

Systematic Palaeontology (Vertebrate Palaeontology)

# Occurrence of *Sanqiaspis*, Liu, 1975 (Vertebrata, Galeaspida) in the Lower Devonian of Vietnam, with remarks on the anatomy and systematics of the Sanqiaspididae

Philippe Janvier<sup>a,\*</sup>, Tong-Dzuy Thanh<sup>b</sup>, Ta Hoa Phuong<sup>b</sup>,  
Gaël Clément<sup>a</sup>, Nguyễn Duc Phong<sup>c</sup>

<sup>a</sup> UMR 5143, CNRS, CP 38, Muséum national d'histoire naturelle, 47, rue Cuvier, 75231 Paris cedex 05, France

<sup>b</sup> Vietnam National University, Department of Geology, 334 Nguyễn Trãi Street, Thanh Xuan, Hanoi, Viet Nam

<sup>c</sup> Institute of Geology and Mineral Resources, Thanh Xuan, Hanoi, Viet Nam

Received 6 August 2008; accepted after revision 3 October 2008

Available online 11 December 2008

Presented by Philippe Taquet

## Abstract

A new species of the huananaspidiform galeaspid genus *Sanqiaspis* is reported from the Lochkovian Si Ka Formation of northern Vietnam and is somewhat older than the previously recorded occurrences of this genus, from the Pragian Posongchong Formation of southern China. This species provides new information about the anatomy of the head shield in the Sanqiaspididae and notably provides evidence of a complete endoskeletal and dermal postbranchial wall, like in osteostracans. The various types of vertebrate assemblages defined in the Lower Devonian of China are discussed, by comparison to the vertebrate faunas hitherto recorded from the Lower Devonian of Vietnam, and it is suggested that their composition is strongly influenced by environmental factors. **To cite this article:** P. Janvier et al., C. R. Palevol 8 (2009).

© 2008 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

## Résumé

**Présence de *Sanqiaspis*, Liu, 1975 (Vertebrata, Galeaspida) dans le Dévonien inférieur du Viêt Nam, avec des remarques sur l'anatomie et la systématique des Sanqiaspididae.** Une nouvelle espèce du genre de galéaspide huananaspidiforme *Sanqiaspis*, est décrite dans la Formation de Si Ka du Lochkovien du nord du Viêt Nam et apparaît plus ancienne que les représentants de ce genre décrits jusqu'alors dans la formation praguienne de Posongchong de Chine du Sud. Cette espèce apporte de nouvelles informations sur l'anatomie du bouclier céphalique des Sanqiaspididae et montre la présence d'une cloison postbranchiale endosquelettique et dermique complète, comme chez les ostéostracés. Les divers types d'assemblages de vertébrés définis dans le Dévonien inférieur de Chine sont brièvement comparés aux faunes de vertébrés reconnues dans le Dévonien inférieur du Viêt Nam et il est suggéré que leur composition est fortement influencée par des facteurs environnementaux. **Pour citer cet article :** P. Janvier et al., C. R. Palevol 8 (2009).

© 2008 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

**Keywords:** Vertebrata; Galeaspida; Anatomy; Systematics; Devonian; Palaeobiogeography; Vietnam; China

**Mots clés :** Vertebrata ; Galeaspida ; Anatomie ; Systématique ; Dévonien ; Paléobiogéographie ; Viêt Nam ; Chine

\* Corresponding author.

E-mail address: [janvier@mnhn.fr](mailto:janvier@mnhn.fr) (P. Janvier).

## 1. Introduction

The Galeaspida, or galeaspids, are an extinct clade of armoured jawless vertebrates which is, to date, exclusively known from the Silurian and Devonian of China and Vietnam [4,5,8,13,14,19,24,25,36]. They are currently regarded as the sister group of osteostracans, or “cephalaspids”, and jawed vertebrates, with which they share a perichondrally calcified, or ossified, braincase [2,3,5,7,8,31]. The braincase of galeaspids is covered dorsally by an extensive dermal bone layer of galespidin, or “head shield”, pierced by widely separated orbits and a presumably incurrent median dorsal opening. The latter is a unique character of galeaspids, alongside the characteristic festooned pattern of the dorsal sensory-line canals of the head shield [8,16,36]. Despite their rather homogeneous overall body shape, galeaspids display a remarkable diversity of head shield morphology, which sometimes mimics that of osteostracans, notably in the development of lateral and rostral processes [5,8,19,36]. In addition, the oralobranchial chamber of the Polybranchiaspidiformes and Huananaspidiformes galeaspids display a very large number of branchial fossae that housed the gills (up to 45 pairs; that is, the highest number of gill units ever recorded in vertebrates [9,19,36]).

