

YOUNGOLEPIS FROM THE XISHANCUN FORMATION (EARLY LOCHKOVIAN) OF QUJING, CHINA

MIN ZHU & JUNHANG FAN

ZHU M. & FAN J. 1995. *Youngolepis* from the Xishancun Formation (Early Lochkovian) of Qujing, China. (*Youngolepis* de la Formation Xishancun (Lochkovien inférieur) de Qujing, Chine). *GEOBIOS, M.S. n° 19* : 293-299.

ABSTRACT

Some vertebrate remains, referred to *Youngolepis* sp., are described from the lower part of the Xishancun Formation (Early Lochkovian, Early Devonian) of Qujing, Yunnan, China. They represent the oldest record of *Youngolepis* so far known.

KEY-WORDS : SARCOPTERYGIANS, LOWER DEVONIAN, CHINA.

RÉSUMÉ

Quelques restes de Vertébrés, rapportés à *Youngolepis* sp., sont décrits. Ils proviennent de la partie inférieure de la Formation de Xishancun (Lochkovien inférieur, Dévonien inférieur) de Qujing (Province du Yunnan, Chine). Ils représentent la plus ancienne découverte de *Youngolepis* connue jusqu'ici.

MOTS-CLÉS : SARCOPTÉRYGIENS, DÉVONIEN INFÉRIEUR, CHINE.

INTRODUCTION

Youngolepis was first described by Chang & Yu (1981) from the Lower Devonian Xitun Formation (the second older formations of the Cuifengshan Group) of Qujing, Yunnan, China. From this formation, numerous well-preserved skulls of *Youngolepis* have been found, and the works of Chang (1982, 1991b) and Chang & Smith (1992) make this genus become one of the best known and most disputed sarcopterygians. Tong-Dzuy & Janvier (1987, 1990) and Smith (1991) described *Youngolepis* from the Sika and Bacun Formations (Lower Devonian) of Trang Xa and Dong Mo, northern Vietnam. As stated by Tong-Dzuy & Janvier (1987, p. 6), the Sika, Bacun and Mialé Formations correspond to the Lianhuashan, Nakoling and Yukiang Formations of Guangxi (South China), respectively. Using biostratigraphic correlation, Zhu *et al.* (1994) considered that the Lianhuashan Formation of Guangxi corresponds to the Xitun and Guijiatun Formations of Qujing, and that the Lianhuashan Formation can not be correlated with the Xishancun Formation (the lowermost formation of the Cuifengshan Group) of Qujing.

Therefore, in our opinion, the Sika Formation, possibly plus the lower part of the Bacun Formation, correspond to the Xitun and Guijiatun Formations of Qujing (cf. Tong-Dzuy & Janvier 1987, fig. 9). The latest report of *Youngolepis* was given by Zhu *et al.* (1994) who described an ethmosphenoid shield of *Youngolepis* from the Guijiatun Formation of Qujing.

The present paper deals with *Youngolepis* from the lower part of the Xishancun Formation in Qujing, Yunnan. It is generally considered that the base of the Xishancun Formation represents roughly the Silurian-Devonian boundary (Zhu 1991 ; Fang *et al.* 1994) and the age of the Xishancun Formation should be Lower Lochkovian (Zhu *et al.* 1994). Therefore, the discovery of *Youngolepis* in the Xishancun Formation represents the oldest occurrence of this genus so far known. Early vertebrates associated with *Youngolepis* in the Xishancun Formation include galeaspids, arthrodiros, petalichthyids and antiarchs (Zhu 1991, 1992, in press ; Zhu *et al.* 1994).

All specimens are housed in the Institute of Vertebrate Paleontology and Paleoanthropology (prefix V), Chinese Academy of Sciences, China.

SYSTEMATIC DESCRIPTION

Class SARCOPTERYGII Romer, 1955

Order Indet.

Genre *Youngolepis* CHANG & YU, 1981

YOUNGOLEPIS SP.

