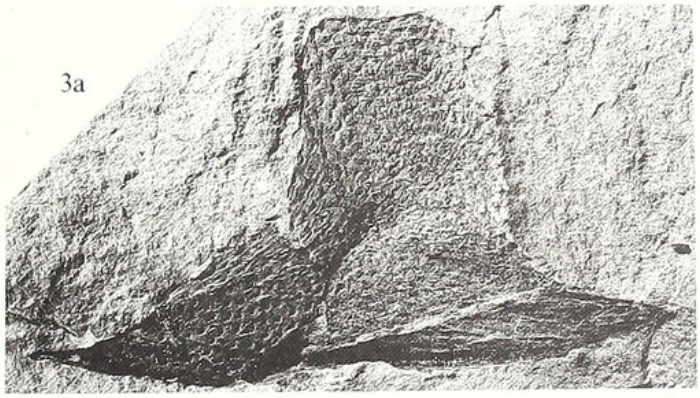
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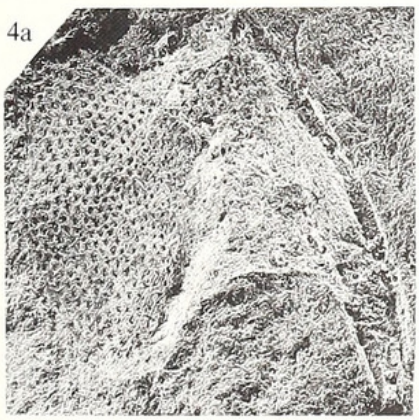
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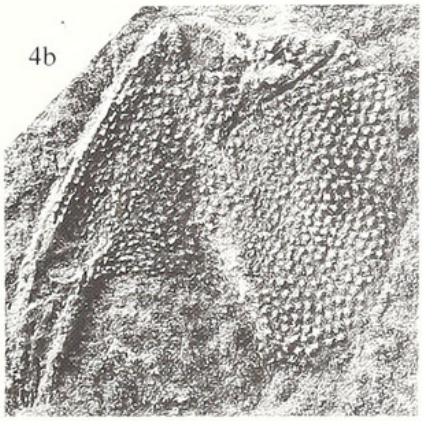
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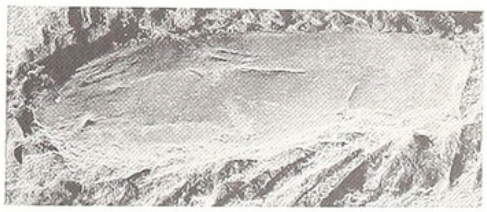
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TONG-DZUY THANH *et al.*, Devonian vertebrates

Superclass GNATHOSTOMATA Cope, 1889
Class PLACODERMI McCoy, 1848
Order ACANTHOTHORACI Stensiö, 1944

The Tong Vai material includes a few placoderm plates which can be referred here to the presumably paraphyletic taxon Acanthothoraci (Goujet 1984), on the basis of their overall morphology and star-shaped ornamentation. They seem to belong to two distinct forms, based on slight differences in the shape of the anterolateral plate. Both forms are probably new, and differ markedly from all previously described acanthothoracids, but we consider that it is preferable to wait for the discovery of cranial material, to ensure a useful systematic analysis, before erecting new species.

ACANTHOTHORACI gen. et sp. indet. 1

Plate 3, figure 3; Text-figure 6A

Material. An anterolateral plate of the right side, associated with the spinal plate (BT 167).

Locality and horizon. Exposure **2** (Text-fig. 1) of the Tong Vai valley, in a thin layer of black shale from the third member of the section (second member of the Khao Loc Formation).

Description. We refer to this first form a complete anterolateral plate, associated with the spinal plate (*AL*, *SP*, Text-fig. 6A), preserved as an impression of its external surface. The dorsal blade of the anterolateral plate is roughly square, and the postbranchial lamina is not clearly distinct from the rest of the plate, yet is covered with crescentiform tubercles (Pl. 3, fig. 3c; *pbrl*, Text-fig. 6A) as in e.g. *Romundina* (Ørvig 1975), *Palaeacanthaspis* and *Kosoraspis* (Stensiö 1944; Denison 1978). The rest of the anterolateral plate is ornamented with large, scattered, star-shaped tubercles (Pl. 3, fig. 3b).