Most galeaspid species are only known from their dermoskeletal head shield, and very few preserve features of the braincase and oralobranchial chamber. Therefore, any information that contributes to the knowledge of the anatomical diversity of the group will help in refining current galeaspid phylogeny [36]. Here we describe a new galeaspid species from the Lochkovian (Lower Devonian) of northern Vietnam, which is referred to the hitherto poorly known genus *Sanqiaspis*, Liu, 1975 [14], and provides new information about its morphology. *Sanqiaspis* was hitherto recorded only from the Lower Devonian of Yunnan, Guangxi and Sichuan, China [33–35,37]. This agrees with its discovery in northern Vietnam, immediately below well-dated Lochkovian-Pragian marine layers, and allows a more precise dating of the Chinese occurrences.

## 2. Material and methods

The specimen described herein is preserved in thin-bedded, slightly bituminous shale from the middle part of the Upper Lochkovian Si Ka Formation of the Lung Cu–Ma Lé section (23° 21' 07" N; 105° 17' 36" E; altitude: 1416 m; Fig. 1). It has been prepared by etching away the bone with 5% hydrochloric acid. After having been photographed (Fig. 2B1), the posterior part of the

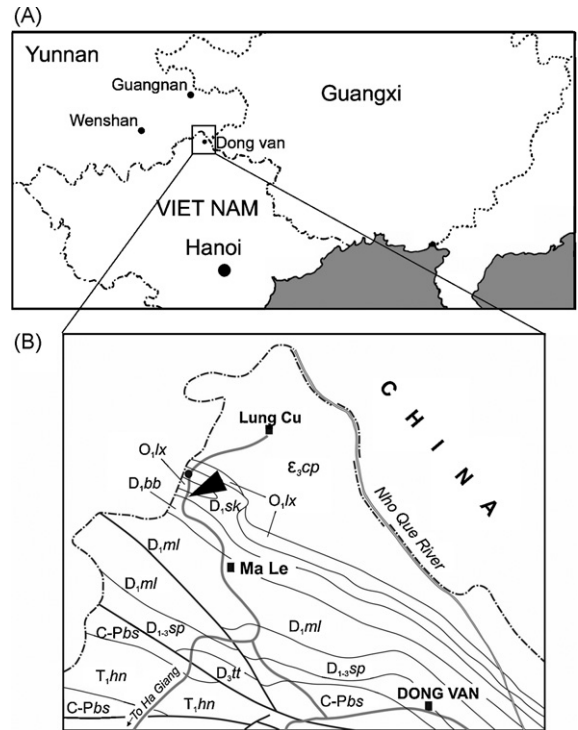


Fig. 1. Locality map. **A.** Location of the Lung Cu area (framed) on the map of northern Vietnam and South China. The closest Lower Devonian vertebrate-bearing localities of China (Wenshan and Guangnan) are added. **B.** Geological sketch of the Dong Van and Lung Cu areas. Arrowhead indicates the type locality of *Sanqiaspis vietnamensis*. Abbreviations:  $\epsilon_3 cp$ , Chang Pung Formation (Upper Cambrian);  $O_1 lx$ , Lut Xia Formation (Lower Ordovician);  $D_1 sk$ , Si Ka Formation (Lochkovian);  $D_1 bb$ , Bac Bun Formation (Lochkovian-Pragian);  $D_1 ml$ , Mia Lé Formation (Pragian);  $D_{1-3} sp$ , Si Phai Formation (Pragian-Frasnian);  $D_3 tt$ , Toc Tat Formation (Frasnian-Famennian);  $C-Pbs$ , Bac Son Formation (Carboniferous-Permian);  $T_1 hn$ , Hong Ngai Formation (Lower Triassic).

Fig. 1. Carte de la localité. **A.** Position de la région de Lung Cu (encadré) sur la carte du Nord du Viêt Nam et du Sud de la Chine. Les gisements de vertébrés dévoniens les plus proches en Chine (Wenshan et Guangnan) sont ajoutés. **B.** Carte géologique simplifiée des régions de Dong Van et Lung Cu. La pointe de flèche indique la localité type de *Sanqiaspis vietnamensis*. Abréviations:  $\epsilon_3 cp$ , Formation de Chang Pung (Cambrien supérieur);  $O_1 lx$ , Formation de Lut Xia (Ordovicien inférieur);  $D_1 sk$ , Formation de Si Ka (Lochkovien);  $D_1 ml$ , Formation de Bac Bun (Lochkovien-Pragien);  $D_1 ml$ , Formation de Mia Lé (Pragien);  $D_{1-3} sp$ , Formation de Si Phai (Pragien-Frasnien);  $D_3 tt$ , formation de Toc Tat (Frasnien-Famennien);  $C-Pbs$ , formation de Bac Son (Carbonifère-Permien);  $T_1 hn$ , formation de Hong Ngai (Trias inférieur).

internal, natural cast of the specimen has been removed with a needle, in order to expose the postbranchial wall and the ventral dermoskeleton of the abdominal division of the shield (Fig. 2B2). An elastomer cast stained in black was made and photographed after being whitened with magnesium oxide. The specimen has been obliquely

