

# Phylogenetic relationships of galeaspids (Agnatha)

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**Abstract** We present the first parsimony analysis of the agnathan subclass Galeaspida based on the analysis of 53 morphological characters. Three most parsimonious cladograms (126 steps in length; CI = 0.508; RI = 0.801) were discovered. An amended classification of the Galeaspida is proposed corresponding to the present analysis. Our results suggest that hanyangaspids, xiushuiaspids and dayongaspids from the Llandovery-Wenlock of Silurian are basal galeaspids. Within the remaining galeaspids, three major monophyletic groups (the Eugaleaspidiformes, the Polybranchiaspidiformes and the Huananaspidiformes) are well supported. It is shown that the dorsal fenestrae of the headshield evolved twice within the Galeaspida, one in the polybranchiaspidiform lineage, and the other in the huananaspidiform lineage (nested within the Huananaspididae). The chronological distribution of galeaspids highlights two radiations of the group, one for basal galeaspids and eugaleaspids in the Telychian (Llandovery) of Silurian, and the other for polybranchiaspidiforms and huananaspidiforms in the Lochkovian of Early Devonian.

**Keywords** galeaspida, Agnatha, phylogeny, classification

## 1 Introduction

Galeaspids are a diversified group of jawless vertebrates, first appearing in the Llandovery (Early Silurian), flourishing in the Early Devonian, and surviving until the Late Devonian. The youngest known galeaspid is an unnamed form from the Famennian of Ningxia, northern China, in association with the Devonian tetrapod *Sinostega* (Zhu et al., 2002) and the antiarch *Remigolepis* (Pan et al., 1987). They are characterized by a large median dorsal opening and the festooned

pattern of sensory canals on the dorsal surface of the headshield, the ventral plate covering the median portion of the ventral surface of head, and aspidine tubercles. Galeaspids are one of four diversified agnathan groups (the other three groups are osteostracans, heterostracans and thelodonts), yet endemic to China (South China, Ningxia and Tarim) and North Vietnam. They were first described by Liu (1965), even if the discovery history can be traced back to Mansuy (1915, also see Tong-Dzuy and Janvier, 1987) and Ting and Wang (1936). It was not until 1975 that a large number of galeaspids began to be described (Liu, 1975; P'an et al., 1975). There are currently 74 galeaspid species assigned to 52 genera, in addition to several unnamed forms. However, few cladistic analyses of galeaspids have been previously attempted.

The Galeaspida, whose monophyly had reached a consensus since Halstead et al. (1979) and Janvier (1981), was first subdivided into two distant lineages (Liu, 1965): *Galeaspis* (subsequently replaced by *Eugaleaspis* because of the homonym) and *Nanpanaspis* allied to the Osteostraci (Cephalaspides), and *Polybranchiaspis* referred to the Heterostraci (Pteraspides). Liu (1975) furthered this diphyletic subdivision to propose two subclasses Galeaspida (= Eugaleaspida of Liu, 1980) and Polybranchiaspida, and placed the order Huananaspidiformes of Janvier (1975) in the subclass Polybranchiaspida. This classification comprised three orders (Huananaspidiformes, Polybranchiaspidiformes and Eugaleaspidiformes) and implied that the former two orders are more closely related to each other than either of them to the Eugaleaspidiformes. The fourth order Hanyangaspidida was erected by P'an et al. (1975), and was considered as a group of polybranchiaspidiforms by Liu (1979) and Halstead et al. (1979). Since then, many newly-described galeaspids such as *Kwangnanaspis* (Cao, 1979), *Xiushuiaspis* (Pan and Wang, 1983), *Dayongaspis* (Pan and Zeng, 1985), *Geraspis* (Pan and Chen, 1993), which cannot be assigned to the Eugaleaspidiformes characterized by longitudinal oval or slit-like median dorsal opening and special sensory canal system, or the Huananaspidiformes defined by laterally projecting

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corners and rostral process, were referred to as the Polybranchiaspidiformes, resulting in a group too mingled to be given a definition.

The first cladogram of galeaspids incorporating 16 genera was tentatively proposed by Janvier (1984) (Fig. 1A). It was first suggested that *Hanyangaspis* is the basal taxon of galeaspids. Janvier (1984) recognized two monophyletic groups (Eugaleaspidiformes and Huananaspidiiformes), and suggested that they were closely allied to each other (cf. Liu, 1975) and in turn were more derived than *Polybranchiaspis*-like forms (= Polybranchiaspidiformes) and *Hanyangaspis*. The similar cladogram was proposed by Wang (1991) to include more galeaspid taxa (Fig. 1B). In Wang's cladogram, three Silurian forms *Dayongaspis*, *Xiushuiaspis* and *Changxingaspis* were referred to the Hanyangaspidida, and *Nanpanaspis* was assigned to the Huananaspidiiformes. The relationships of the remaining taxa were suggestive of Janvier's (1984) cladogram. Janvier (1996) synthesized these two cladograms into a new one (Fig. 1C). Apart from the stem taxa such as *Hanyangaspis* and *Xiushuiaspis*, the galeaspids fall into two major clades, the Eugaleaspidiformes and the clade comprising the Huananaspidiiformes and the paraphyletic ensemble "Polybranchiaspidiformes". However, all these three cladograms were not based on the maximum parsimony analysis. In other words, they are not testable hypotheses of the galeaspid phylogeny.

Based on the dorsal fenestrae on the dorsal surface of the headshield, Pan (1992) subdivided the galeaspids into two groups, one with the fenestrae (Macrothyraspidides) and the

other without the fenestrae (Galeaspidides). Leaving aside the nature of these fenestrae, Pan's classification had given high weights to the character of dorsal fenestrae in his sketchy cladograms (Pan, 1992, Tables 4, 5).

The examination of past phylogenetic hypotheses in galeaspids shows that no cladogram except those of Zhu (1992) and Gai et al. (2005) on the relationships of the Eugaleaspidiformes was based on the principle of parsimony. Since the morphological characters in the evolution of galeaspids are often highly homoplastic, the parsimony should be used as a criterion to discriminate the cladograms. In doing so, morphological studies in galeaspids should be furthered, and many characters should be redefined to be used in the character analysis. In addition, the taxonomic confusions of some galeaspids should be clarified at the start. The objective of this paper is to perform a cladistic analysis of the subclass Galeaspidida, and to provide a cladistically-based classification of the subclass.

## 2 Materials and methods

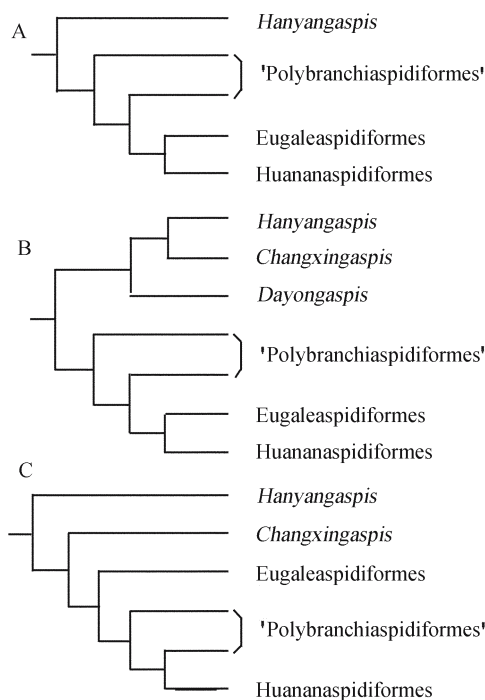
### 2.1 Taxon sampling

By now, 74 galeaspid species assigned to 52 genera have been described in the literature. Among them, 9 species and one genus are cancelled as the junior synonyms, and 5 new combinations are suggested in this work (see below). Since 65 valid species are still too numerous for the phylogenetic analysis with limited characters, a preliminary work has been done to group some species that are evidently closely related. Then, 39 groups with one or more species are adopted as the terminal taxa in the analysis, except two poorly-known species.

#### 2.1.1 Synonym of the species

Liu (1986) suggested that *Sanqiaspis sichuanensis* (P'an and Wang, 1978a) is the junior synonym of *S. rostrata* (Liu, 1975), and the differences between them were due to the preservation of the referred specimens from the same horizon and locality (Pingyipu Formation of Jiangyou, Sichuan). The holotype of *Sanqiaspis sichuanensis* (P'an and Wang, 1978a, pl.38-3) preserved the V-shaped posterior supraorbital sensory canal and two pairs of transverse canals, in addition to a pair of lateral dorsal canals in the holotype of *Sanqiaspis rostrata*. This suggestion is followed in this work.

In addition to the type species, there are eight species referred to the genus *Polybranchiaspis*, and the validity of most *Polybranchiaspis* species is doubtful. Pan (1992) and Tong-Dzuy et al. (1995) suggested that some *Polybranchiaspis* species, such as *P. gracilis*, *P. yunnanensis*, *P. rhombicus* and *P. sinensis* (Cao in Fang et al., 1985), probably reflected the intraspecific variation within *P. liaojiaoshanensis* (Liu, 1965, 1975). In accord with this proposal, *P. miandiancunensis* and *P. zhanyiensis* (P'an and Wang, 1978a) are also regarded as the junior synonyms of *P. liaojiaoshanensis*.



A: simplified from Janvier (1984); B: simplified from Wang (1991); C: simplified from Janvier (1996)

**Fig. 1** Summary of previous hypotheses of galeaspid phylogeny

*Polybranchiaspis minor* (Liu, 1975) is retained here because of its tiny size of the headshield (about 2 cm in length) and the fifth transverse canal. *P. yulongssus* (Liu, 1975) will be dealt with in the section on new combination. A related problem here is the spelling of the type species of *Polybranchiaspis*. Tong-Dzuy et al. (1995) proposed that *P. liaojiaoshanensis* (Liu, 1965) was erroneously spelled as *P. liaojiaoshanensis* by Liu 1975 and several subsequent authors. Tong-Dzuy et al. (1995) were correct in recognizing that *P. liaojiaoshanensis* is the original spelling, however, this original spelling was incorrect due to an inadvertent error. The derivation of the specific name was after the Pinyin (Chinese alphabetic writing) of the type locality (*liao-jiao-shan*), and there is no Chinese character pronounced as “jao”. This incorrect original spelling was corrected by the original author (Liu, 1975), however no explanation was given to this change, which resulted in subsequent confusions. According to the International Code of Zoological Nomenclature (Ride et al., 1985, Article 32c, d), the incorrect original spelling should be corrected, and *P. liaojiaoshanensis* is a valid emendation.

The second species of *Sinoszechuanaspis* (*S. gracilis* P'an et Wang, 1978b) was abandoned by Pan (1992), who considered it as the junior synonym of the type species (*S. yanmenpaensis* P'an et al., 1975). This assignation is also accepted in this work.

Pan (1992) proposed that *Meishanaspis lehmani* (Wang, 1991) is the junior synonym of *Sinogaleaspis zhejiangensis* (Pan, 1986a), and the minor differences between them were caused by the preservation of the shape of median dorsal opening. Based on new materials of *M. lehmani*, which show more differences with *S. zhejiangensis* with regard to the size of the headshield, the sensory canal system and the ornament, Gai et al. (2005) suggested that *Meishanaspis lehmani* is a tenable genus and species, rather than a junior synonym.

### 2.1.2 New combination

Pan (1986b) suggested the new combination of *Hanyangaspis chaohuensis*, which was originally referred to as *Latirostraspis* (Wang et al., 1980). The differences between *H. chaohuensis* and *H. guodingshanensis* (type species of *Hanyangaspis*, Pan et al., 1975) are of specific, not generic, significance. This suggestion was followed by Pan and Dineley (1988) and Wang (1991); however, it was not adopted by Wang (1993). In our opinion, even though the criteria defining genus by respective authors might differ, we should have the species/genus ratio in our classification at a reasonable level. If one genus usually has only one species in our classification, the binominal nomenclature will largely lose its intention for grouping. In fact, we have too many monospecific genera (41 genera) among galeaspids. Therefore, a grouping at a moderate degree will be appropriate in galeaspids, and in some senses this kind of grouping is more important than the erection of a new monospecific genus. Pan's proposal is followed in this work.