PRESERVATION OF THE MATERIAL

The material studied was preserved in a yellowish mudstone. Occasionally, the bone itself can be preserved. However, in most cases it is the tubes or cavities within the bone or the scale that were replaced by very fine grains, so the bone disappeared during fossilization. Therefore, the available specimens of *Youngolepis* include the external mould of the outer surface of the exoskeleton, the internal mould of the tubes within the exoskeleton, the internal mould of the basal surface of the exoskeleton, and few bones and scales. With particular respect to the ethmosphenoid and otoccipital shields, their internal moulds display the dorsal surface of the endocranium. The internal mould of the tubes within the exoskeleton is eroded easily in the fossils; however, it shows the histological structure of the exoskeleton in three dimensions whenever preserved.

SKULL ROOF

Ethmosphenoid shield - The ethmosphenoid shields (V10519.1-4, Pl. 1, figs 1-6) display the same shape and size as those found from the Xitun Formation (Chang & Yu 1981; Chang 1982). Their anterior and anterolateral margins curve downwards to form a rather broad and blunt snout. In anterior view, the ethmosphenoid shields show the notches for the independent premaxillaries (n.Pmx, Fig. 1; Pl. 1, fig. 2). The orbital fenestra is relatively small, and the postorbital division of the shield is much longer than the preorbital division (Table 1). Only one shield shows the external mould (V10519.1, pl. 1, fig. 3), some openings of the supraorbital sensory canals and impressions of the anterior pit-lines are preserve. The intertemporal (dermosphenotic of Chang 1982) can also be outlined in this specimen. It is a small bone at the posterolateral corner of the ethmosphenoid shield.

The internal mould of the shield reflects the dorsal surface of the endocranium, and confirms Chang's (1982, fig. 9, pl. 4) reconstruction. Specimens

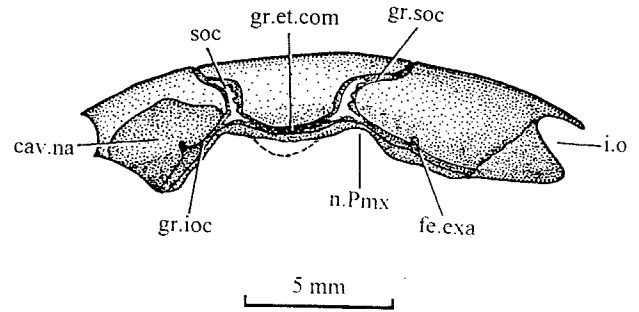


Figure 1 - *Youngolepis* sp., Early Lochkovian (Xishancun Formation), Qujing, Yunnan, China, internal mould of an ethmosphenoid shield in anterior view, V10519.1. **cav.na**, internal mould of nasal cavity; **fe.exa**, anterior exonarial fenestra; **gr.et.com**, groove for ethmoidal commissural canal; **gr.ioc**, groove for anterior portion of infraorbital canal; **gr.soc**, groove for supraorbital canal; **i.o**, orbital notch; **n.Pmx**, notch for premaxillary; **soc**, internal mould of supraorbital sensory canal. *Lochkovien inférieur (Formation de Xishancun), Qujing, Yunnan, Chine, moule interne du bouclier ethmosphénoïdal en vue antérieure, V10519.1. Abréviations: cav.na, moule interne de la cavité nasale; fe.exa, fenêtre exonarinale antérieure; gr.et.com, sillon pour le canal de la commissure ethmoïdienne; gr.ioc, sillon pour la division antérieure du canal infraorbitaire; gr.soc, sillon pour le canal supraorbitaire; i.o, encoche orbitaire; n.Pmx, encoche pour le prémaxillaire; soc, moule interne du canal sensoriel supraorbitaire.*

	V 10519.1	V 10519. 2	V 10519. 3	V 10519. 4
Length (b)	16.3	14.0	13.0	10.5
width at preorbital corner (d)	16.3	12.8	13.3	10.2
length of preorbital division (r)	5.0	4.2	3.6	2.9
length of orbital division (s)	2.5	3.1	3.1	3.0
length of postorbital division (t)	8.8	6.7	6.3	4.6
length of orbital division (l.i.o)	3.1	3.4	3.3	3.0
depth of orbital notch (dp. i. o.)	1.4	1.3	1.3	1.3
l.i.o / dp. i. o.	2.21	2.62	2.54	2.31
r / s+t	0.44	0.43	0.38	0.38
t / r+s	1.17	0.92	0.94	0.78
d / b	1.00	0.91	1.02	0.97
l.i.o. / b	0.19	0.24	0.25	0.29
v / w	0.61	0.70	0.66	0.72

