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A SMALL ANTIARCH, *MINICRANIA LIROUYII* GEN. ET SP. NOV., FROM THE EARLY DEVONIAN OF QUJING, YUNNAN (CHINA), WITH REMARKS ON ANTIARCH PHYLOGENY

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ABSTRACT—A new Early Devonian (Lochkovian) yunnanolepiform-like antiarch *Minicrania lirouyii* gen. et sp. nov. is described from Qujing, Yunnan, southeastern China. This tiny antiarch possesses both a preorbital depression and a preorbital recess. It is characterized by a long and narrow skull-roof, short obstantic margin, large orbital fenestra, fairly short dorsal wall of the trunk-shield and a close fusion of the dermal plates. It shows some neurocranial structures, observed here for the first time in an antiarch. A growth series of the skull-roof shows a slight allometric growth. The phylogeny of antiarchs is discussed on the basis of new character combinations observed in this new form. It is suggested that *Minicrania* is the sister-group of euantiarchs plus sinolepids, sharing with them the preorbital recess. The Yunnanolepidae would be the sister-group of the Chuchinolepidae (i.e., "procondylolepids"), and the Yunnanolepiformes are re-defined here to include only these two groups.

INTRODUCTION

Liu Y.-H. (1963) erected the antiarch genus *Yunnanolepis* on the basis of a skull-roof from the Early Devonian of Qujing, Yunnan, China. At that time, *Yunnanolepis,* first assigned to the Asterolepiformes by Liu Y.-H. (1963), was the earliest known antiarch record. Subsequently, more detailed works (Chang K.-J., 1978; P'an and Wang, 1978; Zhang G.-R., 1978; Zhang M.-M., 1980) showed that *Yunnanolepis* and its relatives represent the most primitive antiarchs, lacking a complex dermal pectoral fin joint. Therefore, a new order Yunnanolepiformes (Zhang G.-R., 1978) was erected to distinguish them from the other antiarchs, although the monophyly of this taxon is poorly supported (Janvier and Pan, 1982). Since the Yunnanolepidae (including *Yunnanolepis*) is the best known family of the Yunnanolepiformes, it has been chosen as the root in the phylogenetic analysis of antiarchs (Zhang and Young, 1992). However, as discussed below, yunnanolepids are relatively specialized in several characters, and their selection as the root for antiarch phylogeny would result in biases in the assessment of character polarities.

In 1988, one of us (Z.M.) collected abundant early vertebrate fossils (galeaspids, acanthodians, sarcopterygians and placoderms) from the Lochkovian Xishancun Formation, in Qujing, Yunnan (Zhu, 1991, 1992, in press). Among this material, more than 40 specimens belong to a new, very small-sized antiarch, *Minicrania lirouyii* gen. et sp. nov., described below. This species is very suggestive of the Yunnanolepidae by its simple pectoral fin joint, but it looks less specialized than the latter in several respects, thereby raising a number of questions as to antiarch phylogeny. All the material of this new form is preserved as internal and external molds in a fine-grained sediment, without any trace of bone. Therefore, it was studied essentially on the basis of elastomere casts.

The growth series of the antiarch *Bothriolepis canadensis* and its significance to antiarch evolution has been studied by Werdelin and Long (1986), and yet another example is given here. The skull-roofs of *M. lirouyii* of various sizes are supposed here to form a relatively complete growth series. The largest skull-roof is about 6 mm in length while the smallest one (supposedly juvenile) is shorter than 2.2 mm in length (that is, the smallest fossil vertebrate head found so far!).

The specimens described below are housed in the Institute of Vertebrate Paleontology and Paleoanthropology (**IVPP**), Academia Sinica, Beijing.

SYSTEMATIC DESCRIPTION

PLACODERMI M'Coy, 1848
ANTIARCHA Cope, 1885

MINICRANIA gen. nov.

Diagnosis—as for the type species (by monotypy).

Type species—*Minicrania lirouyii* gen. et sp. nov.

Etymology—Mini, from *minus* (lat.) = small; crania, from *cranium* (Lat.) = skull.

Remarks—*Minicrania lirouyii,* the only species of the genus, is the smallest antiarch recorded so far. The entire dermal armour (skull-roof and trunk-shield) in the presumed adult is less than 20 mm in length.

Minicrania is very suggestive of the Yunnanolepiformes by its simple pectoral fin articulation and triangular preorbital depression. However, it differs from the typical Yunnanolepidae in the following characters: 1) the skull-roof being more or less square-shaped with the breadth/length ratio approximately 1.0, 2) the presence of a preorbital recess, 3) the short obstantic margin, 4) the closely fused skull-roof and trunk-shield bones, 5) the anterior median dorsal plate roughly hexagonal in shape with a broad anterior margin, 6) the posterior median dorsal plate fairly large and broad, and 7) the crista transversalis interna posterior extending laterally to the posterior ventral process of the PMD plate. The latter character is also found in the yunnanolepiform *Zhanjilepis.*

MINICRANIA LIROUYII sp. nov.
(Figs. 1–11)

Diagnosis—Very small-sized antiarch, with closely fused skull-roof and trunk-shield bones; dermal bones ornamented with comparatively large, closely-set tubercles; obstantic margin short; postpineal plate convex and short; very large preor-

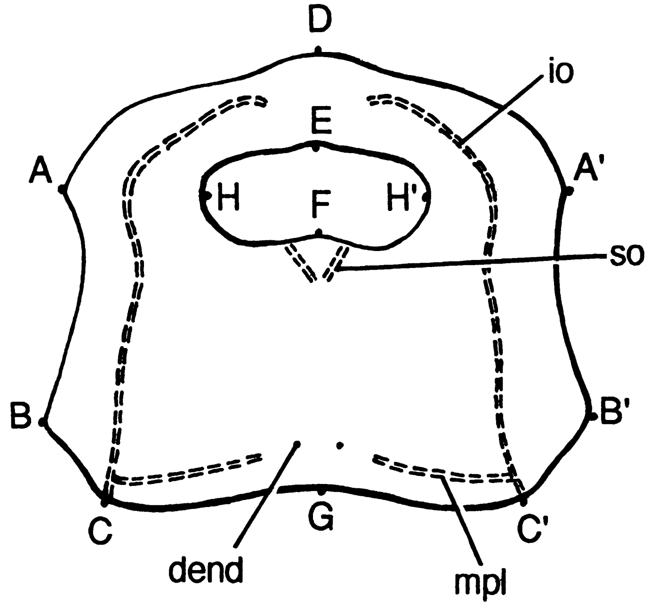

FIGURE 1. Skull-roof of *Minicrania lirouyii* (gen. et sp. nov.), showing the landmarks and distances used in measurements. ***Landmarks of the skull-roof***: A (A') = anterolateral angle of skull-roof, anterior end of lateral skull-roof margin; B (B') = posterolateral angle (preobstantic corner) of skull-roof, posterior end of lateral skull-roof margin; C (C') = postobstantic corner of skull-roof, posterior end of obstantic margin; D = rostral angle of skull-roof; E = middle point of orbital fenestra margin of premedian plate; F = middle point of orbital fenestra margin of postpineal plate; G = posterior angle of skull-roof; H (H') = lateral point of orbital fenestra. *Distances:* AA' = rostral width of skull-roof; BB' = total width of skull-roof; CC' = posterior width of skull-roof; HH' = width of rostral margin; DE = length of premedian plate; preorbital length of skull-roof; EF = length of orbital fenestra; FG = postorbital length of skull-roof; DG = DE + EF + FG, length of skull-roof; AB (A'B') = length of lateral skull-roof margin; BC (B'C') = length of obstantic margin of skull-roof. **dend**, opening of the endolymphatic duct; **io**, infraorbital sensory-line groove; **mpl**, "middle pit-line"; **so**, supraorbital sensory-line groove.

bital depression bounded off by a prominent ridge; small crescentiform preorbital recess lying below the middle part of preorbital depression; anterior ventral process situated between the levels of the tergal angle and the geometric centre of the anterior median dorsal plate; posterior median dorsal plate fairly large and broad; median dorsal ridge and two medial dorsolateral ridges on both sides extending from the tergal angle to the posterior angle; posterior angle spine-shaped.

Holotype—an internal mold of an adult skull-roof, V10505.1 (Figs. 2C, 3A).

Plesiotype—an external mold of the skull-roof associated with the ventral wall of the trunk-shield of a juvenile individual, V10505.2 (Fig. 5C).

Type Locality—Liaoguoshan, Qujing, Yunnan, China.

Type Horizon—Xishancun Formation, Cuifengshan Group (Lochkovian, Early Devonian).

Etymology—A species dedicated to Mr. Li Rou-yi (Qujing, Yunnan) who kindly provided help in collecting the specimens.

Referred Material—skull-roofs (external or internal molds), 10505.3–13, 46; trunk-shields, V10505.14–45.

Description

Measurements—Two systems of measurements of the antiarchs are mentioned in the literature (Young, 1988). One is that of Stensiö (1948), followed and modified by Miles (1968) and Young (1988), and which suits best disarticulated specimens. The other is that of Werdelin and Long (1986) which is appropriate for articulated specimens. However, for articulated specimens whose bone sutures could not be observed, as in the present case, the system of Werdelin and Long has its limits. In fact, a third system (Zhang G.-R., 1978) has been ignored. In the case of articulated skull-roofs, especially when no suture can be seen, the system of Zhang G.-R. (1978) is more convenient and depicts better the overall shape of the skull-roof. In this paper, Zhang's system is modified to accord with the current method of morphometrics (Fig. 1).

Ten distances were measured on eleven skull-roofs of *Minicrania lirouyii* (Table 1), and eight indices were calculated (Table 2). For comparison, the table of Zhang G.-R. (1978) for skull-roofs of *Yunnanolepis chii* was modified into Tables 3 and 4. Since there are individual variations in skull-roofs, these kinds of indices only provide information about their shape and facilitate comparisons.

Skull-roof—The skull-roof of *Minicrania lirouyii* is known from fourteen specimens of various sizes, either in external or internal molds. In general, the skull-roof plates in either adult or juvenile specimens (as assumed on the basis of their relative size), are tightly fused and no suture could be observed. One exception is V10505.5, which is an internal mold of a juvenile skull-roof (Fig. 2B), where impressions of sutures between the premedian and lateral plates are observed.

The skull-roof of *M. lirouyii* is more or less square-shaped, and somewhat suggestive of that of sinolepids. The index between skull-roof length and width (DG/BB') ranges from 90.7 to 102.0 (Table 2). In the Yunnanolepiformes, exemplified by *Yunnanolepis chii,* the skull-roof is much wider than long (Tables 3, 4). The rostral margin (AA') is here only slightly narrower than the skull-roof width (BB'). In other words, the posterolateral corners in *M. lirouyii* do not extend as far laterally as in the Yunnanolepiformes. The lateral margin is somewhat concave. The obstantic margin is fairly short, representing

TABLE 1. Measurements (in millimeters) of the head-shield distances in *Minicrania lirouyii* gen. et sp. nov. (estimated values in italics). See Figure 1 for abbreviations.