Pan (1992, p.41) suggested that *Diandongaspis xishancunensis* (Liu, 1975) is a species of *Laxaspis* (Liu, 1975). Indeed, *D. xishanchunensis* is somewhat similar to *L. qujingensis* in general shape of the headshield and sensory canal pattern. However, these two species are distinct by their ornamentation, indicating the divergence between them. *D. xishancunensis* has very tiny and simple scale-units whereas *L. qujingensis* has fairly large stellated scale-units. Thus, the new combination of *D. xishancunensis* by Pan (1992) is not followed here.

In this work, we propose the new combination of *Polybranchiaspis yulongssus*. *P. yulongssus* has a very developed inner corner, whose posterior end is far behind the posterior middle point of the headshield, and its headshield shape is more suggestive of that of *Laxaspis* than that of *Polybranchiaspis liaojiaoshanensis*. Moreover, the headshield of *P. yulongssus* (Liu, 1975) is about 10 cm in length, much larger than that of *P. liaojiaoshanensis* (4.5–5.5 cm in length). Therefore, it is appropriate to remove *P. yulongssus* out of *Polybranchiaspis*, and assign it to *Laxaspis*.

There are other two species whose genus assignments should be changed, one is *Dongfangaspis qujingensis* (Pan and Wang, 1981; Pan, 1992), the other is *Laxaspis rostrata* (Liu, 1975).

The holotype of *Dongfangaspis qujingensis* is an incomplete headshield. Its restoration (Pan and Wang, 1981) was largely after the headshield of *D. major* (Liu, 1975). The inner corner of *D. qujingensis* has the same relative size as that of *Polybranchiaspis* and *D. major*. In fact, the left inner corner of the holotype did not lose a lot as Pan and Wang (1981) restored, and its posterior middle point of the headshield should be more anteriorly placed. As to the overall headshield shape, *D. qujingensis* is more suggestive of *Laxaspis* than *D. major* and *Polybranchiaspis*. This was well shown in the subsequent restoration of *D. qujingensis* by one of the original authors (Pan, 1992; Fig. 12). In addition to those indicated by Pan and Wang (1981, p.119), there are other major differences between *D. major* and *D. qujingensis* that create obstacles in assigning the latter as *Dongfangaspis*. The first is the overall shape of headshield as stated above. The second is the ornamentation. The scale-units of the headshield in *D. major* are very tiny ones, whereas those in *D. qujingensis* are relatively larger and stellated as in *Laxaspis qujingensis* and *Polybranchiaspis*. The third is the number of branchial fossae. *D. major* has at least 40 pairs of branchial fossae as indicated by the branchial openings (Liu, 1975, pl.II-1), whereas the branchial fossae of *D. qujingensis* are fewer than 20 pairs. In every respect, *D. qujingensis* should be removed out of *Dongfangaspis* to *Laxaspis*, which results in a new problem since the type species of *Laxaspis* is *L. qujingensis* (Liu, 1975). Then a new specific name should be proposed to replace *D. qujingensis*. Nevertheless, since there exists a possibility that *D. qujingensis* is just the junior synonym of *L. qujingensis* if stellated ends of sensory canals are proved to be just reflections of the ornamentation, *D. qujingensis* is cited as “*Dongfangaspis qujingensis*” instead of a replacement name in this work.



The same treatment is given to *Laxaspis rostrata*. The holotype (the only specimen) of *L. rostrata* is incompletely preserved, however, it shows evidently the long rostral process (Liu, 1975, pl. IV-1), by which *L. rostrata* is more suggestive of *Gumuaspis rostrata* than *Laxaspis qujingensis* (Liu, 2002). However, if we assign *L. rostrata* to *Gumuaspis*, the problem of homonym will be produced since the type species of *Gumuaspis* is named as *G. rostrata*. The alternative is to erect a new genus for *L. rostrata*. Currently, *Laxaspis rostrata* retains its original name with quotation marks.

### 2.1.3 Grouping of galeaspids

We identify 38 groups of galeaspids as the terminal taxa for the phylogenetic analysis. Among them, 23 groups are monotypic. Each of the remaining 15 groups includes two or more species, so a preliminary study should be done with these groups. In the data matrix (Appendix 1), each group is represented by the first species listed in Table 1.

**Table 1** The summary and groupings of the galeaspids

1. <i>Hanyangaspis guodingshanensis</i> P'an et Liu, 1975 <i>H. ("Latirostraspis") caohuensis</i> (Wang, Xia et Chen, 1980) <i>Nanjiangaspis kalpinensis</i> Wang et al., 2002 <i>Kalpinolepis tarimensis</i> Wang, Wang et Zhu, 1996 <i>Konoceraspis grandoculus</i> Pan, 1992	<i>Cyclodiscaspis ctenus</i> Liu, 1975
2. <i>Dayongaspis hunanensis</i> Pan et Zeng, 1985 <i>Platycaraspis tianshanensis</i> Wang et al., 2002	16. <i>Dongfangaspis major</i> Liu, 1975
3. <i>Changxingaspis gui</i> Wang, 1991 <i>Xiushuiaspis jiangxiensis</i> Pan et Wang, 1983 <i>X. ganbeiensis</i> Pan et Wang, 1983 <i>Microphymaspis pani</i> Wang et al., 2002	17. <i>Bannhuanaspis vukhuci</i> Janvier, Thanh et Phuong, 1993 <i>Clororbis apronomedianus</i> Pan et Ji, 1993
4. <i>Sinogaleaspis shankouensis</i> Pan et Wang, 1980	18. <i>Geraspis rara</i> Pan et Chen, 1993
5. ' <i>S. xikengensis</i> Pan et Wang, 1980	19. <i>Kwangnanaspis subtriangularis</i> Cao, 1979
6. ' <i>S. zhejiangensis</i> Pan, 1984	20. <i>Duyunolepis paoyangensis</i> (P'an et Wang, 1978a), emended Pan et Wang, 1982 <i>Paraduyunaspis hezhangensis</i> P'an et Wang, 1978a <i>Neoduyunaspis minuta</i> P'an et Wang, 1978a
7. <i>Meishanaspis lehmani</i> Wang, 1991	21. <i>Lopadaspis pinglensis</i> (Wang et al., 2001), emended Wang et al., 2002
8. <i>Anjiaspis reticularis</i> Gai et Zhu, 2005	22. <i>Zhaotongaspis janvieri</i> Wang et Zhu, 1994
9. <i>Yunnanogaleaspis major</i> Pan et Wang, 1980	23. <i>Wenshanaspis zhichangensis</i> Zhao, Zhu et Jia, 2002
10. <i>Nochelaspis maeandrina</i> Zhu, 1992	24. <i>Antiquisagittaspis cornuta</i> Liu, 1985
11. <i>Pterogonaspis yuhaii</i> Zhu, 1992 <i>Tridensaspis magnoculus</i> Liu, 1986	25. <i>Sanchaspis magalarostrata</i> Pan et Wang, 1981
12. <i>Eugaleaspis changi</i> (Liu, 1965) emended Liu, 1980 <i>E. lianhuashanensis</i> Liu, 1986 <i>E. xujiaochongensis</i> Liu, 1975 <i>E. xiushanensis</i> Liu, 1983 † <i>E. qujingensis</i> Cao, in Fang et al., 1985	26. <i>Gumuaspis rostrata</i> Wang et Wang, 1992 " <i>Laxaspis rostrata</i> " Liu, 1975
13. <i>Polybranchiaspis liaojiaoshanensis</i> Liu, 1965 <i>P. minor</i> Liu, 1975 <i>Siyingia altuspinosa</i> Wang et Wang, 1982a † <i>P. miandiancunensis</i> P'an et Wang, 1978a † <i>P. zhanyiensis</i> P'an et Wang, 1978a † <i>P. gracilis</i> Cao, in Fang et al., 1985 † <i>P. rhombicus</i> Cao, in Fang et al., 1985 † <i>P. sinensis</i> Cao, in Fang et al., 1985 † <i>P. yunnanensis</i> Cao, in Fang et al., 1985	27. <i>Pentathyraspis pelta</i> Pan, 1992
14. <i>Laxaspis qujingensis</i> Liu, 1975 <i>Laxaspis</i> (" <i>Polybranchiaspis</i> ") <i>yulongssus</i> (Liu, 1975) " <i>Dongfangaspis qujingensis</i> " Pan et Wang, 1981	28. <i>Microhoplonaspis microthyris</i> Pan, 1992
15. <i>Damaspis vartus</i> Wang et Wang, 1982b <i>Diandongaspis xishancunensis</i> Liu, 1975	29. <i>Sinoszechuanaspis yanmenpaensis</i> (P'an et Wang, 1975) emended P'an et Wang, 1978b † <i>S. gracilis</i> P'an et Wang, 1978b
	30. <i>Macrothyraspis longicornis</i> Pan, 1992 <i>Macrothyraspis longilanceus</i> Wang, Gai et Zhu, 2005
	31. <i>Lungmenshanaspis kiangyouensis</i> P'an et Wang, 1975 <i>L. yunnanensis</i> Wang, Fan et Zhu, 1996
	32. <i>Qingmenaspis microculus</i> Pan et Wang, 1981
	33. <i>Nanpanaspis microculus</i> Liu, 1965
	34. <i>Huananaspis wudinensis</i> Liu, 1975
	35. <i>Asiaspis expansa</i> P'an, in P'an et al., 1975
	36. <i>Sanqiaspis rostrata</i> Liu, 1975 <i>S. zhaotongensis</i> Liu, 1975 † <i>S. sichuanensis</i> P'an et Wang, 1978a
	37. <i>Wumengshanaspis cuntianensis</i> Wang et Lan, 1984
	38. <i>Gantarostrataspis geni</i> Wang et Wang, 1992 Incertae sedis <i>Hyperaspis acclivis</i> Pan, 1992 <i>Pseudoduyunaspis bachuensis</i> Wang, Wang et Zhu, 1996

There are currently 74 galeaspid species assigned to 52 genera; 9 species beginning with the † mark are cancelled as the junior synonyms; the first species in each group is selected as the terminal taxon in the phylogenetic analysis

**Group 1** Four genera are included in this group (*Hanyangaspis*, *Nanjiangaspis*, *Kalpinolepis*, *Konoceraspis*), which have the following shared characters: 1) nearly trapezoid-like headshield; 2) transverse slit-like median dorsal opening; 3) median dorsal opening subterminal in position; 4) lateral transverse canals short; 5) two medial transverse canals; 6) 7 pairs of external branchial openings.

**Group 3** This group consists of three genera (*Xiushuiaspis*, *Changxingaspis*, *Microphymaspis*), and is defined by 1) small headshield (shorter than 35 mm in length); 2) headshield elongated (length/width ratio larger than 1.0); 3) the orbital openings behind the broad, subterminal median dorsal opening; 4) short pre-pineal part of the headshield; 5) long postbranchial wall; 6) six pairs of branchial fossae.

**Group 4–6** Three species were assigned to *Sinogaleaspis* by Pan and Wang (1980) and Pan (1984). However, recent phylogenetic analysis of eugaleaspids indicated that these three species do not form a monophyletic, but a paraphyletic group. The type species of *Sinogaleaspis*, *S. shankouensis* has a

closer relationship to *Yunnanogaleaspis* and higher eugaleaspids than to '*S. zhejiangensis*' and '*S. xikengensis*'. They share such synapomorphies as the anterior end of median dorsal opening away from the rostral margin, the absence of  $ltc_{a-c}$ , and the developed median dorsal canal. '*S. zhejiangensis*' and '*S. xikengensis*' cannot be referred to *Sinogaleaspis* (Gai et al., 2005). So these three species are treated respectively.