Table 1 - Measurements (mm) and proportions of ethmosphenoid shields. v : distance from middle point of orbital notch to anterior end of ethmosphenoid shield; w : distance from middle point of orbital notch to posterior end of ethmosphenoid shield. *Mesures (mm) et proportions des boucliers ethmosphénoïdaux. v : distance du milieu de l'encoche orbitaire au bout antérieur du bouclier ethmosphénoïdal; w : distance du milieu de l'encoche orbitaire au bout postérieur du bouclier ethmosphénoïdal.*

men V10519.3 (Pl. 1, fig. 5) shows clearly the elevation above the pineal body on the dorsal sur-

face of the endocranium, which is situated closely behind the level of the dermal postorbital corner. The supraorbital and infraorbital canals form the deep grooves on the dorsal surface of the endocranium, where the internal moulds of the corresponding sensory canals are visible. The sensory canal is fairly thick with the small tubes communicating with the outside. Specimen V10519.1 exhibits the internal mould of the anterior pitlines (Pl. 1, fig. 1), which is a very thin groove, and extends posteromesially from the posterior end of the supraorbital canal. The groove caused by the supraorbital canal on the dorsal surface of the endocranium is fairly deep anteriorly and becomes shallow posteriorly. The supraorbital and infraorbital canals are separated, and there is no connection between them; this condition is simi-

lar to *Youngolepis* from the Xitun Formation and *Powichthys* (Jessen 1975, 1980). All of four internal mould specimens show the groove caused by the ethmoidal commissural sensory canal (gr.et.com, Fig. 1) and the anterior portion of the infraorbital canal (gr.ioc, Fig. 1) is immediately behind the notch for the premaxillary. This is because the suture between the premaxillaries and the adjacent part of the ethmosphenoid shield is oblique; this is shown clearly on the holotype of *Youngolepis* from the Xitun Formation (Chang 1982). The ethmoidal commissural sensory canal and the anterior portion of the infraorbital canal are situated at the suture.

The anterior exonarinal fenestra (fe.exa, Fig. 1) is a small opening that lies above the anterior por-