	DE	EF	FG	DG	AA'	BB'	CC'	HH'	AB	BC
V10505.1	1.22	0.96	3.40	5.58	5.46	5.73	4.83	2.20	2.95	1.21
V10505.2	0.54	0.50	1.67	2.71	2.58	2.88	2.25	1.31	1.50	0.62
V10505.3	0.41	0.45	1.29	2.15	2.25	2.37	1.75	1.13	1.24	0.50
V10505.4	0.75	0.67	2.13	3.55	3.42	3.73	3.12	1.51	2.33	0.65
V10505.5	*0.46*	*0.42*	1.37	2.25	2.03	2.29	1.85	1.00	1.29	0.46
V10505.6	0.46	0.49	*1.55*	2.50	2.13	2.45	1.92	1.04	1.41	0.58
V10505.7	0.52	0.52	1.63	2.67	2.54	2.71	2.25	1.25	1.67	0.42
V10505.8	0.46	0.58	1.34	2.38	2.18	2.34	1.88	1.13	1.21	0.51
V10505.9	*0.46*	*0.45*	1.31	2.22	1.98	2.22	1.81	1.00	1.25	0.48
V10505.10	0.38	0.46	1.33	2.17	2.17	2.33	2.00	1.02	1.04	0.39
V10505.11	*0.55*	*0.55*	1.67	*2.77*	2.83	3.00	2.50	1.37	1.33	0.50

TABLE 2. Proportions (indices) of the head-shield in *Minicrania lirouyii* gen. et sp. nov. (estimated value in italics). See Figure 1 for abbreviations.

	DG/BB′	DE/DG	EF/DG	FG/DG	DE/FG	HH′/BB′	AA′/BB′	BC/DG
V10505.1	97.4	21.9	17.2	60.9	35.9	38.4	95.3	21.7
V10505.2	94.1	19.9	18.5	61.6	32.3	45.5	89.6	22.9
V10505.3	90.7	19.1	20.9	60.0	31.8	50.2	94.9	23.2
V10505.4	95.2	21.1	18.9	60.0	35.2	40.5	91.7	18.3
V10505.5	98.3	*20.4*	*18.7*	60.1	*33.6*	43.7	88.7	20.4
V10505.6	102.0	18.4	*19.6*	62.0	*29.7*	42.4	86.9	23.2
V10505.7	98.5	19.5	19.5	61.0	31.9	46.1	93.7	15.7
V10505.8	101.7	19.3	24.4	56.3	34.3	48.3	93.2	21.4
V10505.9	100.0	*20.7*	*20.3*	59.0	*35.1*	45.0	89.2	21.6
V10505.10	93.1	17.5	21.2	61.3	28.6	43.8	93.1	18.0
V10505.11	92.3	*19.9*	*19.9*	60.2	*32.9*	45.7	94.3	*18.1*

about 20% of the skull-roof length. In *Yunnanolepis* (Liu, 1963; Zhang G.-R., 1978), the obstantic margin is relatively long, as in *Bothriolepis* (Stensiö, 1948; Denison, 1978).

The orbital (or orbitonasal) fenestra (orbnaf, Fig. 3A) is rather large and occupies a comparatively anterior position on the dorsal surface of the skull-roof. The width of the orbital fenestra (HH′) in the adult specimen V10505.1 represents 38.4% of the skull-roof width (BB′). The index HH′/BB′ in juvenile specimens increases, suggesting allometric growth (Table 2). In *Yunnanolepis chii,* the orbital fenestra is very small and the index HH′/BB′ is lower than 20.0. Taking this character into consideration, *M. lirouyii* is somewhat similar to *Y. parvus,* where the HH′/BB′ index could reach about 31.6. The anterior position of the orbital fenestra is widely distributed among the Yunnanolepiformes and is considered as a plesiomorphic character for antiarchs, since it is closer to the condition in certain acanthothoracid placoderms, thought to be the sister-group of antiarchs.

As in *Yunnanolepis,* the premedian plate (PrM, Fig. 8A, the limits of which can be traced only in the specimen V10505.5) is broad and short. Its orbital width is just a little shorter than its rostral width, but this may be a juvenile feature, as in *Bothriolepis canadensis* (Werdelin and Long, 1986). The alternative reason is that *M. lirouyii* possesses a large orbital fenestra, as in *Y. parvus,* which also retains a high value for the orbital width of the premedian plate. In V10505.6 (Fig. 3D), the space which looks like an "orbital fenestra" is abnormally large, when compared to the other specimens, and it probably includes the notch for the postpineal plate. If this is true, the postpineal plate would be relatively broad and short and, consequently, the nuchal plate of *M. lirouyii* would be comparatively longer than that of *Yunnanolepis,* given that the postorbital portion of the head in these two genera is roughly equivalent in length.

In external skull-roof molds, a preorbital depression (prorbd, Fig. 4) ornamented with tubercles can be clearly observed (Fig. 5A–B). Its shape and relative size are nearly the same as those in *Yunnanolepis* (Zhang G.-R., 1978; Zhang M.-M., 1980), but it is more elliptic in outline, and bounded by a prominent ridge. It extends laterally onto the lateral plates. It is noteworthy that, in addition to the preorbital depression, there is a structure in the posterior portion of the premedian plate, which should be regarded as a preorbital recess (prorbr, Fig. 6A). In internal skull-roof molds, the middle of the anterior margin of the orbital fenestra is often notched anteriorly. Sometimes an arched groove surrounding a small, roughly triangular, or crescentiform and convex, area can be seen (Figs. 2B–D, 3). This small impression is regarded here as the natural mold of the roof of the preorbital recess. When this impression is preserved in the fossil, the ventral lamina which formed the floor of the recess is often completely or partly lost, since it was fairly thin and held a relatively low position. Thus what we see in most specimens is not the natural mold of the entire preorbital recess, but only its anterior boundary.

Behind the orbital fenestra, the dorsal surface of the skull-roof exhibits two pairs of oblique ridges which correspond to the position of the underlying semicircular ridges of the braincase (rasc, rpsc, Figs. 4, 5A, B, 6). These neurocranial ridges also occur in arthrodires (Liu Y.-H., 1979; Goujet, 1984b) and petalichthyids (Zhu, 1991). In most placoderms, a ridge on the dorsal surface of the braincase is not projected through to the external surface of the skull-roof. However, since *M. lirouyii* is a very small fish, and its skull-roof very thin, such ridges can appear on the external surface of the skull-roof. The same is also true for the dome-shaped structure in the middle of the postpineal plate which (as described below) probably corresponds to the position of the posterior dorsal myodome for the superior oblique eye muscle.

The sensory-line grooves could be seen in all external molds and are best preserved in V10505.8. As a whole, the sensory lines of *M. lirouyii* are very similar to those of asterolepidoids and sinolepids. The infraorbital sensory-line grooves (io, Fig. 4) of both sides are more or less parallel. Anteriorly they turn medially onto the premedian plate, lining the anterior margin of the preorbital depression, but they never meet on the premedian plate. A pair of short V-shaped sensory-line grooves (so, Fig. 4) is present on the postpineal plate, as in some of the Yunnanolepidae and Chuchinolepidae (Tong-Dzuy and Janvier, 1990). This pair of grooves has been referred to as the postpineal sensory-line grooves by Tong-Dzuy and Janvier (1990). However, these grooves can be compared to the supraorbital canals in *Romundina* (Ørvig, 1975) which also are situated on the postpineal plate. Therefore, it is better to refer to the postpineal grooves of antiarchs as the supraorbital sensory-line grooves. The so-called "supraorbital sensory-line grooves" (Stensiö, 1948, followed by Miles, 1968 and most other authors,

TABLE 3. Measurements (in millimeters) of the head-shield distances in *Yunnanolepis chii* (after Zhang, G.-R., 1978).

	DE	EF	FG	DG	AA′	BB′	CC′	HH′	AB	BC
V4423.3	6.3	4.0	15.2	25.5	26.3	40.2	34.6	7.6	11.1	10.9
V4423.4	7.2	4.4	17.9	29.5	24.5	37.0	—	6.2	—	12.8
V4423.39	7.6	4.5	18.4	30.5	25.8	40.0	34.0	6.9	—	14.0
V4423.2	9.1	4.4	23.8	37.3	31.7	45.0	39.6	9.0	17.6	13.1
V4423.1	8.8	4.4	23.9	37.1	37.7	57.8	50.0	10.2	15.8	17.0

TABLE 4. Proportions (indices) of the head-shield in *Yunnanolepis chii* (partly after Zhang, G.-R., 1978).

	DG/ BB′	DE/ DG	EF/ DG	FG/ DG	DE/ FG	HH′/ BB′	AA′/ BB′	BC/ DG
V4423.3	63.4	24.7	15.7	59.6	41.4	18.9	65.4	42.7
V4423.4	79.7	24.4	14.9	60.7	40.2	16.8	66.2	43.4
V4423.39	76.3	24.9	14.8	60.3	41.3	17.3	64.5	45.9
V4423.2	82.9	24.4	11.8	63.8	38.2	20.0	70.4	35.1
V4423.1	64.2	23.7	11.9	64.4	36.8	17.6	65.2	45.8

except Stensiö, 1969) on the premedian plate of antiarchs are not homologous to the supraorbital lines of other placoderms, and should be given another name. Just in front of the posterior margin of the skull-roof, the so-called "middle pit-line groove" (mpl, Fig. 4), whose homology with that of other placoderms is also unclear, extends from the infraorbital sensory-line groove onto the nuchal plate. No central sensory-line groove is observed.

Neurocranium—Although no perichondral bone is preserved, the new material provides some information not only on the outline of the neurocranium, but also on its deeper structure, in particular in the occipital region. The fact that the internal cast of the neural canal and part of the brain cavity are preserved in some specimens is evidence for an endoskeletal component. The impression of the neurocranium of *Minicrania lirouyii* is preserved in the holotype V10505.1 (Fig. 2C) and several juvenile individuals (Figs. 2B, D, 3). It is a very thin and easily damaged structure. Its ventral surface is unknown, but some specimens show that the braincase is well preserved, particularly the occipital region, where the internal cast of the entire neural canal is visible (brcav, Fig. 3G2). In all specimens, the perichondral bone lamella which lines it internally and externally is no longer present. It is thus very important to make out the distinction between the filling of the cavities of the braincase (such as the brain cavity and neural canal, Fig. 3A, D, G) and the sediment which replaces the cartilage. The same kind of preservation of the neurocranium is seen in petalichthyids of the same bed (Zhu, 1991). The neurocranium of *M. lirouyii,* although incomplete, is the first record in antiarchs. Previously, the shape of the antiarch neurocranium had only been inferred from the shape of the otico-occipital depression. This is the impression left by the braincase on the visceral surface of the skull-roof, behind and lateral to the orbital fenestra. The shape of the preorbital recess is also instructive in restoring the antiarch neurocranium (Stensiö, 1948, 1969; Young, 1984a). Here, in addition to these impressions, there are also some traces of deeper, perichondrally ossified structures.