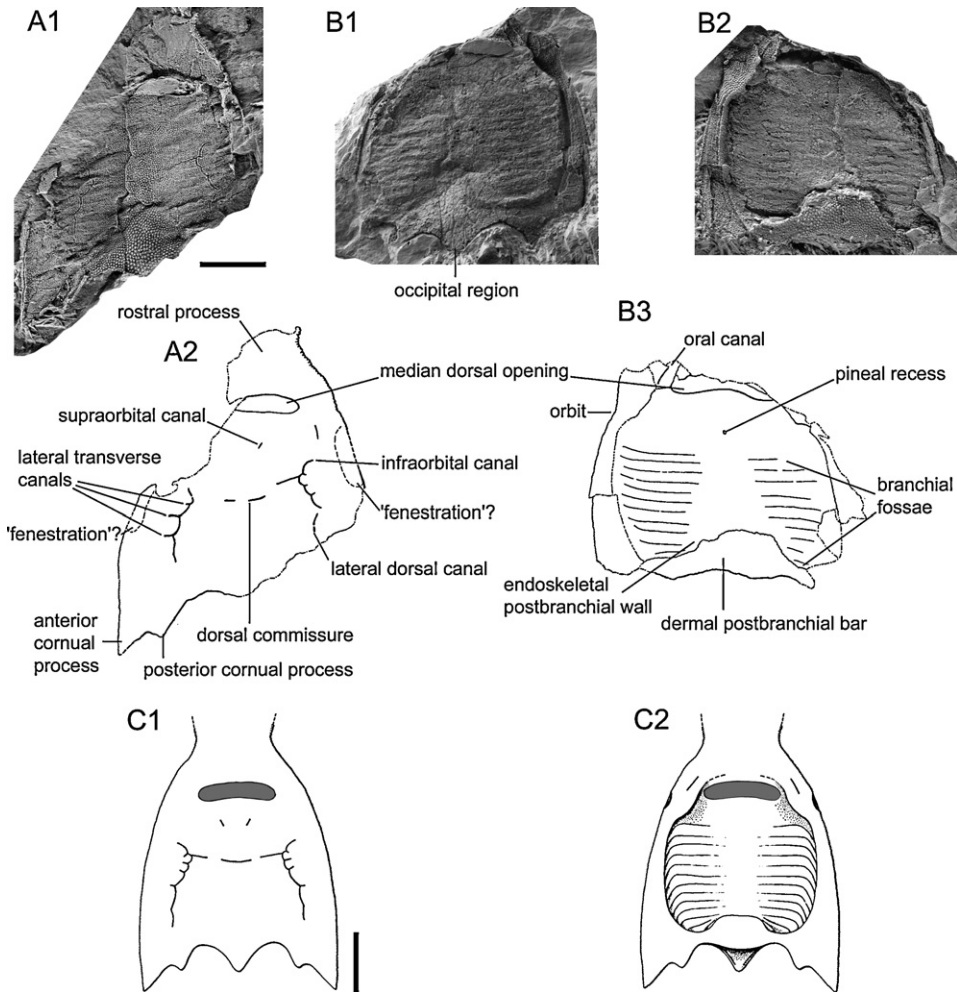


Fig. 2. *Sanqiaspis vietnamensis* n. sp., Si Ka Formation, Lochkovian (Lower Devonian) of Lung Cu, northern Vietnam. **A.** Incomplete head shield (BT 338, holotype) in dorsal view; elastomer cast (A1) and explanatory sketch (A2). **B.** Ventral counterpart of the same specimen before preparation of the postbranchial wall (B1), elastomer cast after preparation exposing the postbranchial wall (B2), and explanatory sketch (B3). **C.** Attempted graphic restoration of the original proportions of the specimen in dorsal (C1) and ventral (C2) view. Scale bar = 10 mm.

Fig. 2. *Sanqiaspis vietnamensis* n. sp., Formation de Si Ka, Lochkovien (Dévonien inférieur) de Lung Cu, Nord du Viêt Nam. **A.** Bouclier céphalique incomplet (BT 338, holotype) en vue dorsale; moulage en élastomère (A1) et schéma explicatif (A2). **B.** Contre-empreinte ventrale du même spécimen avant préparation de la cloison postbranchiale (B1), moulage en élastomère après préparation de la cloison postbranchiale (B2) et schéma explicatif (B3). **C.** Essai de reconstitution graphique des proportions originales du spécimen en vues dorsale (C1) et ventrale (C2). Échelle = 10 mm.

distorted during fossilization (Fig. 2A). Its original shape and proportions have been restored by using the “skew” command of Photoshop, and bringing the commissural sensory line in a transverse position (Fig. 2C).