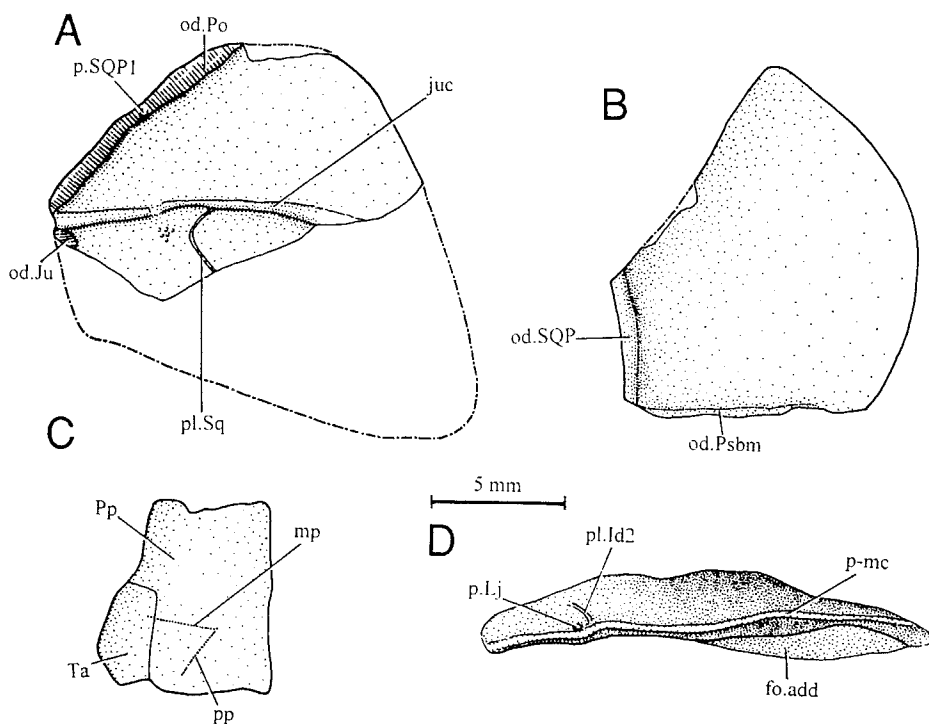


Figure 2 - *Youngolepis* sp., Early Lochkovian (Xishancun Formation), Qujing, Yunnan, China. **A**, external mould of an incomplete compound "squamosal + quadratojugal + preopercular" bone, V10519.8; **B**, external mould of a subopercular, V10519.13; **C**, external mould of the right side of an otoccipital shield, V.10519.6; **D**, external mould of a lower jaw, with internal mould of adductor fossa attached, V10519.12. **fo.add**, internal mould of adductor fossa; **juc**, jugal canal; **mp**, middle pit-line; **od.Ju**, area overlapped by jugal; **od.Po**, area overlapped by postorbital; **od.Psbm**, area overlapped by preoperculo-submandibular; **od.SQP**, area overlapped by compound "squamosal + quadratojugal + preopercular" bone; **pl.Id2**, pit-line of infradentary 2; **p.Lj**, external pit on lower jaw; **pl.Sq**, squamosal pit-line; **p-mc**, preoperculo-mandibular sensory canal; **Pp**, postparietal; **pp**, posterior pit-line; **p.SQP1**, anterior external pit on compound "squamosal + quadratojugal + preopercular" bone; **Ta**, tabular. *Lochkovien inférieur (Formation de Xishancun), Qujing, Yunnan, Chine. A*, moulage externe de l'os squamosal + quadratojugal + préoperculaire composé incomplet, V10519.8; *B*, moulage externe du sous-operculaire, V10519.13; *C*, moulage externe du bouclier otoccipital droit, V.10519.6; *D*, moulage externe de la mandibule droite, avec le moulage interne, V10519.12. **fo.add**, moulage interne de la fosse du muscle adducteur; **juc**, canal jugal; **mp**, pit-line moyenne; **od.Ju**, surface de recouvrement pour le jugal; **od.Po**, surface de recouvrement pour le postorbital; **od.Psbm**, surface de recouvrement pour le préoperculo-sousmandibulaire; **od.SQP**, surface de recouvrement pour l'os "squamosal + quadratojugal + préoperculaire" composé; **pl.Id2**, pit-line de l'infradentaire 2; **p.Lj**, dépression externe sur la mandibule; **pl.Sq**, pit-line squamosal; **p-mc**, canal sensoriel préoperculo-mandibulaire; **Pp**, postpariétal; **pp**, pit-line postérieure; **p.SQP1**, dépression externe antérieure sur l'os "squamosal + quadratojugal + préoperculaire" composé; **Ta**; tabulaire.

tion of the infraorbital sensory canal. Specimen V10519.1 also exhibits part of the internal mould of the right nasal cavity (cav.na, Fig. 1).

Noteworthy there is the internal mould of the meshwork of the bony tubules in the rostrum as well as that of the pore-canal system. Whenever preserved (Pl. 1, figs 3-4), the internal mould of the pore-canal system of cosmine exhibits a thin layer of meshwork. In the rostrum of *Youngolepis*, in addition to this layer of meshwork, there is an additional meshwork beneath it. The latter has several layers and represents the rostral tubuli (rt, Pl. 1, fig. 4). It makes the dorsal surface of the endocranium rather rough in the ethmoidal region (cf. Chang 1982, fig. 9). The canal for the ramus ophthalmicus superficialis can be distinguished easily from other canals.

Otoccipital shield - Both of otoccipital shields of the specimens (V10519.5 and V10519.6) are external moulds with internal moulds of the pore-canal system and pitlines attached on them. The internal mould of the middle and posterior pitlines is very slender (mp, pp, Fig. 2C), like that of the anterior pitline. Specimen V10519.5 (Pl. 1, fig. 7) is a complete otoccipital shield and exhibits only the suture between the two postparietals. Anteriorly, the area overlapped by the ethmosphenoid shield is preserved. In the specimen V10519.6, the suture between the tabular (Ta, Fig. 2C) and the adjacent elements is visible.