The preserved portion of the neurocranium impression (Figs. 6, 7) is mainly the part which extends behind the level of the orbital fenestra, and corresponds to the otico-occipital depression of the dermal skull-roof. On the dorsal surface of the neurocranium impression, a pair of semicircular ridges, caused by the large, underlying semicircular canals (rasc, rpsc, Figs. 3A, 6B), indicate the position of the otic region (asc, psc, Fig. 7). Among antiarchs, similar ridges occur in *Yunnanolepis* and *Bothriolepis,* as inferred from the pattern of the otico-occipital depression (Liu, 1963, pl.I-1; Zhang G.-R., 1978, pl.I-3; Stensiö, 1969; Young, 1984a). Since semicircular ridges on the dorsal surface of the neurocranium are seen in many other placoderms, e.g. actinolepids and petalichthyids (Liu, 1979; Goujet, 1984b; Zhu, 1991), this character can be regarded as plesiomorphic for antiarchs. The semicircular ridges in question occupy almost 2/5 of the skull-roof length. This large size of the semicircular canals should not be surprising, due to the small size of this species. As usual in fishes, the size of the labyrinth is not proportional to that of the entire animal, and small forms have a proportionally larger labyrinth. In the holotype are also seen a pair of endolymphatic tubes (dend, Figs. 2C, 3A, 6B) extending posteromedially from a paired swelling which probably contained the endolymphatic sacs (ends, Figs. 3A, 6, 7).

The anterior postorbital process (apopr, Fig. 6B) of *M. lirouyii* is more posteriorly placed than in *Bothriolepis* (Stensiö, 1948, 1969; Young, 1984, 1988; Long and Werdelin, 1986). In *Bothriolepis, Asterolepis* (Stensiö, 1969), and even *Yunnanolepis* (Liu, Y.-H., 1963), the visceral surface of the skull-roof shows a postorbital crest which bounds the anterior postorbital process of the braincase. In *M. lirouyii,* this dermal crest is weakly marked and extends just in front of the short anterior postorbital process of the braincase (dpor, Figs. 3A, 6A). Behind the anterior postorbital process, and lateral to the junction of the semicircular ridges, a slight lobe of the lateral wall of the braincase could represent the reduced posterior postorbital process (ppopr, Fig. 6B). More posteriorly, there is a pair of anterior and posterior supravagal processes (sva, svp, Figs. 3A, 6B; the "craniospinal processes" of Young 1984a).

On the dorsal surface of the neurocranial impression of the holotype, there are two symmetric sinuous lines (Figs. 2C, 3A), extending behind the orbital fenestra and between the semicircular ridges, which clearly delineate the area where the brain cavity (brcav, Fig. 3A) was directly overlain by the dermal skull-roof, without any intervening neurocranial roof. This area probably corresponds to a large median fontanelle in the braincase. These lines correspond to the position of the inner perichondral lamella (now absent) lining the brain cavity, and the outline of the dorsal part of the brain cavity in *M. lirouyii* can be inferred from their pattern. Although its actual outline remains unknown, the brain cavity seems to have been considerably broadened between the two anterior semicircular ridges, and slightly so between the two posterior semicircular canals (Fig. 7). A comparison with one of the best preserved placoderm brain cavities, that of the acanthothoracid *Brindabellaspis* (Young, 1980), suggests that the anterior swelling (cmet, Fig. 6B) corresponds to the position of the metencephalon (met, Fig. 7), and the posterior swelling (cmyc, Fig. 6B) to that of the myelencephalon (myc, Fig. 7). The latter portion of the brain cavity, or the subsequent neural canal, can be seen in section in the specimen V10505.46 (brcav, Fig. 3G2). Anterior to the area where the brain cavity is exposed, a pair of rounded domes (pdmy, Figs. 3A, 6B) occur just behind the orbital fenestra. A similar structure was present in *Bothriolepis canadensis* (Stensiö, 1948, 1969, fig. 41), as inferred from the paired fossae on the visceral side of the postpineal plate (Stensiö, 1969, fig. 138). Stensiö (1969) did not give any interpretation of these domes. They probably correspond to raised areas of the neurocranium which contained a pair of large, medially directed recesses in the posterior neurocranial wall of the orbital cavities, but certainly do not belong to the brain cavity. These paired raised areas of the neurocranium may correspond to the position of the posterior dorsal (or dorsal) myodome for the superior oblique eye muscle (mobls, Fig. 7). It is important to recall here that, contrary to all other gnathostomes, the superior oblique muscle in placoderms was attached in a dorsal, or posterodorsal myodome, much as in the Osteostraci (Goujet 1984b). Young (1986, p. 50), suggested that the anteriorly placed attachment of this extrinsic eye muscle is a synapomorphy of the crown-group gnathostomes (Chondrichthyes and Osteichthyes). Again, a comparison with *Brindabellaspis* shows that this myodome would occupy very much the same position in the latter if the orbits were more closely and dorsally placed, as in antiarchs. In the posterior part of the braincase, the two endolymphatic ducts (dend, Fig. 6B) arise from large, pear-shaped dorsal expansions which may represent some kind of endolymphatic sacs (ends, Fig. 6B), as in *Brindabellaspis.* The two ducts meet on the midline when reaching the skull-roof. The foramina for the

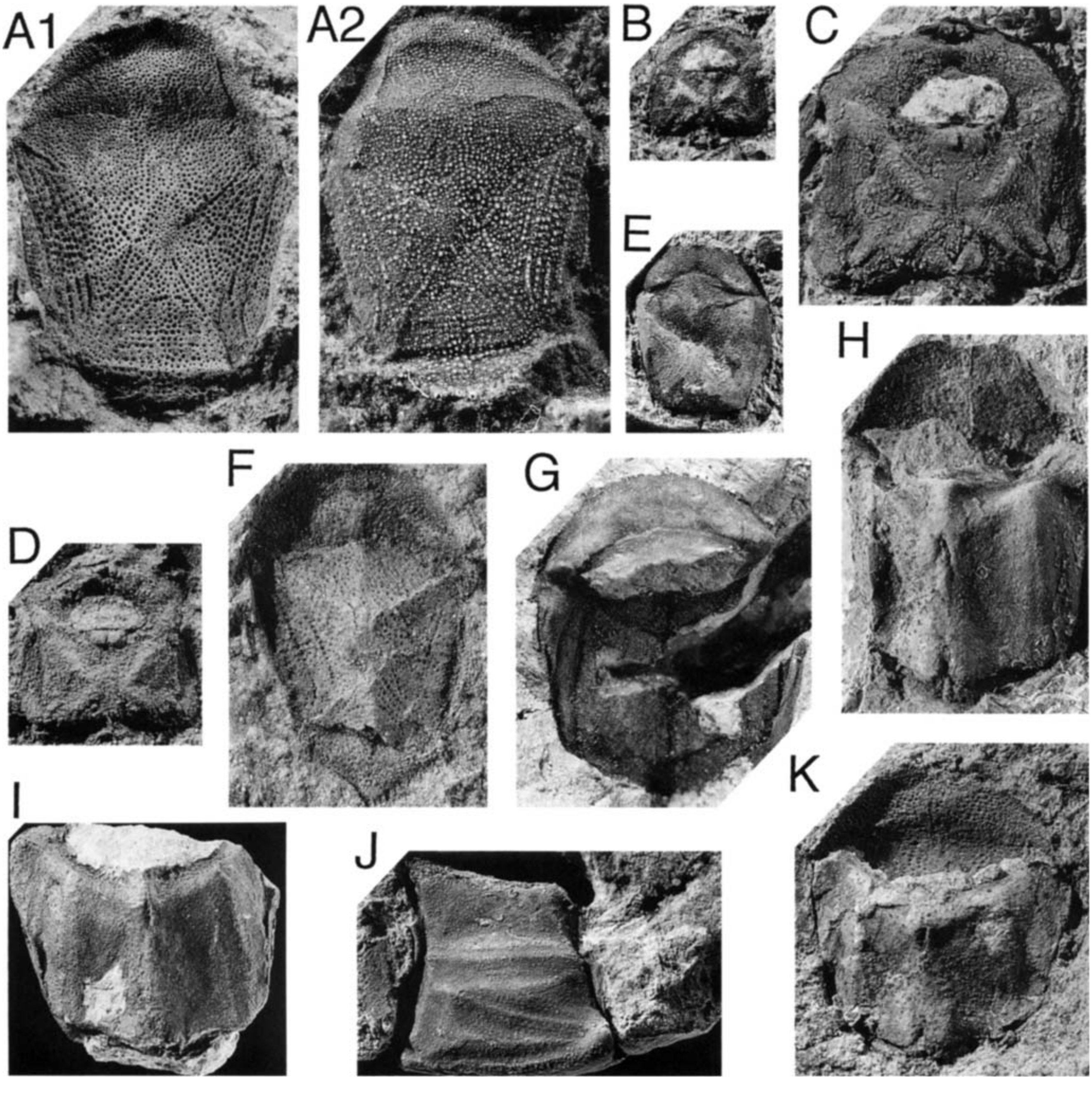

FIGURE 2. *Minicrania lirouyii,* gen. et sp. nov., Xishancun Formation, Early Devonian (Lochkovian), Qujing, Yunnan, China. **A**, natural external mold of the ventral wall of the trunk-shield (**A1**, V10505.17) and its elastomere cast (**A2**); **B**, internal mold of the skull-roof with the neurocranium impression in dorsal view, juvenile individual, V10505.5; **C**, internal mold of the skull-roof with the neurocranium impression in dorsal view, V10505.1 (holotype); **D**, internal mold of the skull-roof with the neurocranium impression in dorsal view, V10505.4; **E**, natural internal mold of the ventral wall of the trunk-shield, juvenile individual, V10505.26; **F**, natural external mold of the ventral wall of the trunk-shield, V10505.18; **G**, natural mold of the trunk-shield (internal cast anteriorly and external cast posteriorly), V10505.21; **H**, natural mold of the trunk-shield, in dorsal view (external cast anteriorly and internal cast posteriorly), V10505.19; **I**, natural internal cast of the trunk-shield in dorsal view, V10505.21; **J**, natural internal cast of the trunk-shield in lateral view, V10505.20; **K**, natural mold of the trunk-shield, in dorsal view (external cast anteriorly, internal cast posteriorly), V10505.15. (A, E–K, ×5; B–D, ×8.)

exit of the cranial nerves cannot be observed and may have been situated essentially on the ventral side of the braincase.

Anteriorly, the margin of the internal surface of the skull-roof is hollowed by a pair of medially placed pits (ap, Figs. 3A, 6A), which are also seen in the premedian plate of the Yunnanolepiformes and may receive either the palatoquadrate or, more likely, the suborbital plate (mental plate of Stensiö, 1948).