### 3. Geological setting

The Lower Devonian of eastern Bac Bo (northeastern Vietnam) is typically composed of a gradual succession of three formations, the Si Ka, Bac Bun and Mia Lé formations, the former two being gathered in the Song Cau Group [27]. The Si Ka Formation generally

consists of reddish sandstone and siltstone, the Bac Bun Formation of siltstone, marl, shale and dolomite, and the Mia Lé Formation of marl, shale, sandstone and limestone. This formation series indicates, from base to top, a progressive installation of a more and more marine environment, in which the fish remains become abundant at the transition between the Si Ka and Bac Bun formations, along with the first marine invertebrates (notably the brachiopod *Howittia wangi*) in the middle part of the Bac Bun Formation [25–27]. This sequence shows some local variations, notably the lack of the arenaceous Si Ka Formation and the predominance of bituminous shale in

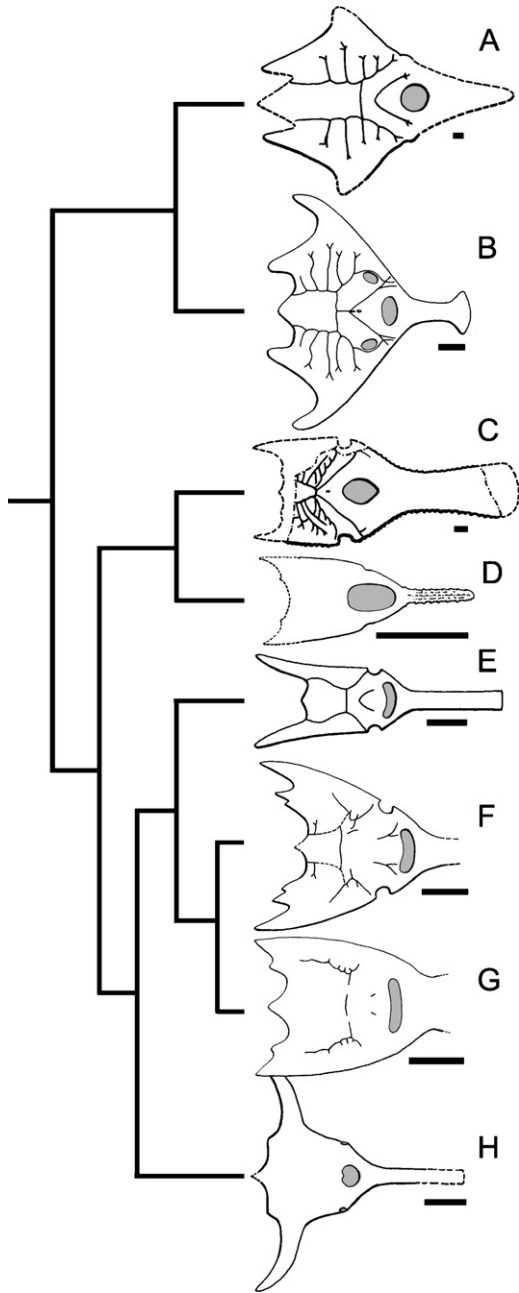


Fig. 3. Phylogenetic relationships of the Huananaspidiformes (after tree topology in Zhu and Gai [36]), with particular reference to the most inclusive taxa of the clade. A. *Antiquisagittaspis*. B. *Sanchaspis*. C. *Gantarostrataspis*. D. *Wumengshanaspis*. E. *Sanqiaspis rostrata*. F. *Sanqiaspis zhaotongensis*. G. *Sanqiaspis vietnamensis*. H. *Huananaspis* and all other Huananaspidiformes. Scale bar = 10 mm. Head shields in dorsal view, redrawn after [15] (A); [21] (B); [29] (C); [32] (D); [34] (E); [30] (F); [14] (H).

Fig. 3. Relations phylogénétiques au sein des Huananaspidiformes (d'après la topologie proposée par Zhu et Gai [36]), en particulier les formes les plus inclusives de ce clade. A. *Antiquisagittaspis*. B. *Sanchaspis*. C. *Gantarostrataspis*. D. *Wumengshanaspis*. E.

the Quan Ba area, north of Ha Giang [22,28], and further west, in the Lai Chau Province.

The specimen described herein comes from the siltstone beds of the middle part of the Si Ka Formation that crops out along the Ma Lé (Mia Lé)–Lung Co road, a classical Devonian section which is known since the early works of Mansuy [18] and Deprat [1,10]. It was found along with plant remains, large arthropod fragments, gastropods, rare lingulids and abundant remains of other fish groups. Among the latter are at least two other galeaspids (probably *Polybranchiaspis* sp. and a large indeterminate form), at least three antiarchs (*Heteroyunnanolepis* sp., *Yunnanolepis* cf. *Y. spinulosa*, Janvier and Ta Hoa, 1999 [10] and *Chuchinolespis* sp.), an indeterminate placoderm (arthrodire or petalichthyid) and at least one sarcopterygian (probably a Youngolepididae).

#### 4. Systematic study

The specimen displays the overall morphology of the two galeaspid species currently referred to the genus *Sanqiaspis* and characterized by a transversely elongated median dorsal opening, elongated head shield, posteriorly directed cornual processes, anterior rostral process and numerous, transversely elongated branchial fossae (Figs. 2 and 3E–G). However, it differs from all other described species of the genus *Sanqiaspis* by its proportions and the shape of its rostral process and is therefore referred to a new species.