EXOSKELETON OF THE CHEEK

"Squamosal + quadratojugal + preopercular" bone

Specimen V10519.7 (Pl. 1, fig. 8) is an external mould of a complete small "Sq+Qj+Pop" bone. Anteriorly, it has the areas overlapped by the postorbital and jugal, as in *Kenichthys campbelli* (Chang & Zhu 1993). The internal mould of the squamosal and quadratojugal pit-lines attaches on the external mould of the bone, and has the same path as in *Youngolepis* from the Xitun Formation (Chang 1991b). Part of the internal mould of the jugal canal in specimen V10519.7 indicates that this canal enters this compound bone at the middle of its suture with the jugal, as in *Thursius wudingensis* (Fan 1992). However, in another larger and incomplete compound bone (V10519.8, Fig. 2A ; Pl. 1, fig. 9) the jugal canal enters this bone crossing the upper part of its suture with the jugal, like that described by Chang (1991b). This is considered as individual variation. Another explanation is that the condition observed in the smaller bone represents a juvenile feature. Specimen V10519.8 shows that the path of the jugal canal is rather straight.

Three pits are visible in V10519.7. Either the middle or the posterior pit has a groove leading posteriorly from it. In contrast, the anterior pit seems to be deficient of this kind of groove. It is found at the anterior margin of the compound bone, similar as in *Kenichthys campbelli*.

PLATE 1

Youngolepis sp., Early Lochkovian (Xishancun Formation), Qujing, Yunnan, China. *Lochkovien inférieur (Formation de Xishancun), Qujing, Yunnan, China.*

Figs. 1, 2 - internal mould of an ethmosphenoid shield in dorsal (1) and anterior (2) views, V10519.1, x 3. **1, 2 - moule interne d'un bouclier ethmosphénoïdal en vue dorsale (1) et en vue antérieure (2), V10519.1, x 3.**

Figs. 3, 4 - external mould of an ethmosphenoid shield (3) and the detail of its ethmoid region (4, showing the internal mould of rostral tubuli (rt, 4), V10519.1, x 3 (3) and x 6 (4). **3, 4 - moule externe d'un bouclier ethmosphénoïdal (3) et le détail de sa région éthmoïde montrant le moule interne des tubuli rostraux, (rt, 4), V10519.1, x 3 (3) et x 6 (4).**

Fig. 5 - internal mould of an ethmosphenoid shield in dorsal view, V10519.3, x 3. **5 - moule interne d'un bouclier ethmosphénoïdal en vue dorsale V10519.3, x 3.**

Fig. 6 - internal mould of an ethmosphenoid shield in dorsal view, V10519.4, x 3. **6 - moule interne d'un bouclier ethmosphénoïdal en vue dorsale, V10519.4, x 3.**

Fig. 7 - external mould of an otoccipital, V10519.5, x 3. **7 - moule externe d'un otoccipital, V10519.5, x 3.**

Fig. 8 - external mould of a compound "squamosal + quadratojugal + preopercular" bone, V10519.7, x 6. **8 - moule externe d'un os composé "squamosal + quadratojugal + préoperculaire", V10519.7, x 6.**

Fig. 9 - external mould of an incomplete compound squamosal + quadratojugal + preopercular bone, V10519.8, x 4. **9 - moule externe d'un os composé "squamosal + quadratojugal + préoperculaire" incomplet, V10519.8, x 4.**