Trunk-shield—As in the skull-roof, the plates of the trunk-shield in *Minicrania lirouyii* are closely united, and all of the trunk-shields are intact. No individual plate of the trunk-shield is recorded in our material. Sutures can occasionally be ob-

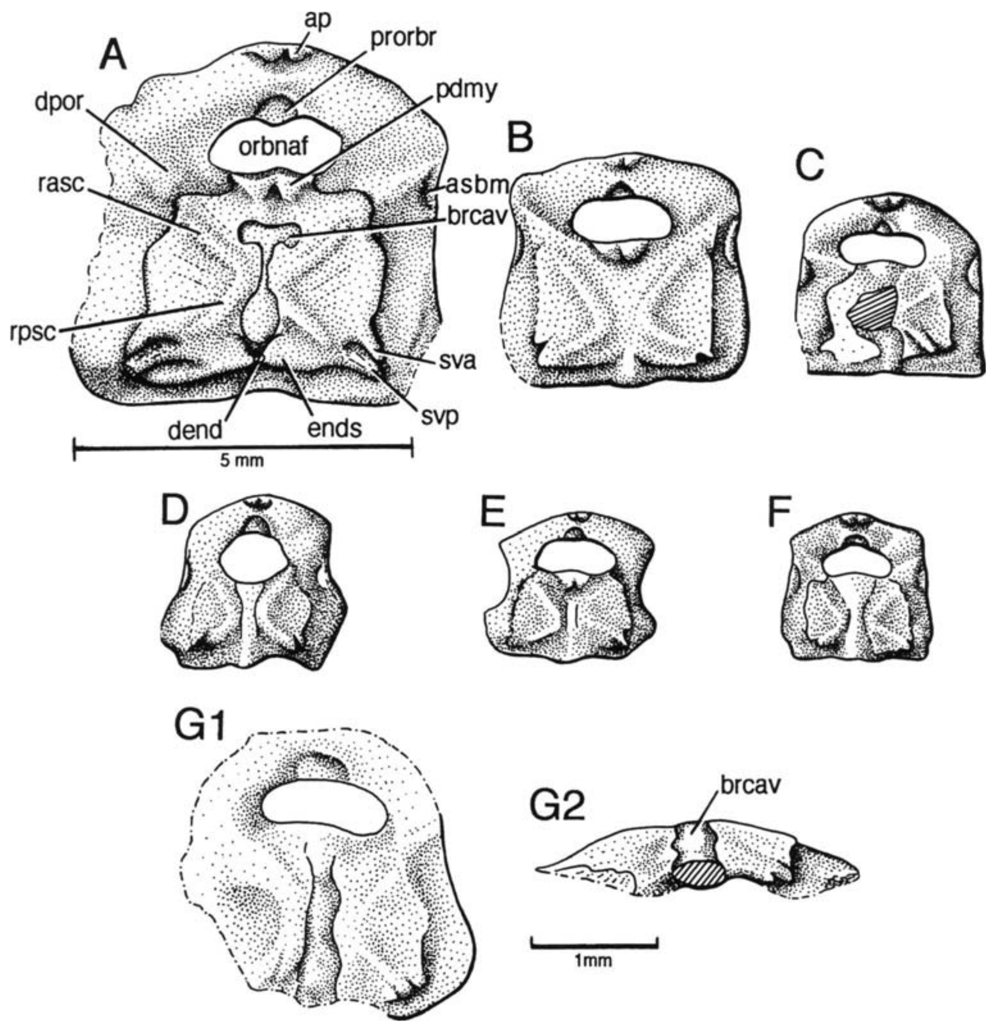

FIGURE 3. *Minicrania lirouyii,* gen. et sp. nov., internal molds of skull-roofs with neurocranium impression and parts of the neurocranial walls, showing the growth series; camera-lucida drawings in dorsal view (**A–G1**) and posterior view (**G2**). **A**, V10505.1 (holotype); **B**, V10505.4; **C**, V10505.7; **D**, V10505.6; **E**, V10505.3; **F**, V10505.9; **G**, V10505.46. **ap**, possible area for attachment of the suborbital plate; **asbm**, articular area for the submarginal plate; **brcav**, brain cavity; **dpor**, dermal postorbital depression; **ends**, cavity for the endolymphatic sac; **orbnaf**, orbital (orbitonasal) fenestra; **prorbr**, preorbital recess; **rasc**, anterior semicircular ridge; **rpsc**, posterior semicircular ridge; **sva**, **svp**, anterior and posterior supravagal processes.

served on the dorsal wall of the trunk-shield, and a small median ventral plate can be traced on the ventral wall in V10505.17 (Figs. 2A2, 8).

The trunk-shield of *M. lirouyii* exhibits a simple pectoral fenestra, which is similar to that of *Yunnanolepis* (Zhang, G.-R., 1978; Zhang, M.-M., 1980), and indicates a simple pectoral fin articulation. Except for this character, it resembles somewhat the trunk-shield of *Microbrachius* (Hemmings, 1978; Pan, 1984). In dorsal view, the trunk-shield is more or less short and broad (Figs. 2G–I, K, 9A). The median dorsal ridge (mdr, Fig. 4) extends as a distinct ridge from the tergal angle to the posterior angle which is produced posterodorsally into a short pointed process. On both sides of the median ridge, from the tergal angle to the posterior angle, there exist a pair of medial ridges (mr, Fig. 4). Anterior to the tergal angle, the dorsal wall slopes gently toward the anterior margin of the shield. Since the dorsolateral ridge (dlr, Fig. 4) has a relatively medial position, the ventral wall of trunk-shield is much wider than the dorsal wall (Fig. 10B). The main lateral-line groove (mll, Fig. 4) runs along the lateral wall below the dorsolateral ridge, and is also lined with a ridge or a row of larger tubercles (Fig. 9A). In ventral view, the ventral wall is flat and extends further anteriorly than the dorsal wall (Figs. 2A, 5D–G, 9, 10A, 11). The length of the ventral wall is about 1.5 times that of the dorsal wall.

The plesiotype V10505.2 (Fig. 5C) shows a skull-roof associated with—but not articulated to—the trunk-shield (the latter is turned on the ventral side and rotated by 90° relative to the skull-roof). If we assume that these two elements belong to the same individual, then the ventral wall of the trunk-shield is about 2.2 times as long as the skull-roof. In correspondence with the length range of the preserved skull-roofs (between 2.2 mm and 5.6 mm) the length of the ventral wall of the preserved trunk-shields (more than 30 in number) ranges from 5 mm to 14 mm. This evidence suggests that the holotype skull-roof, which is about 5.6 mm long, is an adult specimen.

The crista transversalis interna anterior (ctra, Fig. 8B) is developed dorsally and meets the articular fossae (Fig. 10B). The anterior ventral process (pra, Fig. 8) of the anterior median dorsal plate is situated anterior to the geometric center of the plate, but posterior to the tergal angle. The crista transversalis interna posterior (ctrp) is aligned internally with all the poste-

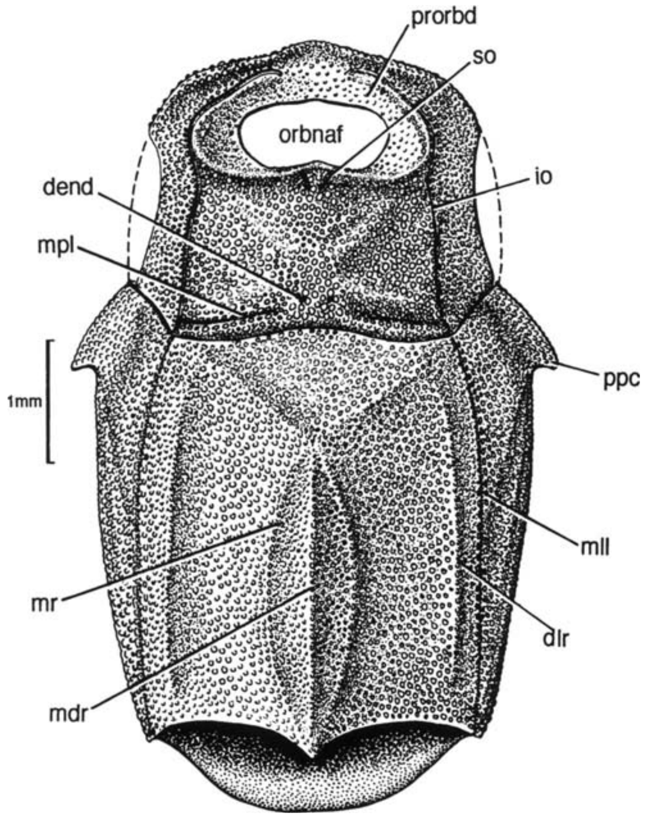

FIGURE 4. *Minicrania lirouyii,* gen. et sp. nov., reconstruction of the dermal armor (skull-roof and trunk-shield) in dorsal view, based on the largest specimens (supposedly adult). **dend**, external opening of endolymphatic duct; **dlr**, lateral dorsolateral ridge; **io**, infraorbital sensory-line groove; **mdr**, median dorsal ridge; **mll**, main lateral-line groove; **mpl**, middle pit-line groove; **orbnaf**, orbital (orbitonasal) fenestra; **mdr**, median dorsal ridge; **mr**, medial dorsolateral ridge; **ppc**, prepectoral corner; **prorbd**, preorbital depression; **so**, supraorbital sensory-line groove.

rior plates of the trunk-shield, as in other antiarchs. Dorsally, the crista transversalis interna posterior lies lateral to the posterior ventral process (prp, Fig. 8A). Between the anterior and posterior ventral processes, a median ventral groove is visible on the internal surface of the anterior and posterior median dorsal plates.

The ornamentation of the trunk-shield (Figs. 5C–G, 9), like that of the skull-roof (Fig. 5A–C), consists of large, closely-set tubercles (Figs. 5C–G, 9), with some tiny tubercles in between. Along the ridges on the trunk-shield (mdr, mr, dlr, Fig. 4), the tubercles are a little larger than those of the rest of the surface, and sometimes spine-shaped in the smallest individuals (Fig. 9B). The tubercles in the anterior part of the median dorsal ridge of the anterior median dorsal plate are also slightly larger (Fig. 9A).

The anterior median dorsal plate (AMD, Fig. 8A) is roughly hexagonal in shape. Its anterior margin is a little broader than its posterior margin, and the anterolateral margin is a little longer than the posterolateral one. The plate reaches its maximum height at the level of the tergal angle, which has a relatively anterior position. In front of the tergal angle the plate slopes anteroventrally. The medial dorsal ridge in the mid-line, and the two medial dorsolateral ridges on both sides, extend posteriorly from the tergal angle to the posterior angle. Internally, the anterior ventral process (pra, Figs. 2H–I, K, 8A) lies between the levels of the tergal angle and the geometric centre of the plate.

The posterior median dorsal plate (PMD, Fig. 8A) is relatively large and broad. The medial dorsal ridge extends posteriorly and dorsally to form a spine-shaped posterior angle (Fig. 11). The median dorsolateral ridges on both sides converge posteriorly toward the posterior angle. Internally, the large posterior ventral process (prp, Fig. 8A) is situated on the crista transversalis interna posterior (ctrp, Figs. 2H–I, K, 8A).