**Group 11** *Pterogonaspis yuhaii* and *Tridensaspis magnoculus* form a monophyletic group as proposed by Zhu (1992) and Gai et al. (2005). The synapomorphies are two homoplastic characters: the rostral process and laterally projecting corner.

**Group 12** *Eugaleaspis* (Liu, 1965, 1975) includes four species, and is defined by the absence of inner corner, the median dorsal opening extending backward to the posterior margin of orbital openings, and the pre-pineal region of the headshield longer than the post-pineal region (Zhu, 1992; Gai et al., 2005). Its ornamentation is fairly specialized and likely to be another synapomorphy of the genus. The interrelationship within the genus was attempted by Zhu (1992) and Gai et al. (2005).

**Group 13** Two genera (*Polybranchiaspis*, *Siyingia*) are included in this group. *Siyingia* (Wang and Wang, 1982a) has only an incomplete headshield resembling *Polybranchiaspis* in shape. Other similarities include the size of the headshield (shorter than 6 cm in length), the ornamentation, the median dorsal opening and the sensory canal pattern.

**Group 14** This group is represented by *Laxaspis* (Liu, 1975), including *L. qujingensis*, *L. yulongssus* and "*Dongfangaspis qujingensis*". In this group, the headshield is relatively broad (length/width ratio about 1.0). Its inner corner is fairly large, and has its posterior end far behind the posterior middle point of the headshield. The scale-unit of the headshield is relatively big, and ornamented with stellated ridges and tiny tubercles. One of the characters used by Liu (1975) to define *Laxaspis* is untenable, that is the end of the sensory canal radiating from a polygonal circle. In our opinion, the supposed end of the canal is caused by the ornament.

**Group 15** Three genera are referred to this group. As to the shape of the headshield, this group is very similar to *Laxaspis*. However, its ornamentation is composed of very tiny scale-units. No further phylogenetic relationship can be obtained among these three genera. The laterally placed orbital opening of *Cyclodiscaspis* is obviously secondary.

**Group 17** *Clarorbis apponomedianus* (Pan and Ji, 1993) is suggestive of *Bannhuanaspis vukhuci* (Janvier et al., 1993) by many lateral transverse canals issued from the infraorbital canal, and the ornamentation of tiny round tubercles.

**Group 20** It includes four genera (all monospecific), exemplified by *Duyunolepis paoyangensis* (P'an and Wang, 1978a; Halstead, 1979), which preserved a mineral replica of the internal anatomy such as the central nervous and vascular systems. In this group, there are more than 20 pairs of branchial fossae. The corner and inner corner are absent. The exoskeleton is ornamented by fairly large, polygonal scale-units.

**Group 26** *Gumuaspsis rostrata* (Wang and Wang, 1992) and "*Laxaspis rostrata*" (Liu, 1975) are referred to this group.

They are more or less similar to *Polybranchiaspis* or *Laxaspis*, however, they have a long rostral process.

**Group 30** Two species in this group are very similar in such characters as armet-like headshield, very developed rostral process and corner, heart-shaped median dorsal opening, paired dorsal fenestra large and bean-shaped, and ornaments with small grain-like tubercles.

**Group 31** This group includes two species of *Lungmenshanaspis* (P'an et al., 1975), defined by heart-shaped median dorsal opening, very long rostral process, corner very developed and projecting laterally, orbital openings dorsally situated, paired dorsal fenestra slender oval-like and laterally positioned (Wang, 1991, 1995).

**Group 36** This group is represented by *Sanqiaspis* (Liu, 1975), defined by narrow headshield, crescent median dorsal opening, and posteriorly projecting corners.

## 2.2 Outgroup of galeaspids

Janvier (1984, 1996) suggested that the Galeaspida is the sister-group of the Osteostraci plus the Gnathostomata. In this work, a basal osteostracan, *Atleaspis tessellata* Traquair (Ritchie, 1967; Janvier, 1984), is selected as the outgroup of galeaspids for the phylogenetic analysis.

## 2.3 Analysis and description of characters

### [1] Median dorsal opening: (0) absent; (1) present.

The median dorsal opening of galeaspids, also termed the naso-hypophysial or exonasal opening, as one of the synapomorphies of the group, had been discussed at length (Liu, 1979, 1985; Pan and Wang, 1981, 1983; Wang and Wang, 1982a; Pan, 1984, 1992; Janvier, 1984; Wang, 1991). It was generally considered as an organ related with the olfactory function. Pan (1984, Fig. 4) described the two small tubes within the median dorsal opening of *Asiaspis expansa* (P'an et al., 1975), the anterior interpreted as the hypophysial duct or the pharyngeal duct and the posterior as the nasal opening proper. Pan (1992) also suggested that the opening was likely to communicate directly with the buccal cavity. Janvier (1993) proposed that the median dorsal opening of galeaspids was homologous to the prenasal sinus in hagfishes, heterostracans and thelodonts. In these forms, the prenasal sinus and the naso-hypophysial duct must be related with the intake of the respiration water. The dorsal migration of the prenasal sinus and the naso-hypophysial duct in galeaspids is one of the synapomorphies of the group, which might have some relationships with its feeding habit.

In galeaspids, the median dorsal opening is fairly large, suggesting its communication with the buccal cavity. The ornamentation on the duct wall in *Polybranchiaspis* (Tong-Dzuy et al., 1995) suggests the inhalant water current through this opening.

### [2] Festooned pattern of sensory canals on the dorsal surface of the headshield: (0) absent; (1) present.

The presence of this characteristic was considered as one of galeaspid's synapomorphies (Janvier, 1984, 1996; Liu,

1986; Zhu, 1992). Liu (1986) gave a systematic description of the sensory canal system of galeaspids. The sensory canals of galeaspids exhibit the festooned pattern, exemplified by *Sinogaleaspis shankouensis* (Pan and Wang, 1980; Fig. 2D).

**[3] Aspidine tubercles: (0) absent; (1) present.**

Another characteristic that can define galeaspids is the histological structure of the exoskeleton which shows a layer of small dermal units fused side by side, and made up of horizontally zonated acellular bone (Janvier, 1990).

**[4] Shape of headshield: (0) trapezoid-like; (1) triangular-like; (2) oval-like; (3) armet-like; (4) fork-like.**

In galeaspids, the shape of the headshield can be roughly classified into five types: the trapezoid-like as in *Hanyangaspis* (Fig. 4A) and *Kalpinolepis*, the triangular-like as in *Dayongaspis* and *Eugaleaspis* (Fig. 2A, H), the oval-like as in *Changxingaspis* and *Duyunolepis* (Fig. 2C, F), the armet-like as in *Sinoszechuanaspis* and *Lungmenshanaspis* (Fig. 2G, 3H), and the fork-like as in *Sanqiaspis* and *Gantarostrataspis* (Fig. 2E, 3C). By the outgroup comparison, the trapezoid-like headshield is likely to be plesiomorphic.

**[5] Margin of headshield: (0) serrated; (1) smooth.**

In some galeaspids (e.g., *Dayongaspis* and *Changxingaspis*), the headshield shows the serrated margin (Fig. 2A, C). The serrated margin also exists in some eugaleaspids such as *Anjiaspis*, '*S.* *xikengensis*' and *Meishanaspis*. By the

outgroup comparison, the smooth margin is likely to be plesiomorphic.

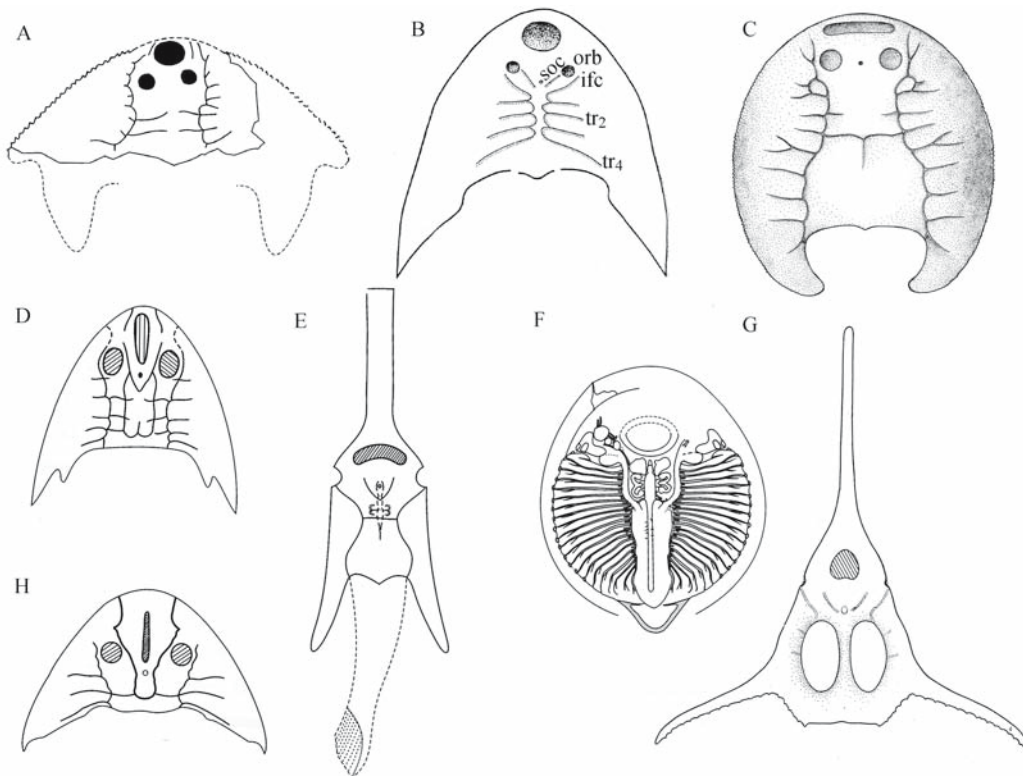
**[6] Shape of median dorsal opening: (0) transverse slit-like; (1) oval-like; (2) slender longitudinal oval.**

**[7] Longitudinal oval dorsal opening: (0) not slit-like (length/width<5); (1) slit-like (length/width>5).**

**[8] Heart-shaped median dorsal opening: (0) absent; (1) present.**

In galeaspids, the shape of the median dorsal opening is a very variable and diagnostic characteristic. Roughly, six types of median dorsal opening are recorded to form a branching transformation series: 0) transverse slit-like as in *Changxingaspis* and *Hanyangaspis* (Fig. 2C, 4A); 1) oval-like as in *Geraspis* and *Gumuaspi* (Fig. 2B, 3B); 2) slender longitudinal oval as in *Yunnanogaleaspis* and *Sinogaleaspis* (Fig. 2D); 3) longitudinal slit-like as in *Pterogonaspis* and *Eugaleaspis* (Fig. 2H, 4C); 4) heart-shaped as in *Huananaspis* and *Sinoszechuanaspis* (Fig. 2G); 5) transverse crescent as in *Sanqiaspis* (Fig. 2E).