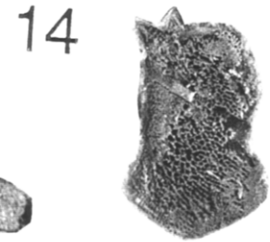
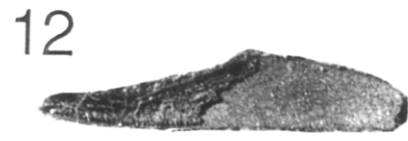
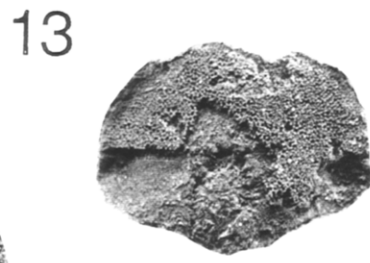
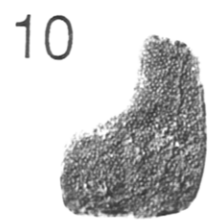
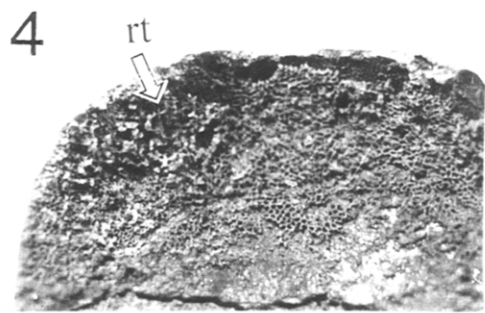
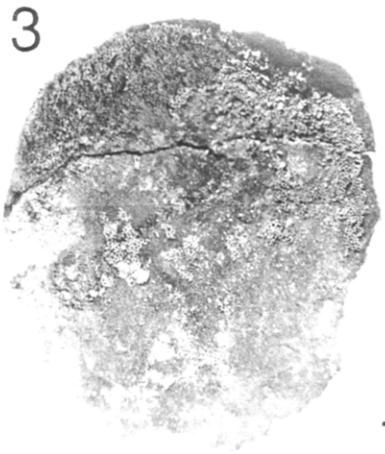
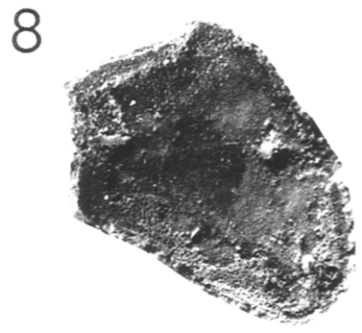
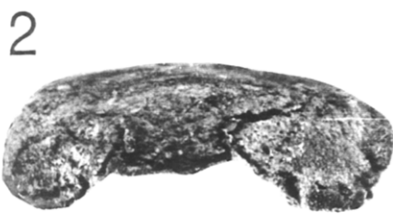
Fig. 10 - a left jugal, V10519.9, x 7. **10 - un jugal gauche, V10519.9, x 7.**

Fig. 11 - internal mould of a lower jaw, V10519.11, x 4. **11 - moule interne d'une mâchoire inférieure, V10519.11, x 4.**

Fig. 12 - external mould of a maxillary, V10519.10, x 5. **12 - moule externe d'un maxillaire V10519.10, x 5.**

Fig. 13 - a dorsal median scale, V10519.14, x 4. **13 - écaille médio-dorsale, V10519.14, x 4.**

Fig. 14 - internal mould of a lateral line scale, V10519.15, x 4. **14 - moule interne d'une écaille de la ligne latérale, V10519.15, x 4.**



Jugal

Specimen V10519.9 (Pl. 1, fig. 10) The jugal is higher than long and has a fairly large orbital notch at its anterodorsal corner. The infraorbital sensory canal runs dorsoventrally near the posterior margin of the bone and then turns anteriorly along its ventral margin.

Maxillary

Only an external mould of the maxillary of *Youngolepis* (V10519.10, Pl. 1, fig. 12) can be identified. Like the maxillary of *Youngolepis* from the Xitun Formation (Chang 1991b, fig. 8), V10519.10 is rather elongated and triangular. It is approximately 5.4 times as long as deep. The marginal teeth are found along the ventral border of the bone.