Since no suture is observed between the anterolateral plate (ADL, Fig. 8A) and the adjoining plates (except the anterior median dorsal plate) the precise shape of the ADL plate is unknown. The same applies to the posterior dorsolateral (PDL, Fig. 8) and posterior lateral plates, and most plates of the ventral trunk-shield wall (AVL, PVL and semilunar plates). The broad lateral division of the crista transversalis interna anterior of the ADL plate is clearly seen ventral to the transverse articular fossa (af, ctra, Figs. 9A, 10B), which is lateral to the anterior margin of the AMD plate. On the lateral wall of the AVL plate, there is a pectoral fenestra which is suggestive of that of *Yunnanolepis* (Zhang G.-R., 1978; Zhang M.-M., 1980). The prepectoral corner (ppc, Fig. 4), which is reminiscent of the spinal plate of other placoderms, borders the pectoral fenestra. In fact, the prepectoral corner is a small tubular structure, filled with the endoskeletal prepectoral process as in arthrodires and petalichthyids (Stensiö, 1963).

Ventrally, the trunk-shield is relatively flat and about 1.5 times longer than broad. In external view, a small diamond-shaped median ventral plate (MV, Fig. 8B) can be inferred from the distribution of the tubercles. Except for this plate, practically no other can be delineated. Noteworthy are two short sensory-line grooves seen on the ventral wall of trunk-shield (all, Figs. 2A, 5G, 8B, 10A). These grooves, termed here as anterolateral lines, lie just behind the corresponding position of the crista transversalis interna anterior and extend posteromedially, and a similar groove was observed in *Chuchinolepis dongmoensis* (Tong-Dzuy and Janvier, 1990). Whether these lines are the anterior ventral transverse pit-line or sensory-line groove of other placoderms is unclear. The trunk-shield extends far anteriorly in front of the crista transversalis interna anterior, whereas the crista transversalis interna posterior lies very close to the posterior limit of the trunk-shield. Anterior to the crista transversalis interna anterior, there is a slight transverse elevation in the floor of the trunk-shield, which may correspond to the postbranchial lamina of most other antiarchs, as in *Yunnanolepis* (Zhang M.-M., 1980; Janvier and Pan, 1982).

DISCUSSION

Allometric Growth of the Skull-roof of *Minicrania lirouyii*

Since only 14 skull-roofs were found and only 11 of these could provide us with measurements, no allometric equation could be obtained. Nevertheless, because these 14 specimens form a relatively continuous growth series, an analysis of allometric growth of the skull-roof could still be attempted, however inconclusive it may be given the small sample.

As stated above, the holotype V10505.1 (5.6 mm in length) may be regarded as an adult specimen while the others are younger or even juvenile ones. Moreover, the ventral wall of the trunk-shield was about 2.2 times as long as the skull-roof. Among all of the trunk-shield specimens (over 30), the largest one (V10505.16, Fig. 5E), which we postulate here to be an adult, is about 14 mm ventrally. Its corresponding skull-roof should be about 6.4 mm in length, that is, just a little larger than V10505.1, assuming the index in the plesiotype V10505.4 (Fig. 5C) could be used as a reference for the adult size. Moreover, in the same bed we found a fairly small skull-roof, about

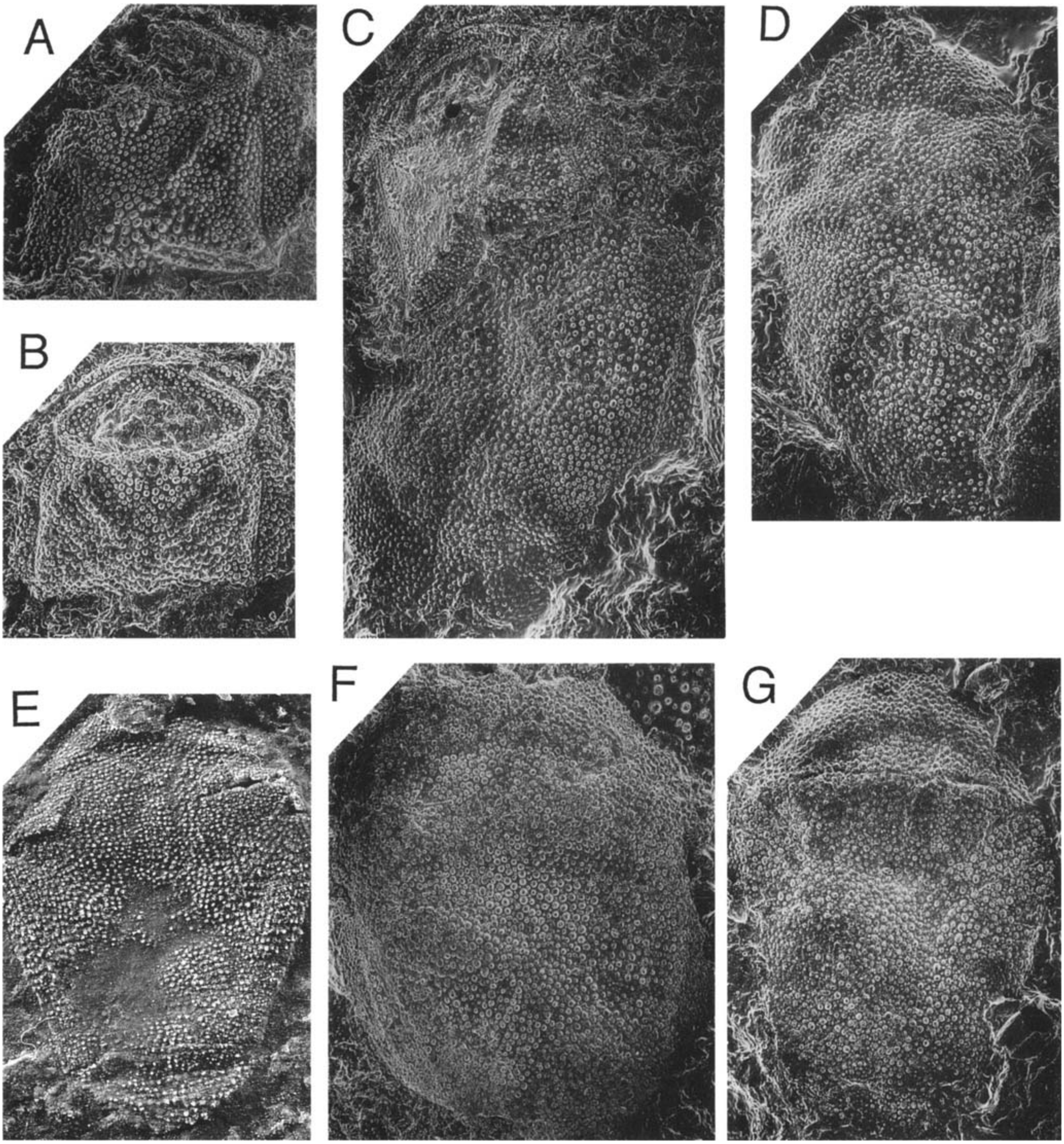

FIGURE 5. *Minicrania lirouyii,* gen. et sp. nov., scanning electron microscope photographs of elastomere casts, unless indicated otherwise. **A–B**, skull-roofs in dorsal view, ×20 (**A**, V10505.11; **B**, V10505.10); **C**, skull-roof in dorsal view, associated with the trunk-shield in ventral view, V10505.2, ×15; **D–G**. ventral surface of trunk-shield (**D**, V10505.29, ×15; **E**, V10505.16, light transmission photograph, ×5, **F**, V10505.44, ×15; **G**, V10505.45, ×15).

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7 mm long, which has been assigned to *Yunnanolepis* (Zhu, in press). Comparing V10505.1 with this *Yunnanolepis* specimen, we find very different proportions between them, thereby ruling out the possibility that *M. lirouyii* is a juvenile stage of *Yunnanolepis* or any other yunnanolepid.

With respect to growth patterns, the following results should be considered.

1) The skull-roof of *Minicrania lirouyii* grows isometrically with respect to the index between the skull-roof length and width.
2) Relative to the maximum skull-roof length, the postorbital distance grows isometrically. In the Yunnanolepidae and Chuchinolepidae, the index FG/DG is comparatively constant (about 60).

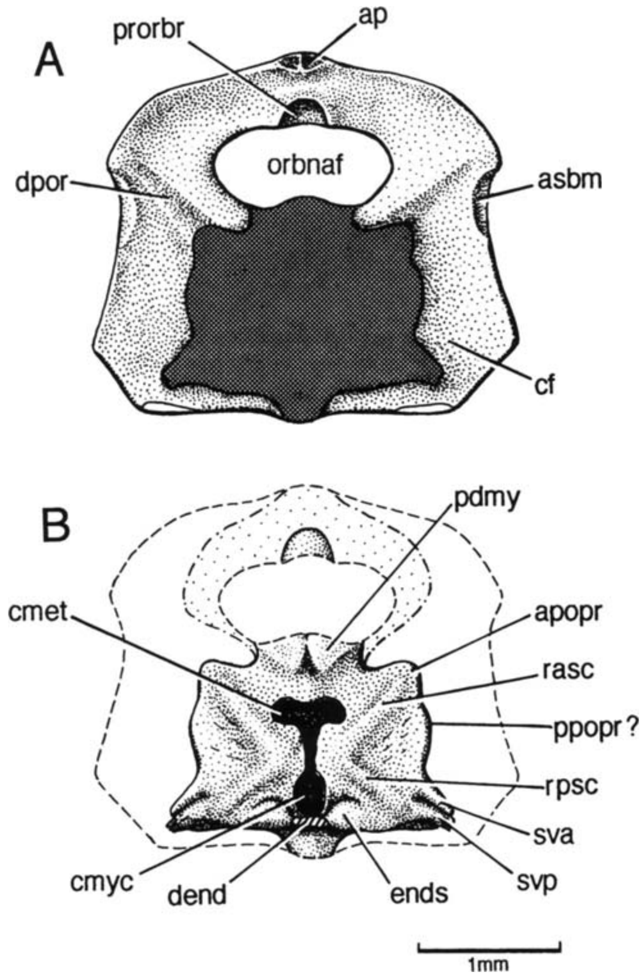

FIGURE 6. *Minicrania lirouyii,* gen. et sp. nov., **A**, reconstruction of the skull-roof in visceral view, position of the neurocranium in grey; **B**, reconstruction of the neurocranium in dorsal view (essentially based on the holotype, outline of the skull-roof in dashed line and unknown, anterior part of the neurocranium stippled). **ap**, possible attachment area for the suborbital plate; **apopr**, anterior postorbital process; **asbm**, articular area for the submarginal plate; **cf**, cucullaris fossa; **cmet**, metencephalic cavity; **cmyc**, myelencephalic cavity; **dend**, external opening of endolymphatic duct; **dpor**, postorbital depression; **ends**, endolymphatic sac; **orbnaf**, orbital (orbitonasal) fenestra; **pdmy**, elevation corresponding to the position of the posterior dorsal myodome in the neurocranium; **ppopr**?, presumed posterior postorbital process; **prorbr**, preorbital recess; **rasc**, ridge caused by anterior semicircular canal; **rpsc**, ridge caused by posterior semicircular canal; **sva**, **svp**, anterior and posterior supravagal processes.