Since the median dorsal opening of galeaspids is homologous to the prenasal sinus in hagfishs, heterostracans and thelodonts, by the outgroup comparison, the transverse slit-like one should be the most plesiomorphic for galeaspids. During the early evolution of galeaspids, because the prenasal sinus migrated onto the dorsal surface of the shield to form the median dorsal opening, and the primitive shape of the

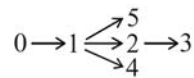


A: *Dayongaspis hunanensis* (from Pan and Zeng, 1985); B: *Geraspis rara* (from Pan and Chen, 1993); C: *Changxingaspis gui* (modified from Wang, 1991); D: *Sinogaleaspis shankouensis* (modified from Pan and Wang, 1980); E: *Sanqiaspis rostrata* (from Zhao et al., 2002); F: *Duyunolepis paoyangensis* (from Pan and Wang, 1978a); G: *Sinoszechuanaspis yanmenpaensis* (from Pan, 1992); H: *Eugaleaspis xujiaichongensis* (from Liu, 1975)

**Fig. 2** Main representatives of galeaspids from China



opening (transverse slit-like) was not adaptable for the efficient intake of the water which would affect the efficiency of the sense organs, the galeaspid burst into a diversification as to the shape of the median dorsal opening. This diversification might have taken place as early as Early Silurian. As the whole states form a continuous series, it is easy to establish the branching character tree. The mix coding method (Wiley et al., 1991) is adopted in the paper. The branching transformation series (TS) is:



By the mix coding method (Wiley et al., 1991), this TS is subdivided into three characters (Characters 6, 7 and 8; the transverse crescent median dorsal opening is omitted in the analysis since it is only found in *Sanqiaspis*).

**[9] Position of median dorsal opening: (0) not subterminal; (1) subterminal.**

Among galeaspid, the median dorsal opening in *Dayongaspis*, *Xiushuiaspis*, *Changxingaspis*, and *Hanyangaspis* has a subterminal position (Fig. 2A, C, 4A), which by the outgroup comparison should be apomorphic for them.

**[10] Anterior end of median dorsal opening: (0) subterminal; (1) some distance behind rostral margin of shield; (2) terminal.**

As the shape of the median dorsal opening transformed from oval-like to longitudinal oval-like, the median dorsal opening extended forward and backward. In some eugaleaspid such as '*S. xikengensis*', '*S. zhejiangensis*' and *Meishanaspis*, the anterior margin of median dorsal opening reached to the rostral margin of the headshield. Thus, the terminal position

of the anterior margin of the median dorsal opening should be apomorphic.

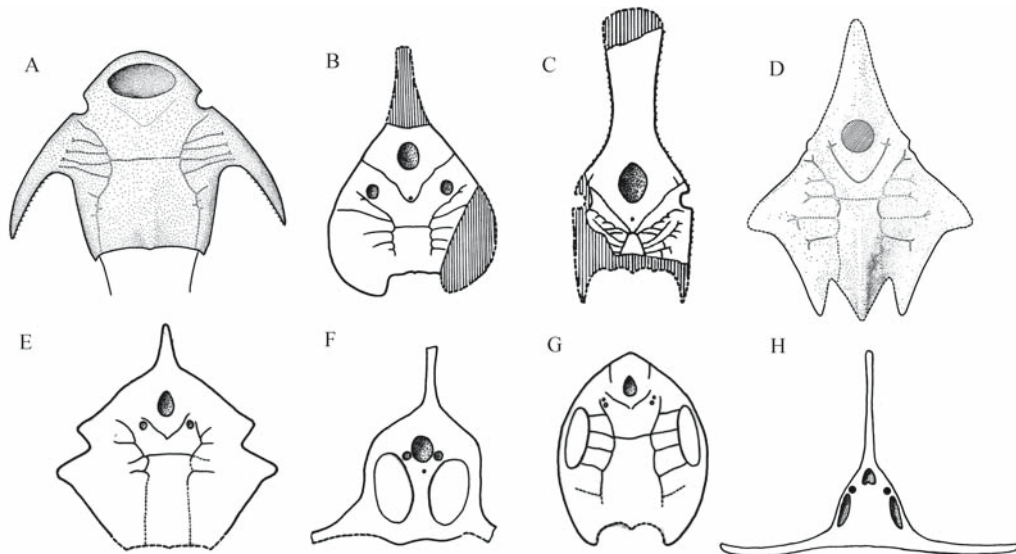
**[11] Posterior end of median dorsal opening: (0) in front of or level with anterior margin of orbital opening; (1) posteriorly beyond anterior margin of orbital opening.**

In most galeaspid, the posterior margin of the median dorsal opening is positioned in front of or level with the anterior margin of the orbital opening. Closely relating to the shape of median dorsal opening transformed from longitudinal oval-like to longitudinal slit-like, some galeaspid with the longitudinal slit-like median dorsal opening such as *Pterogonaspis* and *Eugaleaspis* (Fig. 2H), have the posterior margin of the median dorsal opening extending posteriorly beyond the level of the anterior margin of the orbital opening (Zhu, 1992). In addition, the posterior margin of the median dorsal opening is also situated behind the anterior margin of the orbital opening in *Wumengshanaspis* and *Gantarostrataspis* (Fig. 3C). This is likely to be due to the parallelism.

**[12] Size of orbital openings: (0) large; (1) small.**

In some galeaspid with laterally projecting corner and long rostral process such as *Asiaspis* and *Nanpanaspis* (Fig. 3E), or with dorsal fenestrae such as *Pentathyraspis* and *Lungmenshanaspis* (Fig. 3G, H), the orbital openings are rather small. The small orbital openings are assumed as specialized due to the degeneration of visual sense. The laterally projecting corner, long rostral process, and dorsal fenestrae might have some mechanical or electrical sense functions to compensate the visual sense. So the large orbital openings are likely to be plesiomorphic.

**[13] Position of orbital openings: (0) dorsal position and close to mid-line of headshield; (1) dorsal position and not close to mid-line of headshield; (2) lateral position.**



A: *Zhaotongaspis janvieri* (from Wang and Zhu, 1994); B: *Gumuaspid rostrata* (from Wang and Wang, 1992); C: *Gantarostrataspis geni* (from Wang and Wang, 1992); D: *Antiquisagittaspis cornuta* (from Liu, 1985); E: *Nanpanaspis microculus* (from Liu, 1965); F: *Qingmenaspis microculus* (from Pan and Wang, 1981); G: *Pentathyraspis pelta* (from Pan, 1992); H: *Lungmenshanaspis kiangyouensis* (from P'an et al., 1975)

**Fig. 3** Main representatives of galeaspid, showing rostral process, corner or dorsal fenestrae

By the outgroup comparison, the dorsal position and close to mid-line of the headshield as in *Dayongaspis* and *Changxingaspis* (Fig. 2A, C) should be plesiomorphic for galeaspids. The lateral position in *Hanyangaspis* (Fig. 4A), *Zhaotongaspis* (Fig. 3A), *Cyclodiscaspis*, and some huananaspids (Fig. 2E, G, 3C, D) should be the result of convergence.

**[14] Corner: (0) absent; (1) present.**

Zhu (1992) has discussed in detail the homology problem of the corners among the various galeaspids, and suggested that the so-called “corner” or “pectoral corner” in the Hanyangaspididae and Polybranchiaspididae was in fact equivalent of the inner corner of *Dayongaspis* (Pan and Zeng, 1985) and eugaleaspids. Since the galeaspids do not possess the pectoral fenestra as in the osteostracans, the corner of galeaspids is distinguishable from the pectoral corner of osteostracans. However, they might have the similar function.

**[15] Extending trajectory of corner: (0) projecting posterolaterally; (1) projecting laterally; (2) projecting backward.**

Among galeaspids, the projecting trajectory of corner can be classified into three types: projecting posterolaterally as *Dayongaspis* and *Eugaleaspis* (Fig. 2A, H); projecting laterally as *Sinoszechuanaspis* and *Lungmenshanaspis* (Fig. 2G, 3H); and projecting backward as *Sanqiaspis* and *Gantarostrataspis* (Fig. 2E, 3C). By the outgroup comparison, the posterolaterally projecting corner is like to be a plesiomorphy for galeaspids.

**[16] Portion of headshield behind corner: (0) short; (1) long.**

**[17] Position of corner base: (0) near posterior end of headshield; (1) away from posterior end of headshield.**

Among galeaspids, two types regarding the position of corner base can be recognized: near posterior end of the headshield as in *Qingmenaspis* and *Lungmenshanaspis* (Fig. 3F, H), away from posterior end of the headshield as in *Sinoszechuanaspis* and *Zhaotongaspis* (Fig. 2G, 3A). Among the latter conditions, there exists a region of the headshield behind the corner. The region is short as in *Macrothyraspis* and *Sinoszechuanaspis* (Fig. 2G) and long as in *Zhaotongaspis*, *Antiquisagittaspis*, *Nanpanaspis* and *Sanchaspis* (Fig. 3A, D, E, 4D).

**[18] Spines on corner: (0) absent; (1) present.**

The aculeated spines on the corner are assumed as an apomorphy for *Wenshanaspis* and *Zhaotongaspis* (Fig. 3A).

**[19] Inner corner: (0) present; (1) absent.**

**[20] Shape of inner corner: (0) broad leaf-shaped; (1) spine-shaped.**

Among galeaspids, the inner corner is broad leaf-shaped as in the Hanyangaspididae and Polybranchiaspididae (Fig. 2A, C, 4A), aculeated spine-shaped as in *Anjiaspis* and *Sinogaleaspis* (Fig. 2D), and absent as in *Duyunolepis* and *Eugaleaspis* (Fig. 2F, H).

**[21] Rostral margin of headshield: (0) without rostral angle; (1) with rostral angle.**

The rostral margin of headshield shows a rostral angle in *Pentathyraspis* (Fig. 3G), in comparison with the round

contour in *Polybranchiaspis* (Pan, 1992). However, *Pentathyraspis* has no rostral process. The rostral angle is likely to be the vestige of the rostral process.

**[22] Rostral process: (0) absent; (1) present.**

The presence of rostral process was assumed as an important apomorphy for huananaspids by Janvier (1984) and Wang (1991). Meanwhile, the rostral process is also present in the Eugaleaspidiformes (*Pterogonaspis* and *Tridensaspis*), and the Polybranchiaspidiformes (*Gumuaspis*) (Fig. 3B).

**[23] Shape of rostral process: (0) broad; (1) slender.**

**[24] Spines or tubercles on margin of rostral process: (0) absent; (1) present.**

Among galeaspids with rostral process, three types of rostral process can be recognized: broad as in *Antiquisagittaspis* and *Sanchaspis* (Fig. 3D, 4D), slender as in *Sinoszechuanaspis* and *Lungmenshanaspis* (Fig. 2G, 3H), with spines or tubercles on its margin as in *Wumengshanaspis* and *Gantarostrataspis* (Fig. 3C). The rostral process with spines or tubercles is assumed as an apomorphy.

**[25] Fenestrae on dorsal surface of headshield: (0) absent; (1) present.**

As to the dorsal fenestrae, Pan and Wang (1981) first reported that the headshield of *Qingmenaspis* (Fig. 3F), holds a pair of large openings on its dorsal surface, but owing to the poor preservation, they assumed it as a dorsal branchial opening with reservations. This structure was also recognized later in *Lungmenshanaspis* (Fig. 3H) by Wang (1991). Pan (1992) described the structure in a number of new galeaspids including *Pentathyraspis* (Fig. 3G), *Microhoplonaspis*, *Sinoszechuanaspis* (Fig. 2G), *Macrothyraspis* and renamed it the dorsal fenestra. Liu (1993) had a tentative discussion on the fenestrae and suggested that the fenestra within galeaspids either originated or disappeared more than once. He inclined to that the dorsal fenestrae of galeaspids is not only morphologically comparable with, but also phylogenetically homologous to, the lateral fields of osteostracans and that the feature is shared only by osteostracans and galeaspids within agnathans. However, Wang (1995) argued that the fenestrae of galeaspids were obviously different from the lateral fields of osteostracans and should be regarded as a synapomorphy for the fenestra-bearing galeaspids. He further suggested that the galeaspids with fenestrae is a monophyletic group, indicating that the fenestrae originated only once. Here we prefer to consider that the dorsal fenestra is a synapomorphy for galeaspids and is likely to originate more than once.