LOWER JAW

Two lower jaws of *Youngolepis*, much resembling those from the Xitun Formation in shape, have been found in the collection. Specimen V10519.11 (Pl. 1, fig. 11) is a fairly complete mandible. The internal moulds of the preoperculo-mandibular sensory canal, the horizontal part of mandibular line and the vertical pit-line of infradentaries 2 are preserved; the latter is located much anteriorly. The anterior pit of the lower jaw is found near the intersection of the preoperculo-mandibular sensory canal and the vertical pit-line of infradentary 2, as that described by Chang (1991b, fig. 10). This pit does not connect with the sensory canal nor with the pit-line. In specimen V10519.12, the internal mould of the large adductor fossa (fo.add, Fig. 2D) is preserved. Posteriorly, the preoperculo-mandibular sensory canal (p-mc, Fig. 2D) runs relatively upwards similar to that of *Powichthys* (Jessen 1980, Fig. 1; comment by Ahlberg 1991: 243).

SUBMANDIBULAR AND OPERCULAR SERIES

Subopercular - A detached dermal bone (V10519.13, Fig. 2B) may be interpreted as the subopercular, the shape is suggestive of that of porolepiforms (Jarvik 1972) and *Powichthys* (Jessen 1980). Its anterior margin, where it is overlapped by the compound cheek bone (od.SQP, Fig. 2B), is lower than of *Powichthys*. The ventral margin is relatively long and exhibits an overlapped area (od.Psbm, Fig. 2B). Similar to *Powichthys*, this bone shows no sign of being overlapped by the opercular.

SCALE

Two scales of *Youngolepis* are identified. One is a dorso-median scale (V10519.14, Pl. 1, fig. 13), and

the other is a lateral line scale (V10519.15, Pl. 1, fig. 14), in which the internal mould of the lateral line is preserved. The rhombic scale has a strongly developed dorsal process.

COMMENTS AND CONCLUSIONS

The material of *Youngolepis* that was collected in the Xishancun Formation is not adequate for comparison with *Y. praecursor* (the type and sole species of this genus) because the endocranium is absent although part of the dorsal surface of the endocranium can be recognised from the internal mould of the skull-roof. However, its assignment to *Youngolepis* is certain because its skull-roof has the same shape, size and bone pattern as that of *Y. praecursor*. In addition, these two taxa share the presence of a the compound "squamosal + quadratojugal + preopercular" bone and independent premaxillaries. Thus, the material of the Xishancun Formation is referred to as *Youngolepis* sp.

In the Xitun Formation, the skull-roof of *Youngolepis* is intimately fused to its endocranium; thus, the dorsal surface of the endocranium cannot be directly observed. However, thanks to the work of Chang (1982), the dorsal surface of the endocranium was restored after the wax model using "Sollas" grinding method. In the present study, the internal mould of the skull-roof of *Youngolepis* exhibits directly the dorsal surface of the endocranium, and then can be used to corroborate Chang's restoration. In dorsal view, the anterior part of the endocranium shows two pairs of deep grooves caused by the supraorbital and infraorbital sensory canals respectively. In these grooves, the internal moulds of sensory canals are present in some specimens. As stated by Chang (1982), a connection between the supraorbital and infraorbital sensory canals has not been observed. Specimen V10519.1 exhibits the connection between the supraorbital sensory canal and the anterior pit-line, the latter extends postero-medially from the posterior end of the former.

Chang (1982, 1991a) described the rostral tubuli in *Youngolepis*, it was restored from the grinding series. In the Xishancun material, the internal mould of the rostral tubuli as well as that of pore-canal system can be seen. The rostral tubuli canals are somewhat thicker than those of *Cosmine*. Moreover, the rostral tubuli makes the dorsal surface of the endocranium rather rough in the ethmoid region.

Acknowledgements - The authors are very grateful to Prof. Chang M.-M. for her comment and help. We

also thanks the director fund of the IVPP (Beijing) for partial support of this project. Zhu Min extends his sincere gratitude to the CNRS and WONG foundation for the postdoctoral scholarship in Paris (Laboratoire de Paléontologie et URA 12 du CNRS, Muséum national d'Histoire naturelle)