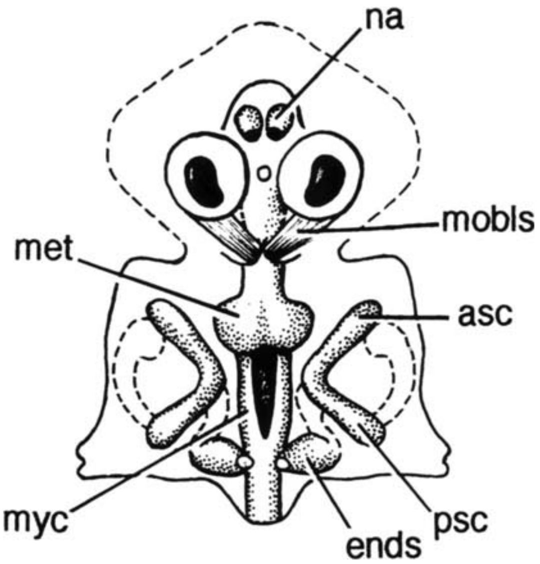

FIGURE 7. *Minicrania lirouyii,* gen. et sp. nov., attempted reconstruction of the soft anatomy of the brain and sensory capsules. **asc**, anterior semicircular canal; **ends**. endolymphatic sac; **met**, metencephalon; **mobls**, superior oblique eye muscle; **myc**, myelencephalon; **na**, nasal cavity; **psc**, posterior semicircular canal.

3) The orbital fenestra grows allometrically (negative allometry), either in length or width. In general, the orbit got proportionally smaller during the growth of the skull-roof. In antiarchs, a negative allometric growth of the orbital fenestra was recorded in *Bothriolepis canadensis* (Werdelin and Long, 1986).
4) The preorbital distance (the length of the premedian plate) was proportionally shorter in the juvenile skull-roof than in the adult. This trend is consistent with that observed in *Bothriolepis canadensis* (Werdelin and Long, 1986). This indicates that during the growth of the skull-roof, the orbital fenestra became more and more dorsal in position. A short premedian plate is assessed as plesiomorphic for antiarchs, by comparison with their presumed out-group, the acanthothoracids, and this seems to be supported by the fact that it is also a juvenile feature.

Re-appraisal of several antiarch characters

Preorbital Depression and Preorbital Recess—The problem of the homology between the preorbital depression and the preorbital recess in antiarchs has been discussed by Janvier and Pan (1982), Long (1983), Young (1984a, b, 1988), Long and Werdelin (1986). A related problem is the position of the nasal capsules in the Yunnanolepidae and other antiarchs which retain the preorbital depression (Chuchinolepidae, Sinolepidae, *Wudinolepis* and perhaps *Microbrachius*).

Janvier and Pan (1982) proposed that the preorbital depression is homologous to the preorbital recess. Meanwhile, they did not consider the hypothesis that the preorbital depression housed the rhinocapsular cartilage as does the preorbital recess. On the contrary, Young (1984a) suggested that the preorbital depression was the site of the rhinocapsular cartilage. However, according to this author, the preorbital depression could not have evolved into a preorbital recess. Until now, there has been no consensus on this issue.

New evidence in *Minicrania lirouyii* indicates that the preorbital depression cannot be homologous to the preorbital recess, and that the preorbital depression is not a plausible site for the rhinocapsular cartilage. In *M. lirouyii,* there is a small triangular preorbital recess which co-exists with a large preorbital depression which is similar to that of the Yunnanolepiformes. This is direct evidence against the homology between the preorbital depression and the preorbital recess [Patterson's (1982) "conjunction test"]. It is noteworthy that a similar condition, i.e., the co-existence of a preorbital depression and a preorbital recess, seems to occur in the Sinolepidae *Grenfellaspis* (Ritchie et al., 1992:fig. 5A, B), where the preorbital recess is, however, long and narrow.

The ornamentation on the preorbital depression has been a controversial problem. The tubercles on the floor of the preorbital depression in *Yunnanolepis* were mentioned by Zhang G.-R. (1978), Zhang M.-M. (1980), Janvier and Pan (1982) and,

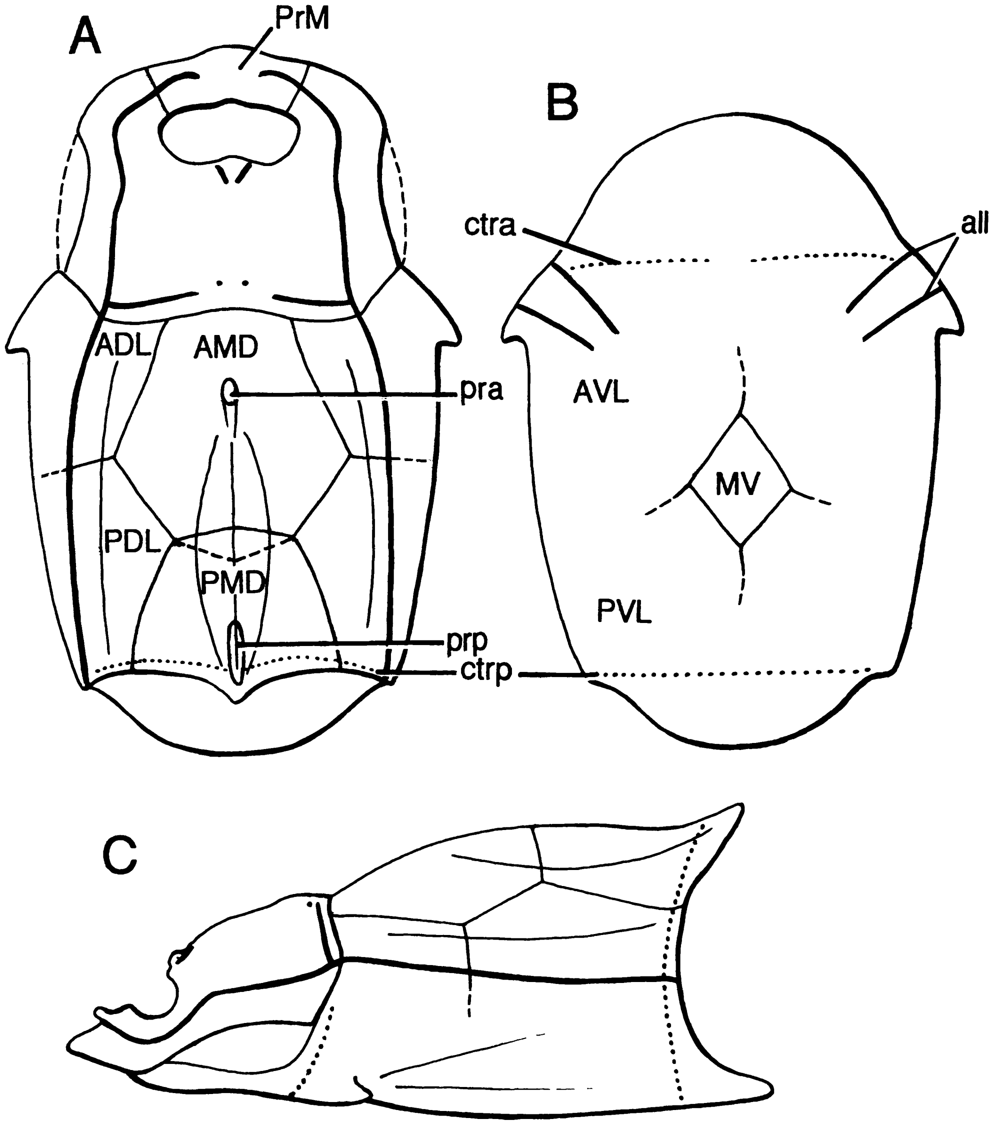

FIGURE 8. *Minicrania lirouyii,* gen. et sp. nov., reconstruction of the dermal armour (skull-roof and trunk-shield), based on several large specimens of approximately similar size, in dorsal (**A**), ventral (**B**) and lateral (**C**) views, and showing some sutures and the relative position of some internal structures; not to scale. **all**, anterolateral sensory-line grooves; **ADL**, anterior dorsolateral plate; **AMD**, anterior median dorsal plate; **AVL**, anterior ventrolateral plate; **ctra**, crista transversalis interna anterior; **ctrp**, crista transversalis interna posterior; **MV**, median ventral plate; **PDL**, posterior dorsolateral plate; **PMD**, posterior median dorsal plate; **pra**, anterior ventral process of the dorsal wall of trunk-shield; **PrM**, premedian plate; **prp**, posterior ventral process of the dorsal wall of trunk-shield; **PVL**, posterior ventrolateral plate.

Long and Werdelin (1986), but Young (1984a) rejected this conclusion on the basis of his personal observations on specimens in the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing. According to Young (1984a), in *Y. chii* the preorbital depression is smooth in the region of the premedian plate which he thought was suitable for the housing of the rhinocapsular cartilage. The situation in *Y. parvus* was less apparent because of its small size (Young, 1984a). However, even though the skull-roof of *M. lirouyii* is very small, the tubercles on the whole of the preorbital depression are fairly clear (Fig. 5A, B) and are nearly the same size as those on the other part of the skull-roof. Therefore, as Janvier and Pan (1982), and Long and Werdelin (1986) argued the preorbital depression certainly did not house any endoskeletal element.

Since the preorbital recess co-exists with the preorbital depression in *Minicrania lirouyii,* the position of the nasal capsule in antiarchs which possess the preorbital depression becomes less controversial. Zhang M.-M. (1980) proposed that nasal capsules in *Yunnanolepis* had a ventral position, beneath the premedian plate, which is consistent with the condition in *M. lirouyii.* The other related problem is the source and fate of the preorbital depression in antiarchs. Janvier and Pan (1982) suggested that the preorbital depression in antiarchs might possibly be homologous to the depression in the "median prerostral plate" (=premedian plate) of *Romundina* (Ørvig, 1975). If, as suggested by Goujet (1984a), antiarchs are the sister group of *Romundina* + *Brindabellaspis* + *Palaeacanthaspis,* then it is most likely that the preorbital depression in antiarchs derives from the depression in the premedian plate of *Romundina* (Janvier and Pan, 1982). The subsequent conclusion would be that the preorbital depression is plesiomorphic for antiarchs. As to its function, it may be envisaged that it served initially in sur-