**[26] Size of dorsal fenestra: (0) small; (1) large.**

**[27] Shape of dorsal fenestra: (0) slender oval-like; (1) broad bean-like.**

**[28] Position of dorsal fenestra: (0) lateral-dorsal position; (1) dorsal position.**

Pan (1992) distinguished the fenestrae in two types by its position, size and shape: the lateral dorsal fenestra, which is narrow and small, existing in *Pentathyraspis* (Fig. 3G), *Microhoplonaspis* as well as *Lungmenshanaspis* (Fig. 3H), and the dorsal fenestra, which is broad and large, found in *Sinoszechuanaspis* (Fig. 2G), *Macrothyraspis* and



*Qingmenaspis* (Fig. 3F). In the work, we used the same term for the lateral dorsal fenestra and dorsal fenestra.

**[29] Position of dorsal fenestra relative to orbital opening: (0) orbital opening inside, fenestra outside; (1) orbital opening outside, fenestra inside.**

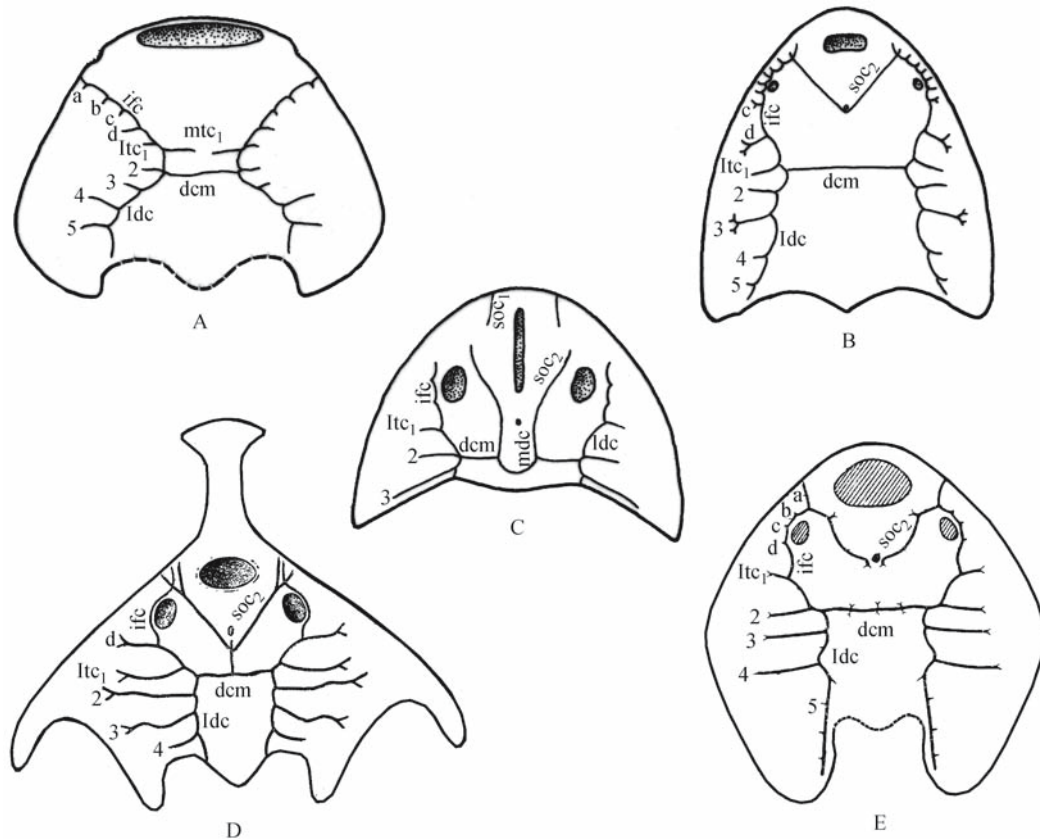
As to the position of dorsal fenestra relative to orbital opening, two types can be distinguished likewise: orbital opening inside, fenestra outside as in *Pentathyraspis* (Fig. 3G), *Microhoplonaspis*, *Lungmenshanaspis* (Fig. 3H) and *Qingmenaspis* (Fig. 3F); orbital opening outside, fenestra inside as in *Macrothyaspis* and *Sinoszechuanaspis* (Fig. 2G).

**[30] Median transverse canals (mtc): (0) two; (1) one; (2) more than two.**

The detailed pattern of sensory canals is the important diagnostic character for galeaspids. The homology of the sensory canal system between galeaspids and other agnathans was well analysed by Liu (1986). It was proposed that different types of the disposition of the sensory canal system in various agnathan groups were derived from a general pattern that is composed of the longitudinal stems and the transverse branches linking them. It is mainly based on the analysis of Liu (1986) that the outgroup comparison is used here to determine the character polarization about the sensory canal system.

Among galeaspids, there exist three conditions with regard to the median transverse canal. In general, when the sensory canals were well preserved, there is only one median transverse canal, which was named as the dorsal commissure (dcm, Fig. 4) (Liu, 1986) or median dorsal commissure (Liu, 1975; Pan, 1992). In *Dayongaspis*, *Changxingaspis*, *Hanyangaspis* (Fig. 2A, C, 4A), there are two median transverse canals. In *Sinogaleaspis shankouensis* (Fig. 2D) (Pan and Wang, 1980) and *Anjiaspis* (Gai and Zhu, 2005) there are more than three median transverse canals. No matter which canal in the latter two conditions is homologous to the dorsal commissure, there must be a dorsal commissure. By the outgroup comparison, the presence of the dorsal commissure should be plesiomorphic.

In several genera, such as *Duyunolepis*, *Paraduyunaspis*, *Neoduyunaspis* (P'an and Wang, 1978a), *Huananaspis* (Liu, 1975), *Wumengshanaspis* (Wang and Lan, 1984), *Lungmenshanaspis* (P'an et al., 1975), *Qingmenaspis* (Pan and Wang, 1980), *Microhoplonaspis*, *Macrothyaspis*, *Sinoszechuanaspis* (Pan, 1992), the sensory canal systems were not preserved (the latter two genera retained the posterior supraorbital canal, the infraorbital canal, and lateral transverse canals), the canal system characters were coded as unavailable.



A: *Hanyangaspis guodingshanensis* (from Pan, 1992); B: *Bannhuanaspis vukhuci* (from Janvier et al., 1993); C: *Eugaleaspis changi* (from Liu, 1965); D: *Sanchaspis magalarostrata* (from Pan and Wang, 1981); E: *Damaspis vartus* (from Wang and Wang, 1982b)

Abbreviations: dcm, dorsal commissure; ifc, infraorbital canal; ldc, lateral dorsal canal; ltc, lateral transverse canal; mdc, medial dorsal canal; mtc, medial transverse canal; soc<sub>1</sub>, anterior supraorbital canal; soc<sub>2</sub>, posterior supraorbital canal

**Fig. 4** The sensory canal system of galeaspids

**[31] Short branches running from posterior supraorbital canal (soc<sub>1</sub>): (0) absent; (1) present.**

**[32] Lateral transverse canal: (0) short; (1) long.**

The lateral transverse canal (ltc, Fig. 4) is present in all galeaspids except those without the sensory canal system preserved. The canals are very short in *Hanyangaspis*, *Changxingaspis*, *Dayongaspis*, *Anjiaspis*, and *Meishanaspis*. By the outgroup comparison, the short lateral dorsal canal is assumed as the plesiomorphic characteristic for galeaspids.

**[33] Branching end of lateral transverse canal: (0) absent; (1) present.**

By the outgroup comparison, the lateral transverse canal with branching end as *Bannhuanaspis* and *Sanchaspis* (Fig. 4B, D) is assumed apomorphic for galeaspids.

**[34] Lateral transverse canals leaving from infraorbital canal: (0) present; (1) absent.**

**[35] The lateral transverse canals leaving from infraorbital canal before ltc<sub>4</sub>: (0) present; (1) absent.**

**[36] Fourth lateral transverse canal (ltc<sub>4</sub>): (0) present; (1) absent.**

**[37] Lateral transverse canals behind ltc<sub>4</sub>: (0) present; (1) absent.**

In general, the Heterostraci, e.g., pteraspids, possess four pairs of lateral transverse canals which were assumed as the ancient agnathan character. It is assumed here that the presence of four pairs of lateral transverse canals (ltc<sub>1-4</sub>) is a plesiomorphy for galeaspids. The ltc<sub>1-4</sub> are also present in most galeaspids in which the sensory canal system was well preserved, and are assumed phyletically homologous among galeaspids in this work. Moreover, in many galeaspids, there are 1–6 pairs of lateral transverse canals running from the infraorbital canal (ifc, Fig. 3) before ltc<sub>1</sub> and 1–3 pairs running from lateral dorsal canals behind the ltc<sub>4</sub> as in *Hanyangaspis* and *Bannhuanaspis* (Fig. 4A, B). These canals are coded as the apomorphy for galeaspids. On the other hand, the fourth lateral transverse canal (ltc<sub>4</sub>) is lost in some eugaleaspids as *Eugaleaspis*, *Yunnanogaleaspis*, *Nochelaspis* and *Pterogonaspis*, being also coded as an apomorphy.

**[38] Anterior supraorbital canal (soc<sub>1</sub>): (0) absent; (1) present.**

This canal is also termed the anterior marginal canal (Liu, 1975; Pan, 1992). We consider that the soc<sub>1</sub> labeled in *Sanchaspis*, *Polybranchiaspis*, and *Laxaspis* (Liu, 1986), was not real an anterior supraorbital canal, but the branching end of the posterior supraorbital canal (soc<sub>2</sub>) or the extension of the infraorbital canal. The anterior supraorbital canal (soc<sub>1</sub>) only evidently exists in some eugaleaspids as *Sinogaleaspis* and *Eugaleaspis* (Fig. 2D, H, 4C) as well as *Pentathyraspis* (Fig. 3G) and can be regarded as an apomorphy.

**[39] Posterior supraorbital canal (soc<sub>2</sub>): (0) present; (1) absent.**

This canal is also termed the supraorbital canal (Liu, 1975; Pan, 1992). By the outgroup comparison, its absence in *Dayongaspis*, *Changxingaspis* and *Hanyangaspis* (cf. Janvier, 1984; Liu, 1986) is apomorphic.

**[40] Posterior supraorbital canals (soc<sub>2</sub>) meet with infraorbital canal (ifc): (0) no; (1) yes.**

**[41] Posterior supraorbital canals (soc<sub>2</sub>): (0) funnel-shaped; (1) parallel; (2) V-shaped.**

**[42] Branching end of posterior supraorbital canals (soc<sub>2</sub>): (0) absent; (1) present.**

As to the trajectory of posterior supraorbital canals (soc<sub>2</sub>), three types can be recognized: funnel-shaped as in '*S. zhejiangensis*' and *Geraspis* (Fig. 2B); parallel as in *Anjiaspis* and *Meishanaspis*; V-shaped as in polybranchiaspids and huananaspids (Fig. 4B, D).

The V-shaped posterior supraorbital canals in turn can be classified into three types: connecting with infraorbital canal as in *Bannhuanaspis* and *Damaspis* (Fig. 4B, E); with branching end as in *Sanchaspis* and *Antiquisagittaspis* (Fig. 4D, 3D); with short branches running from it as in *Dongfangaspis* and *Damaspis* (Fig. 4E). By the mix coding method (Wiley et al., 1991), this transformation series is subdivided into four characters (Characters 31, 40, 41 and 42).

**[43] Medial dorsal canal (mdc): (0) developed; (1) degenerated; (2) absent.**

This canal is present in eugaleaspids (mdc, Fig. 4C), and is plesiomorphic by the outgroup comparison. In *Polybranchiaspis*, *Laxaspis* and *Damaspis* (Fig. 4E), the medial dorsal canal is less developed as a vestige (Liu, 1986), whereas in the other galeaspids it is completely lost.