REFERENCES

- AHLBERG P.E. 1991 - A re-examination of sarcopterygian interrelationships, with special reference to the Porolepiformes. *Zoological Journal of the Linnean Society, London*, **103** : 241-287.
- CHANG M.-M. 1982 - The braincase of *Youngolepis*, a Lower Devonian crossopterygian from Yunnan, south-western China. Ph. D. dissertation, Stockholm University, GOTAB, Stockholm : 1-113.
- CHANG M.-M. 1991a - Rhipidistians, dipnoans and tetrapods. In SCHULTZE H.-P. & TRUEB L (eds) : Origins of the major groups of tetrapods : controversies and consensus. Cornell University Press, Ithaca : 3-28.
- CHANG M.-M. 1991b - Head exoskeleton and shoulder girdle of *Youngolepis*. In CHANG M.-M., LIU Y.-H. & ZHANG G.-R. (eds) : Early Vertebrates and related problems of evolutionary biology. Science Press, Beijing : 355-378.
- CHANG M.-M. & SMITH M.M. 1992 - Is *Youngolepis* a porolepiform? *Journal of Vertebrate Paleontology*, **12** : 294-312.
- CHANG M.-M. & YU X.-B. 1981 - A new crossopterygian *Youngolepis praecursor* gen. et sp. nov. from Lower Devonian of E. Yunnan, China. *Scientia Sinica*, **24** : 89-97.
- CHANG M.-M. & ZHU M. 1993 - A new Middle Devonian osteolepidid from Qujing, Yunnan. *Memoirs of the Association of the Australasian Palaeontologists*, **15** : 183-198.
- FAN J.-H. 1992 - A new species of *Thursius* from Wuding, Yunnan. *Vertebrata Palasiatica*, **30** : 195-209 [In Chinese with English summary].
- FANG Z.J. 1994 - New advance in the study of the Silurian-Devonian boundary in Qujing, East Yunnan. *Journal of Stratigraphy*, **18** (2) : 81-90 [In Chinese].
- JARVIK E. 1972 - Middle and Upper Devonian Porolepiformes from East Greenland with special reference to *Glyptolepis groenlandica* nov. sp. *Meddelelser Grønland*, **187** : 1-295.
- JESSEN H. 1975 - A new choanate fish, *Powichthys thorsteinssoni* nov. gen., nov. sp., from the early Lower Devonian of the Canadian Arctic Archipelago. *Colloques internationaux Centre national de la Recherche scientifique*, Paris, **218** : 213-222.
- JESSEN H. 1980 - Lower Devonian Porolepiformes from the Canadian Arctic with special reference to *Powichthys thorsteinssoni* JESSEN. *Palaeontographica, A*, **167** : 180-214.
- SMITH M.M. 1991 - Microstructure of enamel in the tusk teeth of *Youngolepis*, compared with enamel in crossopterygian teeth and with a youngolepid-like tooth from the Lower Devonian of Vietnam. In CHANG M.-M., LIU Y.-H. & ZHANG G.-R. (eds) : Early Vertebrates and related problems of evolutionary biology. Science Press, Beijing : 341-353.
- TONG-DZUY T. & JANVIER P. 1987 - Les vertébrés dévoniens du Vietnam. *Annales de Paléontologie*, **73** (3) : 165-194.
- TONG-DZUY T. & JANVIER P. 1990 - Les vertébrés du Dévonien inférieur du Bac Bo oriental (province de Bac Thai et Lang Son, Viet Nam). *Bulletin du Muséum national d'Histoire naturelle, Paris, section C, 4e série*, **12** (2) : 143-223.
- ZHU M. 1991 - New information on *Diandongpetalichthys* (Placodermi : Petalichthyida). In CHANG M.-M., LIU Y.-H. & ZHANG G.-R. (eds) : Early Vertebrates and related problems of evolutionary biology. Science Press, Beijing : 179-194.
- ZHU M. 1991 - Two new galeaspids, with a discussion on eugaleaspid phylogeny. *Vertebrata Palasiatica*, **30** (3) : 169-184 [In Chinese with English summary].
- ZHU M., WANG J.-Q. & FAN J.-H. 1994 - Early Devonian fishes from Guijiatun and Xujiachong Formations of Qujing, Yunnan, and related biostratigraphic problems. *Vertebrata Palasiatica*, **32** (1) : 1-20 [In Chinese with English summary].

M. ZHU & J. FAN

Institute of Vertebrate Paleontology
and Paleoanthropology
Chinese Academy of Sciences
Beijing 100044, China