ACANTHOTHORACI gen. et sp. indet. 2

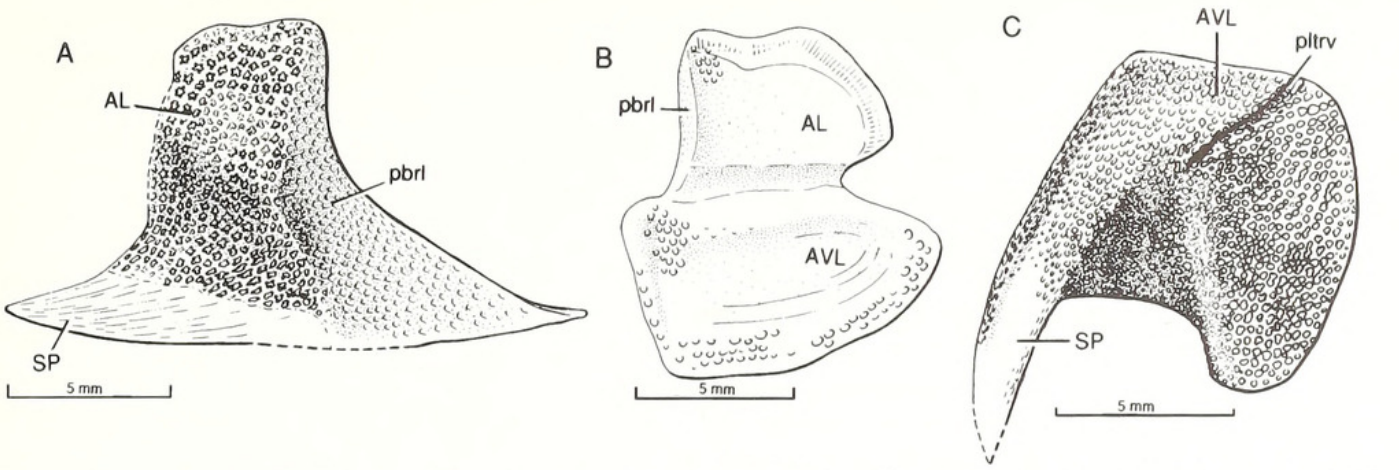
Plate 3, figures 4–5; Text-figure 6B–C

Material. Impression of the anterior ventrolateral and spinal plates of the right side (BT 165); fragmentary impression of an anterior ventrolateral plate of the left side (BT 166); indeterminate plate fragment (BT 164), with the same ornamentation as BT 165; associated anterolateral and anterior ventrolateral plates of left side (BT 168).

Locality and horizon. All specimens referred to this form come from exposure **1** (Text-fig. 1) of the Tong Vai valley and are from the shaly basal part of the third member of the section (second member of the Khao Loc Formation).

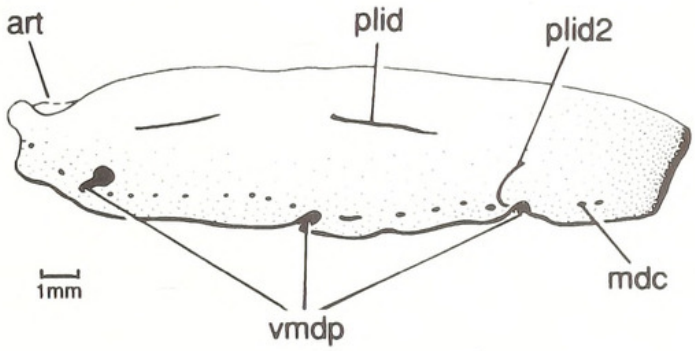
Description. This second form is represented by the external impression of an anterior ventrolateral plate and the associated spinal plate (*AVL*, *SP*, Text-fig. 6C), and two associated anterior ventrolateral and anterolateral plates (*AL*, *AVL*, Text-fig. 6B). They all differ from the preceding form by their larger, more rounded and closely-set tubercles, as well as by the rounded shape of the dorsal blade of the anterolateral plate, and the medially directed postbranchial lamina (*pbrl*, Text-fig. 6B). Since the bone was very thin, the impressions of the internal and external surfaces are somewhat superimposed, and observation of the specimens in immersion reveals traces of the overlap areas. A clear overlap area for the anterior dorsolateral plate, and possibly the posterolateral plate, is visible in the anterolateral plate (Text-fig. 6B). There seems also to be an overlap area for a posterior ventrolateral plate on the anterior ventrolateral plate. In the anterior part of the latter there is an oblique groove for the ventral transverse pit-line (*pltrv*, Text-fig. 6C).