**[44] Medial dorsal canal and posterior supraorbital canal: (0) unjointed; (1) contact.**

**[45] U-shaped medial dorsal canal: (0) absent; (1) present.**

**[46] Portion of headshield behind dorsal commissure proportionally: (0) long; (1) short.**

The short portion of the headshield behind the dorsal commissure is assumed as an apomorphic character for eugaleaspids.

**[47] Postbranchial wall: (0) short; (1) long.**

The postbranchial wall in galeaspids is the ventral portion of the headshield behind the branchial region, corresponding to the ventral median abdominal division of the headshield of osteostracans (Janvier, 1985). The long postbranchial wall is assumed as an important apomorphic characteristic for *Xiushuiaspis* and *Changxingaspis*.

**[48] Elongated branchial region: (0) absent; (1) present.**

**[49] Number of branchial fossae: (0) 5–7 pairs; (1) 9–17 pairs; (2) more than 20 pairs.**

Among galeaspids, the number of branchial fossae ranges from five to thirty-five pairs and possibly up to about forty-five pairs. Current galeaspid phylogenies (Wang, 1991; Zhu, 1992; Janvier, 1996) suggest that the taxa that have the lowest gill number (5–7), such as *Hanyangaspis*, *Changxingaspis* and the *Eugaleaspidiformes*, display the most generalized condition. The outgroup comparison also indicates that the few numbers of branchial chambers is a plesiomorphy.

The large number of branchial fossae occurs in the *Polybranchiaspidiformes* and *Huananaspisidiformes*, and is remarkable among vertebrates. Janvier (2004) thought that the large number of branchial fossae is likely to be correlated

with the flattening of the entire headshield because the height of the headshield in certain polybranchiaspidiforms was probably not more than 1/10 of its total length. Thus, the strategy of galeaspids was possibly to have more and more gill units to compensate the flattening of their branchial fossae. So it is reasonable to assume that polybranchy is a specialized condition among galeaspids.

**[50] Maximum width of headshield placed: (0) posteriorly; (1) medially.**

In *Hanyangaspis*, *Dayongaspis*, eugaleaspids and huananaspidiiforms (excluding the rostral process and corners from the calculation), the maximum breadth of the headshield is posteriorly placed. In comparison with thelodonts, the above state is assumed as plesiomorphic. The derived state is the middle position as in *Changxingaspis* and *Damaspis* (Fig. 2C, 4E).

**[51] Width/length in oval-like headshield: (0) < 1; (1) > 1.**

The headshields of *Laxaspis* and *Damaspis* (Fig. 4E) are especially broad in the galeaspids with oval-like headshield, being assumed apomorphic.

**[52] Nearly parallel lateral margins of headshield: (0) absent; (1) present.**

The lateral margins of the headshield are nearly parallel in *Wumengshanaspis*, *Sanqiaspis* and *Gantarostrataspis* (Fig. 2E, 3C), being assumed as an apomorphic characteristic.

**[53] Broad and large middle dorsal spine of headshield: (0) absent; (1) present.**

The broad and large middle dorsal spine of headshield in *Antiquisagittaspis* and *Sanchaspis* (Fig. 3D, 4D) is considered as apomorphic.

## 2.4 Tree calculations

A taxon-character matrix (Appendix 1) was compiled using 39 terminal taxa (Table 1) and 53 characters, and analyzed

using the PAUP 3.1.1, cladistics package (Swofford, 1993). In the calculation, we used heuristic tree search routines. All characters are set as equal weight and unordered. The random addition sequence was used with 10 replicates. The tree bisection-reconnection branch swapping algorithm was used. MacClade 4.0 (Maddison and Maddison, 2000) was used to trace character transformation in the preferred cladogram.

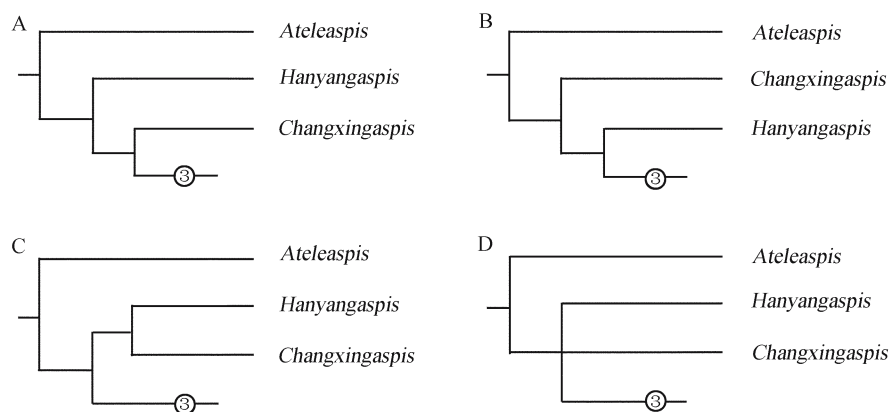
## 3 Results

The phylogenetic analysis resulted in three equally most parsimonious (MP) trees that only differed in the relationship between *Hanyangaspis* and *Changxingaspis*. These trees have a length of 126 steps, a consistency index (CI) of 0.508, and a retention index (RI) of 0.801. The strict consensus tree suggested the basal nodes of galeaspids unresolved. We select the third tree to find character changes.

The monophyly of the Galeaspida (Node 1 in Fig. 6) is well defined by the median dorsal opening, the festooned pattern of sensory canals on dorsal surface of headshield, and aspidine tubercles.

The close affinity between *Hanyangaspis* and *Changxingaspis* (Node 2 in Fig. 6) is supported by their transverse slit-like median dorsal opening. However, this clade is just one of three possibilities in our analysis (Fig. 5), needing further clarification.

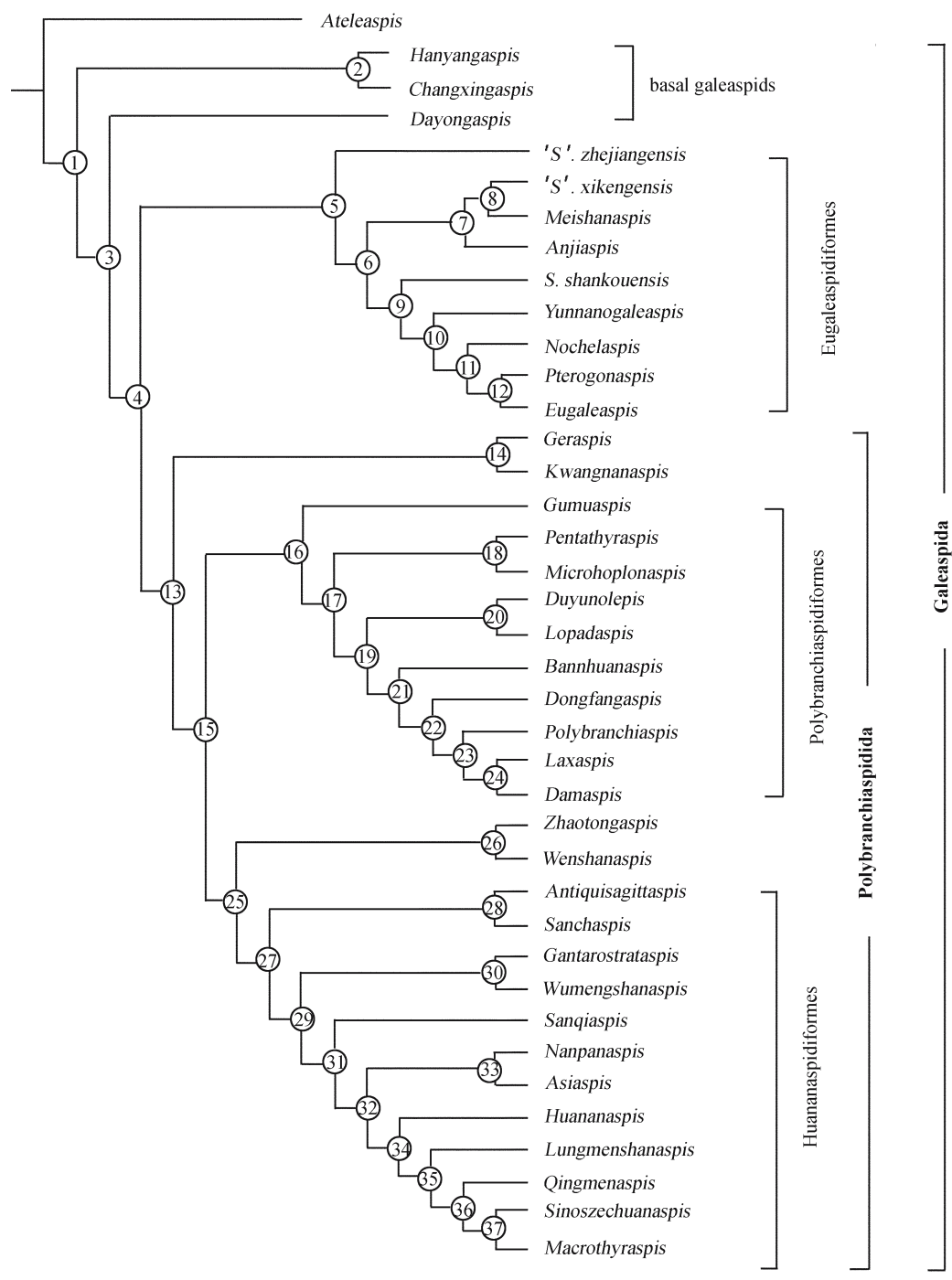
In all three MP trees, another early form, *Dayongaspis*, is left as the most basal offshoot of the remaining galeaspids (Node 3 in Fig. 6), which comprise three major groups of galeaspids: the Eugaleapidiiformes (Node 5 in Fig. 6), Polybranchiaspidiiformes (Node 16 in Fig. 6) and Huananaspidiiformes (Node 27 in Fig. 6). The Polybranchiaspidiiformes and Huananaspidiiformes have a closer relationship than either to the Eugaleaspidiiformes.



Node 3 represents a monophyletic clade shown in Fig. 6

**Fig. 5** Three maximum parsimony trees (A–C) based on the data in Appendix 1 analyzed using PAUP 3.1.1 (Swofford, 1993), and the strict consensus tree (D)





See Appendix 2 for the characters supporting the numbered nodes  
**Fig. 6** One of the maximum parsimony trees resulted from the present analysis

## 4 Discussion

### 4.1 Polyphyly of the galeaspids bearing dorsal fenestrae

Pan (1992) subdivided the Galeaspida (Galeaspidomorphi of Pan, 1992) into two subclasses: the Macrothyraspidides with the dorsal fenestrae (including the lateral dorsal fenestra of

Pan, 1992) and the Galeaspidides without that structure. This classification argued the monophyletic origin of the dorsal fenestrae in galeaspids. However, it sacrificed a large number of other characters, resulting in similar forms (e.g., *Huananaspis* and *Macrothyraspis*) in different higher taxa, since it had given very high weights to the dorsal fenestrae. If all characters are unweighted, the cladogram proposed by Pan (1992) is fairly unparsimonious.

The present analysis suggests that the dorsal fenestrae were derived twice amongst galeaspids, one at Node 18 (Pentathyraspididae, including *Pentathyraspis* and *Microhoplonaspis*) within the Polybranchiaspidiformes lineage, and the other at Node 35 (Macrothyraspinae, including *Lungmenshanaspis*, *Qingmenaspis*, *Sinoszechuanaspis* and *Macrothyraspis*) within the Huananaspidiiformes lineage (Fig. 6). The subclass Macrothyraspidides proposed by Pan (1992) turns out to be polyphyletic.