Subclass Galeaspida Halstead, Tarlo, 1967 [23]

Order Huananaspidiformes, Janvier, 1975 [4]

Family Sanqiaspididae, Liu, 1975 [14]

Genus *Sanqiaspis*, Liu, 1975 [14]

*Sanqiaspis vietnamensis* n. sp.

(Fig. 2)

Diagnosis: A *Sanqiaspis* species with short and distally expanded rostral process. The maximum breadth of the head shield is about thrice that of the median dorsal opening and the length of the cornual processes is about half the breadth of the median dorsal opening.

Type specimen: An incomplete and slightly distorted head shield (Museum of the Geological Survey of Vietnam, Hanoi, BT338) (Fig. 2A, B).

*Sanqiaspis rostrata*. F. *Sanqiaspis zhaotongensis*. G. *Sanqiaspis vietnamensis*. H. *Huananaspis* et tous les autres Huananaspidiformes. Échelle = 10 mm. Boucliers céphaliques en vue dorsale, redessinés d'après [15] (A); [21] (B); [29] (C); [32] (D); [34] (E); [30] (F); [14] (H).



Type locality: Lung Cu–Ma Lé section, Lung Cu village, Dong Van district, Ha Giang Province, northern Vietnam.

Age: Lower Devonian (Lochkovian), middle part of the Si Ka Formation.

Referred material: The holotype only.

Remarks: *Sanqiaspis vietnamensis* clearly differs from the type species of the genus *Sanqiaspis*, *Sanqiaspis rostrata*, Liu, 1975 [14] (Fig. 3E) by its much broader head shield and much shorter rostral process, which expands distally at a short distance from its root, as in *Sanchaspis magalorostrata* Pan and Wang, 1981 [21] (Fig. 3B). *Sanqiaspis vietnamensis* is, however, more closely similar to *S. zhaotongensis*, Liu, 1975 [14] (Fig. 3F), from which it differs by its slightly different sensory line pattern and shorter cornual processes [29]. A third species, *Sanqiaspis sichuanensis*, Pan and Wang, 1978 [20], was described on the basis of a very poorly preserved specimen and later regarded as a junior synonym of *Sanqiaspis rostrata* [16]. Zhu and Gai [36] provided the first extensive phylogenetic analysis of the Galeaspida, which resulted in three equally parsimonious trees, differing only in the position of the most inclusive (Silurian) galeaspid genera *Hanyangaspis*, *Changxingaspis* and *Dayongaspis*. These trees also yield much the same major clades as defined in earlier works [4,5,8], namely the Eugaleaspidiformes and Huananaspidiformes, but show the Polybranchiaspidiformes as monophyletic (contra [5,8]). *Sanqiaspis* (Fig. 3E–G) is nested within the Huananaspidiformes, as the sister group of a clade comprising seven genera (*Nanpanaspis*, *Asiaspis*, *Huananaspis* [Fig. 3H], *Lungmenshanaspis*, *Qingmenaspis*, *Sinoszechuanaspis*, *Sanqiaspis* and *Macrothyriaspis*). Apart from the question of the position of *Antiquisagittaspis* (Fig. 3A; a large but poorly known form [15]), the monophyly of the Huananaspidiformes is well supported and the members of the group are readily recognized by their generally long rostral process.

## 5. Description

Thanks to acid preparation, the cast of *Sanqiaspis vietnamensis* shows a number of details that had never been observed in the previously described *Sanqiaspis* material from China. Galeaspids are generally depressed fishes and their endoskeletal head shield is weakly ossified. Moreover, their dermoskeleton is very thin and made up by small and poorly consolidated units [6,12,31], hence the frequent distortion of their head shield. The entire dermoskeletal shield of *Sanqiaspis vietnamensis* is ornamented with small, pointed and

costulate tubercles of variable size. The largest tubercles are located near the midline both on the dorsal surface and the dermal covering of the postbranchial wall and the smallest ones lie dorsal to the branchial region of both sides (Fig. 2A1). The head shield of *Sanqiaspis vietnamensis* displays the characteristic festooned pattern of the dorsal sensory-lines of all galeaspids [36], which were mainly located in grooves, but partly enclosed in canals, as in, for example, *Polybranchiaspis* [22,26,28]. Surprisingly the dorsal sensory line pattern appears quite different from that of *S. zhaotongensis* (Fig. 3F) [34], otherwise very similar to *Sanqiaspis vietnamensis* by the overall shape of its head shield. By contrast, the sensory line pattern of *Sanqiaspis vietnamensis* resembles more closely that of more generalized Huananaspidiformes, such as *Antiquisagittaspis* or *Sanchaspis* (Fig. 3A, B) [15,29]. Like in all other *Sanqiaspis* (and most other Huananaspidiformes) species, the orbits of *Sanqiaspis vietnamensis* are opening laterally and there is no pineal opening (a variable character in galeaspids). Yet, the internal surface of the dermoskeleton shows the impression of a pineal recess (Fig. 2B3). The median dorsal opening is elliptic in shape and transversely elongated, as in the other *Sanqiaspis* species. The cornual process is preserved only on the left side and shorter than in *Sanqiaspis zhaotongensis*, but similarly double, with a large anterior process and a smaller one, separated by an embayment (Fig. 2A2). The rostral process is incomplete, but its preserved distal extremity suggests that it was somewhat broadened distally, as is also the case in *Sanqiaspis rostrata* (Fig. 3E) and other generalized Huananaspidiformes, such as *Sanchaspis* and *Gantarostrataspis* (Fig. 3B, C). Moreover, and like in the latter genus, the margin of the rostral process bears a single series of enlarged tubercles.