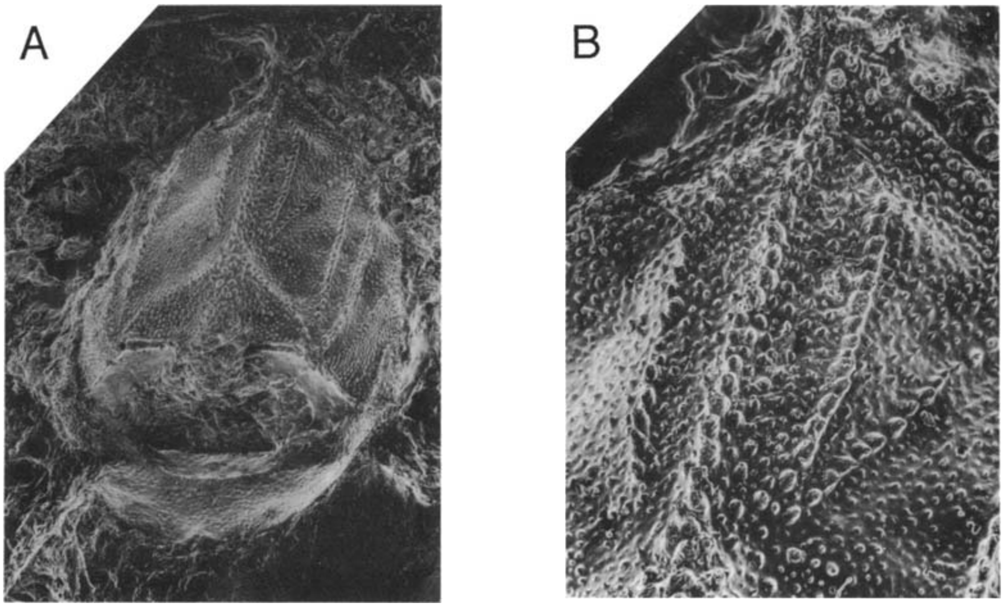

FIGURE 9. *Minicrania lirouyii,* gen. et sp. nov., scanning electron microscope photograph of an elastomere cast of the trunk-shield in anterodorsal view, V.10505.40. **A**, general view (×15); **B**, detail of the posterior part of the dorsal part of the trunk-shield (×45), showing an additional oblique ridge on the left side.

rounding the nostrils and protecting them from being invaded by sand or mud, given that these animals are thought to have had a benthic mode of life. In higher antiarchs, this depression is lacking since the nostrils are situated higher on the top of the head. In the latter, the preorbital depression no longer represented a significant advantage.

In contrast, by outgroup comparison with yunnanolepiforms, it is reasonable to assume that the preorbital recess is an apomorphy at a certain level of antiarch phylogeny. As will be discussed below, the Chuchinolepidae might be the sister group of the Yunnanolepidae. Since we can not find any synapomorphy shared only by euantiarchs on the one hand and the Yunnanolepiformes (Yunnanolepidae + Chuchinolepidae) on the other, we regard the preorbital recess as a synapomorphy shared by *Minicrania lirouyii* and euantiarchs, but possibly lost in the Sinolepidae and, among euantiarchs, the Microbrachiidae (the latter are included in the Bothriolepidoidea in the cladogram of Fig. 12).

Orbital Fenestra and Suborbital Fenestra—This problem is related to that of the homology of the preorbital depression. If the preorbital depression housed the rhinocapsular cartilage, as suggested by Young (1984a), the orbital fenestra of *Yunnanolepis chii* was indeed homologous to the suborbital fenestra of *Bothriolepis* (i.e., the fenestra at the level of the floor of the preorbital recess), and the orbital fenestra in various antiarchs with a preorbital depression was thus misnamed. This comparison could be traced back to Liu (1963) and was followed by Werdelin and Long (1986) and Ritchie et al. (1992). One of Young's (1984a) arguments is that the small size of the orbital fenestra in *Yunnanolepis* prevents the nasal capsules from lying beneath it. In our opinion, the nasal capsules could have been situated below the premedian plate and they did not have a direct bearing on the size of the orbital fenestra which is only large enough to have housed the eyeballs and the nasal tubes. Moreover, the small size of the orbital fenestra in *Yunnanolepis* is likely to be unique to this genus. In *Minicrania lirouyii,* the orbital fenestra is a comparatively large space (by comparison to other Early Devonian antiarchs), and, as suggested by the growth series of various antiarchs, a larger orbital fenestra is often a juvenile feature and therefore may be regarded as plesiomorphic for antiarchs. Since the preorbital recess is found in *M. lirouyii,* which retains the preorbital depression, a direct comparison between *Minicrania* and *Bothriolepis* could be made. It is concluded that the orbital fenestra was correctly named in Zhang G.-R. (1978) and in Janvier and Pan (1982).

The enlarged orbital fenestra had been used as a character to define the Asterolepidoidea (Young, 1984b, 1988). As suggested above, the moderatedly large orbital fenestra is here considered as plesiomorphic and the small orbital fenestra in *Yunnanolepis chii* apomorphic, as is probably the very large fenestra of some asterolepidoids. However, the large orbital fenestra in asterolepidoids cannot be regarded as a synapomorphy of this taxon as a whole.

Shape of the Skull-roof and Lateral Plate—Janvier and Pan (1982) considered the narrow lateral plate to be a synapomorphy of the Asterolepidoidea. Among them, *Stegolepis jugata* (Malinovskaya, 1973) was regarded as the most generalized form because it retains relatively broad lateral plates (Janvier and Pan, 1982, p. 383; see also Pan et al., 1987). Their argument was that the broad lateral plate was present in the Yunnanolepiformes, Bothriolepidoidea and *Sinolepis* (Liu and P'an, 1958). The shape of the lateral plate has a direct bearing on the shape of the skull-roof. In the Asterolepidoidea, the skull-roof is more or less narrow and elongated, whereas the skull-roof is broad and short in the Bothriolepidoidea, Yunnanolepidae, Chuchinolepidae and some sinolepids which possess a broad lateral plate. In fact, the shape of the skull-roof and lateral plate in the Yunnanolepidae, which were regarded as the primitive antiarchs at that time, had a major influence on the decision for the polarity of this character. However, when we compare antiarchs with acanthothoracids, it is clear that the long and narrow skull-roof, as in *Minicrania,* should be regarded as plesiomorphic. In contrast, if arthrodires are regarded as the sister-group of antiarchs, then a broad skull-roof is likely to be the general condition for the latter. The precise shape of the lateral plate in *Minicrania* is unknown at present, but from the sutures between the premedian and lateral plates, the posterior position of the posterolateral corner of the skull-roof and the

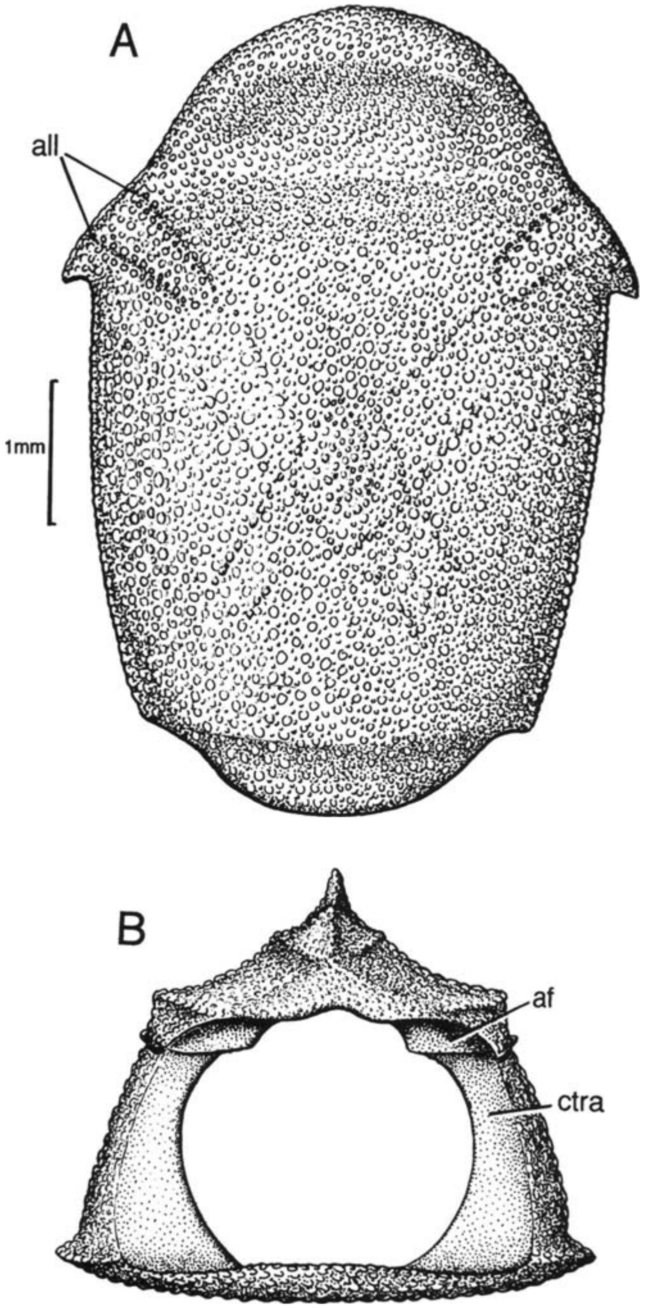

FIGURE 10. *Minicrania lirouyii,* gen. et sp. nov., reconstruction of the trunk-shield, based on the largest specimens (supposedly adult), in ventral (**A**) and anterior (**B**) views. **af**, articular fossa on ADL plate; **all**, anterolateral sensory-line grooves; **ctra**, crista transversalis interna anterior.

shape of the skull-roof, we can reasonably say that it is long and narrow as in asterolepidoids. Consequently, in light of the new information provided by *Minicrania* a re-analysis on the interrelationships of asterolepidoids is needed.

Anterior Margin of the Anterior Median Dorsal Plate—The anterior margin of the anterior median dorsal plate has been used as one of the important characters in cladistic analyses of antiarch phylogeny. Young (1984b, 1988) suggested the broad anterior margin of the anterior median dorsal plate was a synapomorphy of bothriolepidoids. Zhang and Young (1992) argued that, during bothriolepidoid evolution, the anterior margin of the AMD plate became broader and broader. Their main argument was that the primitive antiarch *Yunnanolepis* had an anteriorly pointed AMD plate. A similar idea was proposed by Ritchie et al. (1992, fig. 34) in an analysis of the interrelationships of the Sinolepidae. They also argued this point on stratigraphical grounds, i.e. that all known Early Devonian antiarchs, and most Middle Devonian taxa, have a narrow anterior margin of the AMD plate. However, if outgroup comparison is used, the conclusion reached is just the contrary. In all other placoderms, such as actinolepids, petalichthyids, or acanthothoracids, the median dorsal plate has a broad anterior margin. However, there remains a doubt as to the homology between the latter and the AMD plate of antiarchs. None the less, the criterion of outgroup comparison should be preferred to the stratigraphical argument. However, before the discovery of *Minicrania lirouyii,* the conclusion based on outgroup comparison was not supported by the then presumed most primitive antiarchs, i.e., the Yunnanolepiformes.

In addition, there may be ontogenetic evidence for the primitiveness of the broad anterior margin of the AMD plate. The AMD plate in the juvenile specimens of *Asterolepis* described by Upeniece and Upenieks (1992), clearly has a broad anterior margin which makes it resemble that of bothriolepidoids.

Since *Minicrania* possesses a broad anterior margin of the AMD plate as well as yunnanolepiform-like brachial articulation, the argument of Zhang and Young (1992) is no longer valid. It is suggested here that the anteriorly pointed anterior margin of the Yunnanolepidae and Chuchinolepidae is a derived character, and the same character occurs in some asterolepidoids (e.g., *Asterolepis, Remigolepis*) by homoplasy. Clearly, the character assemblage of *Minicrania lirouyii,* implies a reconsideration of antiarch phylogeny.