#### 4.2 Basal galeaspids

Our analysis shows that some early forms of galeaspids (Groups 1–3) constitute the most basal branches of galeaspids. In all three maximum parsimonious trees, *Hanyangaspis* and *Changxingaspis* represent two most basal taxa, and *Dayongaspis* is sister to the remaining galeaspids. This scheme generally conforms to the previous hypothesis (Janvier, 1984, 1996; Wang, 1991). The *Hanyangaspis* + *Changxingaspis* group was considered either monophyletic (Wang, 1991; Fig. 1B) or paraphyletic (Janvier, 1996; Fig. 1C). This issue has not been resolved by the present analysis, though we selected one cladogram to trace character changes.

With regard to the phylogenetic position of *Dayongaspis*, the present analysis is different from that of Wang (1991), which proposed that *Dayongaspis* was closely allied with *Hanyangaspis* and *Changxingaspis*. Based on his hypothesis of galeaspid phylogeny, Wang (1991) also expanded the Hanyangaspidida to include *Changxingaspis*, *Xiushuiaspis* and *Dayongaspis*. This suggestion did not receive support from our analysis. Since the resolution of basal galeaspid split remained labile, we suggest that the Hanyangaspidida keeps its original definition to exclude the Xiushuiaspidae and the Dayongaspidae.

#### 4.3 Eugaleaspidiformes

The monophyly of the Eugaleaspidiformes has been ascertained (Janvier, 1984; Wang, 1991; Liu, 1986; Pan, 1992; Zhu, 1992; Gai et al., 2005). Regarding the relationships of the Eugaleaspidiformes, the present analysis corroborates Gai et al. (2005) to reject the monophyly of *Sinogaleaspis* (including *S. shankouensis*, '*S. xikengensis*', '*S. zhejiangensis*'). In our cladograms, *Anjiaspis*, '*S. xikengensis*' and *Meishanaspis* form a monophyletic group and '*S. zhejiangensis*' occupies the most basal position in the eugaleaspid lineage. The type species of *Sinogaleaspis*, *S. shankouensis*, is sister to *Yunnanogaleaspis* and the remaining eugaleaspids.

The parsimony analysis shows that the eugaleaspidiforms (Node 5 in Fig. 6) occupy a basal position relative to polybranchiaspidiforms and huananaspidiiforms, in accordance with Janvier (1996), but distinguishable from Janvier (1984) and Wang (1991).

#### 4.4 Polybranchiaspidiformes

The Polybranchiaspidiformes were considered as paraphyletic by Janvier (1984) and Wang (1991), who used *Polybranchiaspis*-like forms to represent this group. In our cladograms, the monophyly of the Polybranchiaspidiformes is robustly supported (Node 16 in Fig. 6), if we remove *Xiushuiaspis*, *Dayongaspis*, *Kwangnanaspis* and *Geraspis* from this group. *Xiushuiaspis* and *Dayongaspis*, as well as the Hanyangaspidae, are basal taxa of the Galeaspidida as discussed above. *Kwangnanaspis* and *Geraspis*, forming a monophyletic group, the Geraspididae (Node 14 in Fig. 6), turn out to be the sister group of the Polybranchiaspidiformes plus the Huananaspidiiformes and can be designated as the stem taxa of the Polybranchiaspidida (Janvier, 1996; Node 13 in Fig. 6).

In our analysis, the Polybranchiaspidiformes consists of *Gumuaspidis*, the Pentathyraspididae, the Duyunolepididae and the Polybranchiaspididae. *Gumuaspidis*, which was referred to the Huananaspidiiformes by Wang and Wang (1992), and to the Polybranchiaspidiformes by Liu (1993), occupies the most basal position in the Polybranchiaspidiformes.

Pan (1992) assigned the Pentathyraspididae to the Macrothyraspidides, which turn out to be polyphyletic in our analysis. Liu (1993) considered that *Pentathyraspis* is closely related to polybranchiaspidiforms rather than huananaspidiiforms or eugaleaspids in such characters as the shape of headshield, the lobe-shaped inner corner, and the positions of median dorsal opening and orbital openings. He argued that *Pentathyraspis* is likely to be a specialized polybranchiaspidiform. In our cladograms, *Pentathyraspis* and *Microhoplonaspis* form a monophyletic group, the Pentathyraspididae, which is the sister group of Duyunolepididae + Polybranchiaspididae, corroborating Liu's opinion.

The Duyunolepididae was not discussed by Janvier (1984) and Wang (1991). Liu (1993) suggested that duyunolepids, which lost inner corners and had over 20 branchial fossae, should be a specialized subgroup of the Polybranchiaspidiformes. This suggestion is well supported by the present analysis. The Duyunolepididae (Node 20 in Fig. 6), including *Duyunolepis*, *Paraduyunaspis*, *Neoduyunaspis*, *Lopadaspis*, is the sister group of the Polybranchiaspididae (Node 21 in Fig. 6), which includes *Bannhuanaspis*, *Clororbis*, *Dongfangaspis*, *Polybranchiaspis*, *Siyingia*, *Laxaspis*, *Diandongaspis*, *Damaspis* and *Cyclodiscaspis*.

#### 4.5 Huananaspidiiformes

The monophyly of the Huananaspidiiformes was proposed by Janvier (1984, 1996) and Wang (1991), however doubted by Wang and Wang (1982b), Liu S F (1986), Liu (1993), and Janvier et al. (1993). The present analysis corroborates the monophyly of the Huananaspidiiformes (Node 27 in Fig. 6), which consists of the Sanchaspididae, the Gantarostraspididae, the Sanqiaspidae, and the Huananaspidae. However, *Gumuaspidis*, used to be assigned as a huananaspidiiform (Wang

and Wang, 1992), should be removed from this group. In our cladograms, *Gumuaspis* is the most basal taxon of the Polybranchiaspidiformes.

The Sanchaspididae (including *Sanchaspis* and *Antiquisagittaspidis*) with broad rostral process, was referred to the Huananaspidae by Pan and Wang (1981) and Liu (1985), but referred to the Polybranchiaspidiformes by Wang and Wang (1982b). In our cladograms, the Sanchaspididae occupies the most basal position in the huananaspidae lineage.

*Wumengshanaspis* was referred to Huananaspidae by Wang and Lan (1984). In our cladograms, *Wumengshanaspis* and *Gantarostrataspidis* are closely allied to each other, and share the characteristics such as the nearly parallel lateral margins of headshield, spines on rostral process, corner projecting backward and large medial dorsal opening. Thus, *Wumengshanaspis* should be removed from the Huananaspidae, and referred to the Gantarostrataspididae.

The remaining huananaspids with slender rostral process, laterally projecting corner and small orbital openings are referred to the Huananaspidae. *Lungmenshanaspis*, *Qingmenaspis*, *Sinoszechuanaspis* and *Macrothyraspis*, four genera bearing the dorsal fenestrae, form a subgroup (Subfamily Macrothyraspinae) nested within the Huananaspidae. The Sanqiaspididae, a monogeneric family, is the sister group of the Huananaspidae (Node 32 in Fig. 6).

The Zhaotongaspididae, including *Zhaotongaspis* and *Wenshanaspis* which have no rostral process, is sister to the Huananaspidae in our cladograms.

#### 4.6 Chronological distribution of galeaspid

Our cladograms, when projected against stratigraphy, highlight that early forms make up basal sections of the galeaspid lineage (Fig. 7). These trees are quite compatible with the chronological distribution of fossil records.

As discussed above, apart from those basal taxa (*Xiushuiaspis*, *Dayongaspis*, *Hanyangaspis* and *Kalpinolepis*), the Galeaspida could be subdivided into two major lineages: one represented by the Eugaleaspidiformes (Node B in Fig. 7), the other is represented by the Polybranchiaspidida (Node C in Fig. 7). The first lineage, like the basal galeaspid, had its early diversification in the Telychian, Llandovery of the Silurian. The early galeaspid underwent a mass extinction during the Ludlow, however some eugaleaspid survived until the late Pragian of the Devonian.

The second lineage had its first appearance in the Telychian of the Silurian, but did not radiate until the beginning of the Early Devonian (Fig. 7). As shown by the present analysis, the diversification of the Polybranchiaspidiformes (Node D in Fig. 7) may predate that of the Huananaspidae (Node E in Fig. 7). The diversity of galeaspid suddenly decreased by the end of the Pragian. Few galeaspid survived into the Middle Devonian (Pan and Ji, 1993) and had its last

occurrence in the Famennian of the Late Devonian (Pan et al., 1987).

#### 4.7 Classification of galeaspid

On the basis of the present analysis, we propose a cladistically-based classification of the Galeaspida as follows:

Subclass Galeaspida Tarlo, 1967

Family Hanyangaspididae P'an et Liu, 1975

*Hanyangaspis* P'an et Liu, 1975

*Nanjiangaspis* Wang et al., 2002

*Kalpinolepis* Wang, Wang et Zhu, 1996

*Konoceraspis* Pan, 1992

Family Xiushuiaspididae Pan et Wang, 1983

*Xiushuiaspis* Pan et Wang, 1983

*Changxingaspis* Wang, 1991

Family Dayongaspididae Pan et Zeng, 1985

*Dayongaspis* Pan et Zeng, 1985

*Platycaraspis* Wang et al., 2002

Order Eugaleaspidiformes Liu, 1980

'S'. *zhejiangensis* Pan, 1984

*Anjiaspis* Gai et Zhu, 2005

'S'. *xikengensis* Pan et Wang, 1980

*Meishanaspis* Wang, 1991

*Sinogaleaspis* Pan et Wang, 1980

Family Eugaleaspididae Liu, 1980

*Yunnanogaleaspis* Pan et Wang, 1980

*Nochelaspis* Zhu, 1992

*Pterogonaspis* Zhu, 1992

*Tridensaspis* Liu, 1986

*Eugaleaspis* Liu, 1980

Supraorder Polybranchiaspidida

Family Geraspididae Pan et Chen, 1993

*Geraspis* Pan et Chen, 1993

*Kwangnanaspis* Cao, 1979

Family Zhaotongaspididae Wang et Zhu, 1994

*Zhaotongaspis* Wang et Zhu, 1994

*Wenshanaspis* Zhao, Zhu et Jia, 2002

Order Polybranchiaspidiformes Liu, 1965

*Gumuaspis* Wang et Wang, 1992

Family Pentathyraspididae Pan, 1992

*Pentathyraspis* Pan, 1992

*Microhoplonaspis* Pan, 1992

Family Duyunolepididae P'an et Wang, 1978a

*Duyunolepis* Pan et Wang, 1982

*Paraduyunaspis* P'an et Wang, 1978a

*Neoduyunaspis* P'an et Wang, 1978a

*Lopadaspis* Wang et al., 2002

Family Polybranchiaspididae Liu, 1965

*Bannhuanaspis* Janvier, Tong-Dzuy et

Ta-Hoa, 1993

*Clororbis* Pan et Ji, 1993

*Dongfangaspis* Liu, 1975

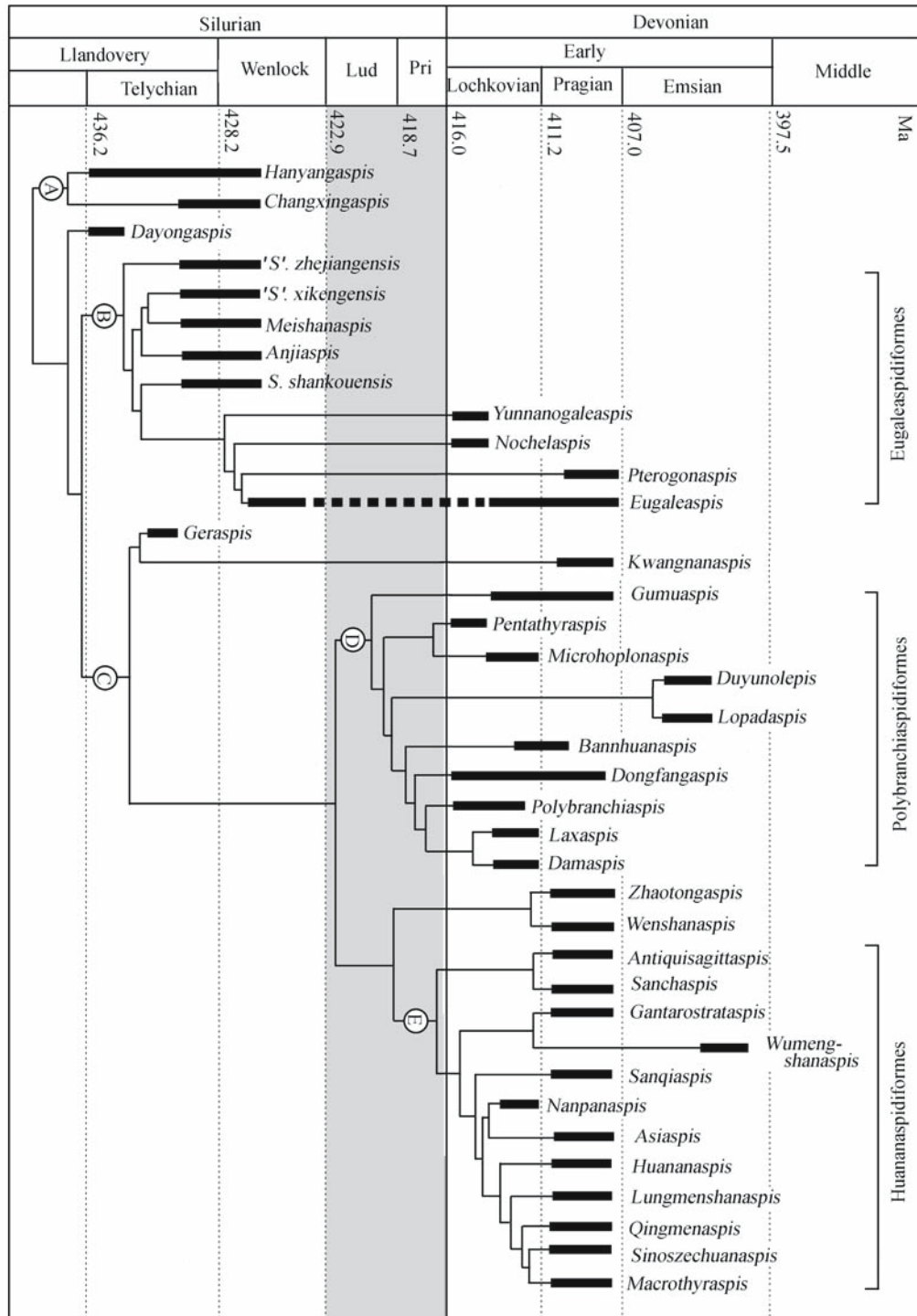
*Polybranchiaspis* Liu, 1965

*Siyingia* Wang et Wang, 1982a



*Laxaspis* Liu, 1975  
*Diandongaspis* Liu, 1975  
*Damaspis* Wang et Wang, 1982b  
*Cyclodiscaspis* Liu, 1975  
 Order Huananaspidiiformes Janvier, 1975  
 Family Sanchaspididae Pan et Wang, 1981

*Sanchaspis* Pan et Wang, 1981  
*Antiquisagittaspis* Liu, 1985  
 Family Gantarostraspidae Wang et Wang, 1992  
*Gantarostrataspis* Wang et Wang, 1992  
*Wumengshanaspis* Wang et Lan, 1984  
 Family Sanqiaspididae Liu, 1975



Solid columns represent known time ranges, thin lines represent 'ghost lineages'

**Fig. 7** A phylogenetic tree of galeaspids projected against stratigraphy

- Sanqiaspis* Liu, 1975  
 Family Huananaspidae Liu, 1973  
*Asiaspis* P'an, in P'an et al., 1975  
*Nanpanaspis* Liu, 1965  
*Huananaspis* Liu, 1973  
 Subfamily Macrothyraspinae Pan, 1992  
*Lungmenshanaspis* P'an et Liu, 1975  
*Qingmenaspis* Pan et Wang, 1981  
*Sinoszechuanaspis* P'an et Wang, 1975  
*Macrothyraspis* Pan, 1992

#### Incertae sedis

- Hyperaspis* Pan, 1992  
*Pseudoduyunaspis* Wang, Wang et Zhu, 1996

## 5 Conclusions

Here, we present the first cladistic analysis of the agnathan subclass Galeaspida based on the analysis of 53 morphological characteristics and the principle of parsimony. In this study, some taxonomic issues of galeaspids are discussed and 38 groups of galeaspids are identified as the terminal taxa for the phylogenetic analysis. The maximum parsimony cladograms suggest that the Hanyangaspididae and the Xiushuiaspididae constitute basal taxa of galeaspids, and the Dayongaspididae is the sister group of the remaining galeaspids, which can be subdivided into two major clades, the Eugaleaspidoformes and the Polybranchiaspidida. The Geraspididae including *Geraspis* and *Kwangnanaspis* is the basal taxon of the Polybranchiaspidida. The monophyly of the Polybranchiaspidiformes (including *Gumuaspidis*, the Pentathyraspididae, the Duyunolepididae and the Polybranchiaspididae) is well supported. The Zhaotongaspididae is sister to the Huananaspidoformes, a monophyletic group including the Sanchaspididae, the Gantarotraspididae, the Sanqiaspididae and the Huananaspidae. The dorsal fenestrae evolved twice within the Galeaspida, one in the polybranchiaspidiform lineage, and the other in the huananaspidoform lineage (nested within the Huananaspidae). The Macrothyraspididae proposed by Pan (1992) turns out to be polyphyletic. An amended classification of the Galeaspida is proposed corresponding to our cladistic analysis.

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Appendix 1 Data Matrix of Characters

Taxon	111111111122222222233333333334444444445555
	1234567890123456789012345678901234567890123
<i>Ateleaspis</i>	00001??0???000?????00?????00?????01???0?0?000???
<i>Anjiaspis</i>	1111020001000100000100??0????200000??0001001110000?00
<i>Antiquisagittaspis</i>	111411?001002101100011000?????1011010100021200001?0?01
<i>Asiaspis</i>	111311?001011110000111100?????10?011?10002020000110?00
<i>Banxhuanaspis</i>	111211?0010010????0000?0?????101100000012020000111?00
<i>Changxingaspis</i>	111200?0100000????0000?0?????0001000001???20001001000
<i>Damaspis</i>	111211?0010010????0000?0?????11110000001201000011110?
<i>Dayongaspis</i>	111101?010000100000000?0?????00000000?1???20000000?0?
<i>Dongfangaspis</i>	111211?0010010????0000?0?????111100000012020000121000
<i>Duyunolepis</i>	111211?0010110????1?00?0?0?????0?????0?????00121000
<i>Eugaleaspis</i>	1111121001101100001?00?0?0?????101011111001001110000?00
<i>Gantarostrataspis</i>	111411?001102120000111010?????01101010002120000110?10
<i>Geraspis</i>	111111?001001100001?00?0?0?????010110100000200?0010?00
<i>Gumaspis</i>	111411?0010010????0011000?????1010010?00020200001?1000
<i>Hanyangaspis</i>	111010?0100020????0000?0?????0000000001???20000?00?0?
<i>Hunanaspis</i>	111311?10101211?001011100?????0?????????????????01?0?00
<i>Kwangnanaspis</i>	111111?001001100001?00?0?0?????10?011?10?????200?0010?0?
<i>Laxaspis</i>	111211?0010010????0000?0?????11110000001201000011110?
<i>Lopadaspis</i>	111211?0010010????1?00?0?0?????101101010012020000121000
<i>Lungmenshanaspis</i>	111311?101011110001?111010000?0?????????????????0110?00
<i>Macrothyraspis</i>	111311?101012110101?11101111110?????1???0002020000110?00
<i>Meishanaspis</i>	1111020002001100000100??0????10000001?0010??110000?00
<i>Microhoplonaspis</i>	111211?0010010????0000?10000?0?????0?????00111000
<i>Nanpanaspis</i>	111311?001011111101?11100?????10101101000202000011100?
<i>Nochelaspis</i>	1111121001001100000000?0?????10101111?001001110000?00
<i>Pentathyraspis</i>	111211?0010110????0010??1000010?0?1011002020000111000
<i>Polybranchiaspis</i>	111211?0010010????0000?0?????111000000012010000111000
<i>Pterogonaspis</i>	1111121001101110000011100?????101011111001001110000?00
<i>Qingmenaspis</i>	111311?001010110001?111011110?0?????????????????01?0?00
<i>Sanchaspis</i>	111411?001001101100011000?????101101010012120000110?01
<i>Sanqiaspis</i>	111411?001002120001?11000?????10?011?0002020000110?10
<i>'S'. zhejiangaspis</i>	1111120002001100000100??0????10100001?00002?010000?00
<i>'S'. xikengensis</i>	1111020002001100000100??0????10?????????????????10000?00
<i>S. shankouensis</i>	1111120001101100000100??0????201000011002001110000?00
<i>Sinoszechuanaspis</i>	111311?101012110111?111011111?0?0110100020200001?0?00
<i>Wenshanaspis</i>	111411?001002100010000?0?????201101000002120000120?00
<i>Wumengshanaspis</i>	111411?001?02120000111110?????0?????????????????0110?10
<i>Funnanogaleaspis</i>	1111120001001100000000?0?????101011111001001110000?00
<i>Zhaotongaspis</i>	111411?001002101110100?0?????101101010002?20000120?00

## Appendix 2 List of synapomorphies of a selected most parsimonious tree of the Galeaspida

Asterisks indicate ambiguous character states resolved using DELTRAN; Character state is (1), unless marked otherwise

Node 1: [Galeaspida] 1, 2, 3, 43(2)

Node 2: [Hanyangaspididae + Xiushuiaspididae] 6(0)

Node 3: [Dayongaspididae + (Eugaleaspidiformes + Polybranchiaspidida)] 4, 6\*, 14

Node 4: [Eugaleaspidiformes + Polybranchiaspidida] 9(0), 10, 13, 30, 32, 37, 39(0)

Node 5: [Eugaleaspidiformes] 6(2), 20, 46

Node 6: 41, 43(0), 44\*, 45

Node 7: 5(0), 32(0)

Node 8: 10(2)

Node 9: 38

Node 10: [Eugaleaspididae] 20(0), 34, 35, 36

Node 11: 7

Node 12: 11

Node 13: [Polybranchiaspidida] 35, 49

Node 14: [Geraspidae] 19, 34

Node 15: [Polybranchiaspidiformes + (Zhaotongaspididae + Huananaspidiformes)] 4(4), 41(2), 48

Node 16: [Polybranchiaspidiformes] 14(0), 50

Node 17: 4(2)

Node 18: [Pentathyraspididae] 25

Node 19: [Dyunolepididae + Polybranchiaspididae] 33, 40

Node 20: [Dyunolepididae] 19, 49(2)

Node 21: [Polybranchiaspididae] 35(0), 37(0)

Node 22: 31

Node 23: 43

Node 24: 51

Node 25: [Zhaotongaspididae + Huananaspidiformes] 13(2), 33, 42

Node 26: [Zhaotongaspididae] 18, 49(2)

Node 27: [Huananaspidiformes] 21, 22

Node 28: [Sanchaspididae] 16, 17, 53

Node 29: 15(2)

Node 30: [Gantarostrataspididae] 20\*, 24, 52\*

Node 31: [Sanqiaspidae + Huananaspididae] 19, 33(0), 34, 42(0)

Node 32: [Huananaspididae] 4(3), 12, 15, 23

Node 33: 13

Node 34: 8

Node 35: [Macrothyraspinae] 25

Node 36: 26, 27, 28

Node 37: 17, 29