The dermoskeletal postbranchial bar is generally regarded as lacking in galeaspids, except in the two plesiomorphic genera *Xiushuiaspis* and *Changxingaspis* [36]. This is probably because of the lack of preparation of the ventral side of the head shield of most galeaspids. However, *Sanqiaspis vietnamensis* shows an extensive postbranchial bar that covers ventrally the abdominal division of the head shield and bounds off posteriorly the oralbranchial fenestra, like in osteostracans [8] (Fig. 2B3). This agrees with the presence of an equally extensive endoskeletal postbranchial wall that closes posteriorly the oralbranchial chamber (Fig. 2B3). The endoskeletal roof of the oralbranchial chamber is poorly preserved but shows indications of at least 11 pairs of transversely elongated branchial fossae (Fig. 2B); that is, far less than the 17–19 pairs that are visible in *Sanqiaspis rostrata* [14,32]; their number in *Sanqiaspis zhaoton-*

*gensis* is unknown. The posteriormost branchial fossae are slightly oblique relative to the midline and extend on the postbranchial wall, as in osteostracans, and there seems to be a single large median postbranchial opening. The lateral margins of the oralbranchial fenestra are embayed by branchial notches that are bordered by minute tubercles (Fig. 2B2).

The ventral counterpart of the specimen, before preparation of the postbranchial wall, showed the trace of the posteriorly tapering occipital region and, at the limit between the endoskeleton and dermoskeleton, an extensive subaponevrotic vascular network (Fig. 2B1).

The lateral part of the dorsal dermoskeleton that overlies the oralbranchial chamber shows, at any rate on the right side, a small gap (Fig. 2A2) that is suggestive of the “fenestrations” mentioned in various galeaspid taxa, notably Huananaspidifomes [36], and once regarded as either homologues of the “lateral cephalic fields” of osteostracans [17], or dorsal external branchial openings. Janvier [8] doubted both interpretations (except perhaps for *Microhoplaspis*, in which these dorsal openings show a distinct margin lined with endoskeleton), and considered that these fenestrations are an artefact of preservation due to the fragility of the very thin dermoskeleton in this particular region of the head shield, where the roof of the branchial fossae is directly in contact with the dermoskeleton. Similar dorsal gaps are also found in some specimens of *Polybranchiaspis*, whose dorsal dermoskeleton is normally not fenestrated [22].

## 6. Discussion and conclusion

Despite its poor preservation, *Sanqiaspis vietnamensis* shows that preparation of galeaspids in the form of natural moulds and casts provides a wealth of hitherto unavailable detail information, in particular as to the ornamentation of the dermoskeleton. The discovery of a complete postbranchial wall in *Sanqiaspis* suggests that this feature is more widespread in galeaspids than previously thought and is yet another character shared by this taxon and the osteostracans.

The discovery of *Sanqiaspis* in northern Vietnam increases the distribution of this huananaspidiform genus in the Devonian of the South China Block. The two previous occurrences from China, in Jiangyou, Sichuan and Zhaotong, northeastern Yunnan suggested possible endemism [14,28,30], until it turned up in the Pragian of Wenshan, Yunnan [34]. The type horizon of *Sanqiaspis zhaotongensis* was initially referred to the Late Lochkovian “Cuifengshan Formation” but later correlated with the Pragian Posongchong Formation