Phylogenetic position of *Minicrania lirouyii* and interrelationships of antiarchs

Comparing *Minicrania lirouyii* and *Yunnanolepis* the similarities include:

1. Simple pectoral fin joint.
2. Large triangular to oval preorbital depression, extending over the premedian and lateral plates.
3. Semicircular ridges of neurocranium caused by semicircular canals.
4. Premedian plate short, orbital fenestra relatively anterior in position.
5. Anterior ventral process of the AMD plate situated at midway between the anterior and posterior margins of the plate.

We suggest that all the similarities cited above are symplesiomorphies for antiarchs, and do not define a group including *M. lirouyii* and *Yunnanolepis.* Differences include:

6. The skull-roof of *M. lirouyii* is more or less square-shaped, whereas that of *Yunnanolepis* is short and broad.
7. The anterior margin of the AMD plate of *M. lirouyii* is broad, and that of *Yunnanolepis* pointed.
8. The skull-roof and trunk-shield bones are closely fused in *M. lirouyii,* whereas the sutures are clearly visible in *Yunnanolepis.*
9. The crista transversalis interna posterior is lateral to the posterior ventral process of the PMD plate in *M. lirouyii,* and posterior to it in *Yunnanolepis.*
10. The dorsal wall of the trunk-shield is much shorter than the ventral wall in *M. lirouyii,* whereas in *Yunnanolepis* the dorsal wall is only a little shorter than the ventral wall.
11. The preorbital recess is present in *M. lirouyii,* and absent in *Yunnanolepis.*

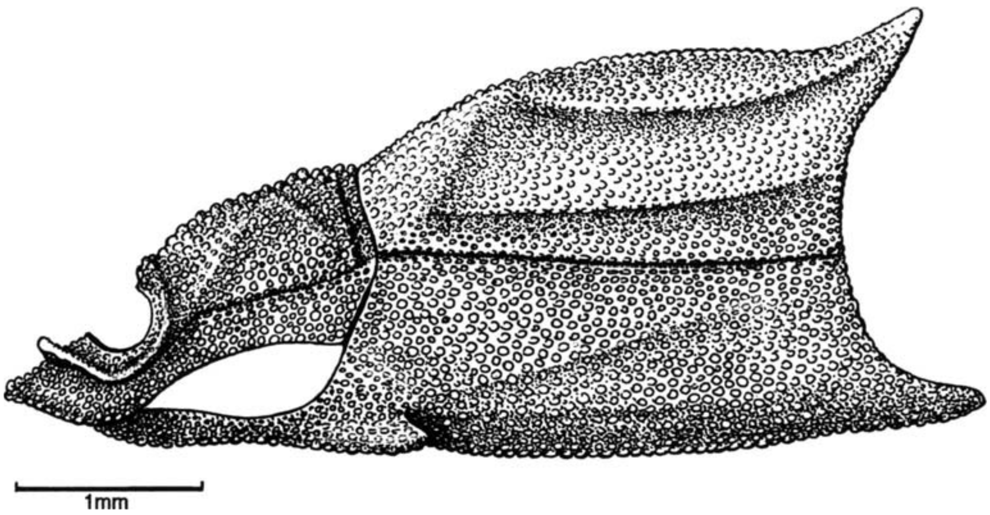

FIGURE 11. *Minicrania lirouyii,* gen. et sp. nov., reconstruction of the dermal armor (skull-roof and trunk-shield) in lateral view, based on the largest specimens (Presumably adult). The suborbital, gnathal and cheek plates are unknown to date.

12. The obstantic margin of *M. lirouyii* is short, whereas that of *Yunnanolepis* is long.
13. The infraorbital groove does not extend anteriorly to the skull-roof margin in *Minicrania lirouyii,* whereas in *Yunnanolepis,* this groove gives off a branch toward the shield margin.
14. The orbital fenestra of *M. lirouyii* is large, whereas that of *Yunnanolepis* is small. (although this is true of *Y. chii,* this is not the case in *Y. parvus*).

By outgroup comparison, the long and narrow skull-roof and the broad anterior margin of the AMD plate in *M. lirouyii* should be assessed as plesiomorphic, as discussed above. The close fusion of the plates of the skull-roof and trunk-shield is likely to be apomorphic for this genus. In some outgroups, such as actinolepids, phlyctaeniids, petalichthyids and acanthothoracids, the bones of the skull-roof are in general closely fused, and it is difficult to identify the sutures, but those of the thoracic armor remain well separated, except in phlyctaeniids, where it may also be a derived condition. As to other differences, since there is no possibility of clear-cut outgroup comparison, the polarities remain ambiguous.

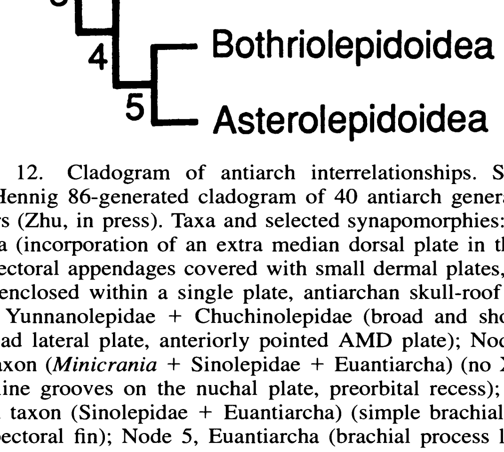

FIGURE 12. Cladogram of antiarch interrelationships. Simplified from a Hennig 86-generated cladogram of 40 antiarch genera and 66 characters (Zhu, in press). Taxa and selected synapomorphies: Node 1, Antiarcha (incorporation of an extra median dorsal plate in the trunk-shield, pectoral appendages covered with small dermal plates, pectoral fenestra enclosed within a single plate, antiarchan skull-roof pattern); Node 2, Yunnanolepidae + Chuchinolepidae (broad and short skull-roof, broad lateral plate, anteriorly pointed AMD plate); Node 3, unnamed taxon (*Minicrania* + Sinolepidae + Euantiarcha) (no X-shaped sensory-line grooves on the nuchal plate, preorbital recess); Node 4, unnamed taxon (Sinolepidae + Euantiarcha) (simple brachial process, jointed pectoral fin); Node 5, Euantiarcha (brachial process large and helmet-shaped, crista transversalis interna posterior situated behind the posterior ventral process of the PMD plate, short postorbital part of the skull-roof).

Paraphyly or Monophyly of the Yunnanolepiformes—The taxon Yunnanolepiformes was erected by Zhang G.-R. (1978), mainly on the basis of two plesiomorphic antiarch characters: the preorbital depression extending over the premedian and lateral plates, and the simple pectoral fin articulation (no brachial process). Its monophyly was questioned by Janvier and Pan (1982) and Young (1984b), since there was no clear synapomorphy to define this group, even though for operational reasons it was considered as monophyletic by various authors (Zhang, 1984; Pan et al., 1987; Tong-Dzuy and Janvier, 1990). On this basis, *Minicrania* would be referred to as one of the Yunnanolepiformes. *Zhanjilepis* (Zhang G.-R., 1978) is likely to be related to the Yunnanolepidae as it holds an anteriorly pointed AMD plate, but since there is no information about its skull-roof, its phylogenetic position is difficult to assess. Moreover, the Chuchinolepidae are removed from the Yunnanolepiformes since they have been proved to be procondylolepiforms (Tong-Dzuy and Janvier, 1990; Zhu, in press) in possessing a derived pectoral fin articulation.

From the comparisons above, we know that there exist important differences between *Minicrania* and the Yunnanolepidae, as exemplified by *Yunnanolepis,* and all their similarities are plesiomorphic characters. Therefore, the monophyly of the Yunnanolepiformes as defined previously can not be corroborated. Since *Minicrania* is here considered to be the sister-group of the Sinolepidae and Euantiarcha (Fig. 12), the Yunnanolepiformes sensu Zhang G.-R. (1978) could turn out to be paraphyletic.

By contrast, some similarities shared by *Yunnanolepis* and *Chuchinolepis* (procondylolepiforms, Zhang, 1984; Tong-Dzuy and Janvier, 1990) are plausible synapomorphies. These include: 1) the broad and short skull-roof, and the broad lateral plate (homoplastic with the condition in bothriolepidoids) and

2) the anteriorly pointed AMD plate (homoplastic with the condition in some asterolepidoids). Since the pectoral fin articulation of Chuchinolepidae is completely different from that of the Sinolepidae and Euantiarcha, it is impossible to imagine how the pectoral fin articulation of the latter could be directly derived from that of the Chuchinolepidae (cf. Zhang, 1984; Young and Zhang, 1992). We suggest that the Chuchinolepidae and the Sinolepidae + Euantiarcha represent two different strategies in the development of an exoskeletal articular device for the pectoral fin plates. Moreover, as to the interrelationships between *Minicrania,* the Yunnanolepidae (considered here as monophyletic) and the Chuchinolepidae, the latter two groups are more closely related to each other than either is to *Minicrania.* When the Yunnanolepiformes are redefined with the following synapomorphies: broad and short skull-roof, broad lateral plate and anteriorly pointed AMD plate, this taxon consists of two clearly monophyletic groups: the Yunnanolepidae and the Chuchinolepidae, and is consistent with the original classification of the Yunnanolepiformes (Zhang G.-R., 1978).

Interrelationships of Antiarchs—At present, antiarchs can be subdivided into six monophyletic taxa:the Yunnanolepidae, Chuchinolepidae, Sinolepidae, Asterolepidoidea, and Bothriolepidoidea, and *Minicrania.* When considering only these six taxa, our view of antiarch interrelationships can be expressed in a cladogram (Fig. 12), which is derived from a more complete analysis of 40 antiarch genera (Zhu, in press), generated by the Hennig86 program.

When compared to previous hypotheses on antiarch interrelationships (Janvier and Pan, 1982; Long, 1983; Young, 1984c, 1988; Ritchie et al., 1992) this new cladogram differs mainly in the position of the Chuchinolepidae when *Minicrania* is added. It is proposed here that the Chuchinolepidae are the sister group of the Yunnanolepidae, instead of that of the Euantiarcha and Sinolepidae, as previously believed on the basis of the seemingly derived brachial articulation. *Minicrania* is placed here as the sister group of the Euantiarchs and Sinolepidae, on the basis of the presence of a preorbital recess and some other apomorphies. The Yunnanolepidae and Chuchinolepidae are derived, in particular in the skull-roof pattern, whereas *Minicrania* retains a generalized antiarchan condition. The more complex brachial articulation of the Chuchinolepidae would thus be an advanced condition (relative to the Yunnanolepidae) which vaguely parallels that in the Sinolepidae and Euantiarcha. This would explain the difficulty in finding any reliable homology between the structure of the branchial articulation in the Chuchinolepidae on the one hand, and the Sinolepidae and Euantiarcha on the other. Also, this is in accord with the Yunnanolepidae and Chuchinolepidae both being endemics of the South China block.

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