By its broad anterior ventrolateral plate, this form clearly differs from all other acanthothoracids described to date in which this plate is very narrow. However, there is a number of still undescribed forms (e.g. from Siberia and Saudi Arabia) with a similar, broad anterior ventrolateral plate (D. Goujet, pers. comm. 1994). A small acanthothoracid is present in the Cuifengshan Group of Yunnan (Zhu Min, pers. comm. 1994) which



TEXT-FIG. 6. A–C, Acanthothoraci gen. et sp. indet., Khao Loc Formation, Tong Vai, Ha Giang Province, Vietnam. A, Acanthothoraci gen. et sp. indet. 1, BT 167, right anterolateral and spinal plates in lateral view, camera lucida drawing of an elastomere cast of a specimen preserved as an impression. B–C, Acanthothoraci gen. et sp. indet. 2; B, BT 168, left anterolateral and anterior ventrolateral plates preserved essentially as an impression of the internal surface, with some patches of exoskeleton and external ornamentation, camera lucida drawing; C, BT 165, right anterior ventrolateral plate and spinal plate in ventral view, camera-lucida drawing of an elastomere cast of the specimen preserved as an impression. Abbreviations: *AL*, anterolateral plate; *AVL*, anterior ventrolateral plate; *pbrl*, postbranchial lamina of the anterolateral plate; *pltrv*, transverse ventral pit-line; *SP*, spinal plate.

TEXT-FIG. 7. *Youngolepis praecursor* Zhang and Yu, BT 169, Khao Loc Formation, Tong Vai, Ha Giang Province, Vietnam. Camera-lucida drawing of the right lower jaw in lateral view. Abbreviations: *art*, glenoid articular fossa; *mdc*, pores of the mandibular sensory-line canal; *plid*, horizontal part of infradentary pit-line; *plid2*, vertical pit-line of infradentary 2; *vmdp*, ventral mandibular pits.



seems to be identical to this second form from Tong Vai. All the acanthothoracids known to date are Late Lochkovian to Early Emsian in age.

Class OSTEICHTHYES Huxley, 1880
Subclass SARCOPTERYGII Romer, 1955
Infraclass DIPNOMORPHA Ahlberg, 1991

Genus YOUNGOLEPIS Zhang and Yu, 1981

Youngolepis praecursor Zhang and Yu, 1981

Plate 3, fig. 6; Text-figure 7

Material. A single lower jaw of the right side (BT 169).

Locality and horizon. Exposure **1** (Text-fig. 1) of the Tong Vai valley.

Description. A small right lower jaw of a cosmine-covered sarcopterygian is similar to that of *Youngolepis praecursor*, described by Chang (1991), and shows the characteristic ventral series of large sensory pits (*vmdp*, Text-fig. 7). The pores of the mandibular canal are relatively large (*mdc*, Text-fig. 7), and the horizontal and vertical pit-lines (*plid*, *plid2*, Text-fig. 7) are well marked. The articular area is poorly preserved (*art*, Text-fig.

7). In addition, there are some cosmine-covered dermal bone fragments with very large and closely-set pores, which may belong to a different taxon.

CONCLUSIONS

The vertebrate fauna from Tong Vai accords with the '*Polybranchiaspis liaojaoshanensis – Dongfangaspis qujingensis* palaeocommunity' as defined by S. T. Wang (1991) from the base of the Xishancun Formation of the Cuifengshan Group of Qujing, Yunnan. However, *P. liaojaoshanensis* is known to extend into the overlying Xitun Formation, where it occurs in association with *Youngolepis praecursor* (Chang 1982). We would thus be inclined towards correlating the fish horizon in Tong Vai with the Xitun Formation of the Cuifengshan Group of Yunnan which is referred to the Late Lianhuashanian – Early Nagaolingian. Although fragments with a *Polybranchiaspis*-like ornamentation occur also in the more southerly situated Vietnamese localities of Trang Xa and Dong Mo, the material referred to by Tong-Dzuy Thanh and Janvier (1990) as '*Polybranchiaspis* sp.' from Dong Mo probably belongs to a different genus. Its ornamentation of small, isometric and rounded tubercles, and the lack of basal recesses are rather suggestive of *Bannhuanaspis*, yet its size is much smaller than that of the latter. Two forms of acanthothoracid placoderms have been described herein, one of which is unquestionably new. The occurrence of this taxon is consistent with the Pragian age of this locality.

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