of Wenshan and Guangnan of southern Yunnan, where *Sanqiaspis rostrata* also occurs [34,37], and which are the Chinese vertebrate-bearing localities that lie closest to Lung Cu in Vietnam (Fig. 1). The marine invertebrate fauna of the Bac Bun Formation that immediately overlies the vertebrate-bearing shale at Lung Cu is widely accepted as essentially Late Lochkovian in age (with a possibly Early Pragian top part) [27]. Therefore *Sanqiaspis vietnamensis*, which clearly comes from the underlying Si Ka Formation, is Lochkovian in age; that is, older than the Chinese occurrences of *Sanqiaspis*. So far, none of the other Lower Devonian vertebrate faunas hitherto recorded from Vietnam has ever yielded *Sanqiaspis*, despite the abundance of galeaspids in certain outcrops of the Bac Bun and Si Ka formations, notably *Polybranchiaspis* and *Laxaspis*, which also occur in the Lochkovian Xishancun Formation (Cuifengshan group) of Yunnan [11,22,24,26,28,33]. One must, however, consider with caution the age of these Lower Devonian vertebrate occurrences of the South China Block, which are rarely associated with unambiguously marine invertebrates. *Sanqiaspis* belongs to the “*Sanchaspis–Asiaspis*” assemblage III [35,37], which is known from the Posongchong, Xujachong and Nagaolin formations of Yunnan (Zaotong, Wenshan), Sichuan (Jiangyou) and Guangxi (Liuqing), respectively. In China, this assemblage is dated as Pragian on the basis of associated invertebrate faunas, including conodonts and palynomorphs [33,35]. This contrasts with the Lochkovian age of the Vietnamese *Sanqiaspis* occurrence. Moreover, *Sanqiaspis vietnamensis* is found in association with taxa that are regarded as typical for the Late Lochkovian “*Diabolepis–Nanpanaspis*” assemblage II, such as the antiarch *Chuchinolepis* [35]. However, in the same beds also occur taxa, such as the antiarch *Heteroyunnanolepis*, which are referred to the Early Lochkovian “*Polybranchiaspis liaojiaoshanensis–Laxaspis qujingensis*” assemblage I [35]. Therefore, we suspect that the galeaspid occurrences are strongly facies-bound and the galeaspid taxa may either not be entirely reliable guide fossils, or some of the vertebrate assemblages defined in China are imperfectly dated. The four major Lower Devonian vertebrate faunas hitherto described from the Bac Bun Formation (or the transition between the latter and the underlying Si Ka Formation) of northern Vietnam (i.e., from Trang Xa, Ban Nhuan, Dong Mo and Tung Vai, respectively [10–12,22,25,26,28]) all occur below the first *Howittia wangi*-bearing beds and yield taxa that generally belong to the Lochkovian assemblages I and II. A possible exception is Tung Vai [22,28], whose vertebrate fauna is dominated

by *Polybranchiaspis*, *Laxaspis*, *Minicrania* and *Heteroyunnanolepis* but devoid of *Chuchinoalepis*, and likely to be older than all other Early Devonian vertebrate faunas from Vietnam.

## References

- [1] J. Deprat, Études géologiques sur les régions du Haut Tonkin (feuilles de Pakha, Hagiang, Mapilo, Yenminh), Mem. Serv. Geol. Indochine 5–4 (1916) 1–176.
- [2] P.C.J. Donoghue, M.P. Smith, The anatomy of *Turinia pagei* (Powrie) and the phylogenetic status of the Thelodonti, Trans. R. Soc. Edinb. Earth Sci. 92 (2001) 15–37.
- [3] P.C.J. Donoghue, P.L. Forey, R.J. Aldridge, Conodont affinity and chordate phylogeny, Biol. Rev. 75 (2000) 191–351.
- [4] P. Janvier, Anatomie et position systématique des Galéaspides (Vertebrata, Cyclostomata), Céphalaspidomorphes du Dévonien inférieur du Yunnan (Chine), Bull. Mus. Natl. Hist. Nat. Ser. III 278 (1975) 1–6.
- [5] P. Janvier, The affinities of the Osteostraci and Galeaspida, J. Vertebr. Paleontol. 3 (1984) 315–321.
- [6] P. Janvier, La structure de l'exosquelette des Galeaspida, C. R. Acad. Sci. Paris Ser. II 130 (1990) 655–659.
- [7] P. Janvier, The dawn of the vertebrates: characters versus common ascent in the rise of current vertebrate phylogenies, Palaeontology 39 (1996) 259–287.
- [8] P. Janvier, Early Vertebrates, Oxford University Press, Oxford, 1996.
- [9] P. Janvier, Early specialization in the branchial apparatus of jawless vertebrates: a consideration of gill number and size, in: G. Arratia, M.V.H. Wilson, R. Cloutier (Eds.), Recent Advances in the Origin and Early Radiation of Vertebrates, Verlag Dr. Friedrich Pfeil, Munich, 2006, pp. 29–52.
- [10] P. Janvier, P. Ta Hoa, Les Vertébrés (Placodermi, Galeaspida) du Dévonien inférieur de la coupe de Lung Cô-Mia Lé, province de Hà Giang, Viêt Nam, avec des données complémentaires sur les gisements à Vertébrés du Dévonien du Bac Bo oriental, Geodiversitas 21 (1999) 33–67.
- [11] P. Janvier, T. Tong-Dzuy, The Silurian and Devonian vertebrates of Vietnam: a review, J. Geol. (Dia Chât) Hanoi B 11–12 (1998) 18–28.
- [12] P. Janvier, T. Tong-Dzuy, P. Ta Hoa, A new Early Devonian galeaspid from Bac Thai Province, Vietnam, Palaeontology 36 (1993) 297–309.
- [13] Y.H. Liu, New Devonian agnathan from Yunnan, Vertebr. Palasiat. 9 (1965) 125–134 (in Chinese).
- [14] Y.H. Liu, Lower Devonian agnathans of Yunnan and Sichuan, Vertebr. Palasiat. 10 (1975) 202–216 (in Chinese with English abstract).
- [15] Y.H. Liu, A galeaspid (Agnatha), *Antiquisagittaspis cornuta* gen. et sp. nov., from the Lower Devonian of Guangxi, China, Vertebr. Palasiat. 23 (1985) 247–254 (in Chinese with English abstract).
- [16] Y.H. Liu, The sensory system of Galeaspida, Vertebr. Palasiat. 24 (1986) 245–259 (in Chinese with English abstract).
- [17] Y.H. Liu, Do the lateral field exist in some galeaspids (jawless fishes)? Vertebr. Palasiat. 31 (1993) 315–322 (in Chinese with English abstract).
- [18] H. Mansuy, Contribution à l'étude de l'Ordovicien et du Gothlandien du Tonkin, Mem. Serv. Geol. Indochine 4 (1915) 1–17.
- [19] J. Pan, New Galeaspids (Agnatha) from the Silurian and Devonian, Geological Publishing House, Beijing, 1992.
- [20] J. Pan, S. Wang, Group Agnatha, in: Chengdu Institute of Geology and Mineral Resources (Ed.), Atlas of Fossils of Southwest China, Sichuan, Part I: from Sinian to Devonian, Geological Publishing House, Peking, 1978, pp. 487–493 (in Chinese).
- [21] J. Pan, S. Wang, New discoveries of polybranchiaspids from Yunnan Province, Vertebr. Palasiat. 19 (1981) 114–121 (in Chinese with English abstract).
- [22] P. Racheboeuf, P. Janvier, P. Ta Hoa, J. Vannier, S.-Q. Wang, Lower Devonian vertebrates, arthropods and brachiopods from northern Vietnam, Geobios 38 (2005) 533–551.
- [23] L.B.H. Tarlo, Agnatha, in: W.B. Harland, et al. (Eds.), The Fossil Record, The Geological Society of London, 1967, pp. 629–636.
- [24] T. Tong-Dzuy, P. Janvier, Les Vertébrés dévoniens du Viêt Nam, Ann. Paleontol. 73 (1987) 165–194.
- [25] T. Tong-Dzuy, P. Janvier, Les Vertébrés dévoniens du Bac Bo oriental (Provinces de Bac Thái et Lang Son, Viêt Nam), Bull. Mus. Natl. Hist. Nat. Paris Ser. III 12C (1990) 143–223.
- [26] T. Tong-Dzuy, P. Janvier, The Early Devonian vertebrate fauna from Trang Xa (Bac Thai, Viet Nam), with remarks on the distribution of the vertebrates in the Song Cau Group, J. S. E. Asian Earth Sci. 10 (1995) 235–243.
- [27] T. Tong-Dzuy, K. Vu (Eds.), Stratigraphic Units of Vietnam, Vietnam National University Publishing House, Hanoi, 2006.
- [28] T. Tong-Dzuy, P. Janvier, P. Ta Hoa, Lower Devonian biostratigraphy and vertebrates of the Tong Vai Valley, Vietnam, Palaeontology 38 (1995) 169–186.
- [29] J.Q. Wang, N.Z. Wang, Early Devonian galeaspid Agnatha from Southeast of Yunnan, China, Vertebr. Palasiat. 30 (1992) 185–194 (in Chinese with English abstract).
- [30] J. Wang, J. Fan, M. Zhu, Early vertebrate fossils from the Early Devonian of Zhaotong district, northeastern Yunnan, Vertebr. Palasiat. 34 (1996) 1–17 (in Chinese with English abstract).
- [31] N.Z. Wang, P.C.J. Donoghue, M.M. Smith, I.J. Sansom, Histology of the galeaspid dermoskeleton and endoskeleton, and the origin and early evolution of the cranial endoskeleton, J. Vertebr. Paleontol. 25 (2005) 745–756.
- [32] S.T. Wang, C.H. Lan, New discovery of polybranchiaspids from Yiliang county, Northeast Yunnan Province, Bull. Geol. Inst. 9 (1984) 113–123 (in Chinese with English abstract).
- [33] W.-J. Zhao, M. Zhu, Diversification and faunal shift of Siluro-Devonian vertebrates of China, Geol. J. (2007) 351–370.
- [34] W.-J. Zhao, M. Zhu, L.-T. Jia, New discovery of galeaspids from Early Devonian of Wenshan, southeastern Yunnan, China, Vertebr. Palasiat. 40 (2002) 97–113 (in Chinese with English abstract).
- [35] M. Zhu, M. Catalogue of Devonian vertebrates in China, with notes on bio-events, Cour. Forsch. Inst. Senckenberg 223 (2000) 373–390.
- [36] M. Zhu, Z. Gai, Phylogenetic relationships of galeaspids (Agnatha), Front. Biol. China 2 (2007) 151–169.
- [37] M. Zhu, N.-Z. Wang, J.-Q. Wang, Devonian macro- and microvertebrate assemblage of China, Cour. Forsch. Inst. Senckenberg 223 (2000) 361–372.