International Symposium on Triassic and later Marine Vertebrate Faunas

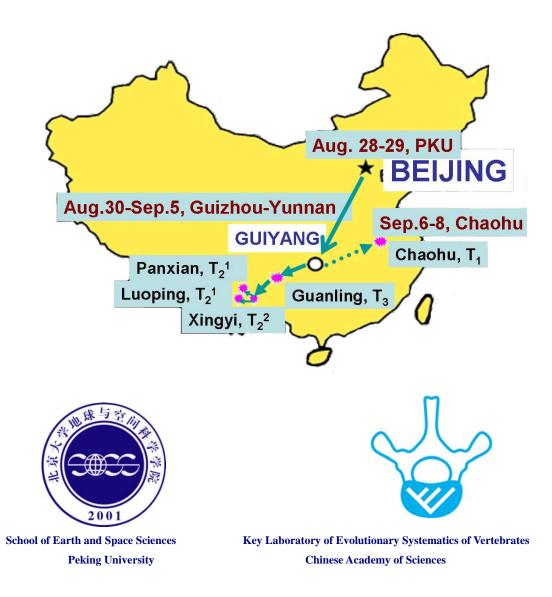
Workshop of Major International Joint Research Project 40920124002, National Science Foundation of China



August 28-September 8

Program and Abstract

Geological Museum and Department of Geology School of Earth and Space Sciences Peking University, Beijing 100871, China





Dear colleagues,

Since the first report on the fossil reptiles from the Late Triassic of Guanling, Guizhou Province, in China in 1999, the Triassic marine vertebrate faunas of Guizhou-Yunnan, including the Guanling Biota, the Xingyi Fauna, the Panxian Fauna and Luoping Fauna, have been attracting much greater interests from scientists all over the world. Research on these faunas featured prominently at the 2nd IPC and at the 64th, 65th, 66th, 67th, 68th, 69th SVP meetings. To provide an opportunity to review progress of research in recent years, and to further discuss the Triassic marine vertebrates from Guizhou-Yunnan, "The International Symposium on Triassic and later Marine Vertebrate Faunas" will be held at Peking University on August 28-29, 2010, sponsored by Peking University and Key Laboratory of Evolutionary Systematics of Vertebrates, Chinese Academy of Sciences, combined with a post-symposium field trip to Guanling, Xingyi, Panxian (Guizhou), Luoping (Yunnan) and Chaohu (Anhui).

The major academic topic of the symposium is: "Triassic marine vertebrate faunas in southwestern China: The evolution, paleogeography, paleoenvironment, paleoecology and the response to the recovery of the Triassic biosphere". This is augmented by the overview of the evolution of marine vertebrates after the Triassic.

A discussion forum will be held around Triassic Paleontology and interrelated subjects such as the construction of geological parks, development of a local museum, the organization of international cooperation and talent cultivation at the site of Guanling after the symposium during the field trip to Guizhou-Yunnan.

Other than the abundant and well-preserved Triassic marine vertebrate fossils and typical stratigraphic sections, there are a lot of beautiful landscape sites, charming minor nationality's cultural sites and ecological villages in the mountains, too. You are welcome to visit Peking University, Beijing and southwestern China, and to experience these natural and cultural rarities.

Chairs,

PAN Mao, HAO Wei-cheng, ZHU Min Olivier Rieppel, Andrea Tintori, Ryosuke Motani

Persons interested in attending the symposium who need more information, please contact:

Dr. JIANG Da-yong, Professor
Secretariat of symposium
Department of Geology and Geological Museum
School of Earth and Space Sciences
Peking University
Yiheyuan Str. 5, Haidian District, Beijing 100871
P. R. China
Email: djiang@pku.edu.cn
Fax: +86-10-62754154

OR please visit the website: <u>http://marinereptile.org/</u>

1 Events of the symposium

1.1 The academic activities

- Symposium: Triassic and later marine vertebrate faunas: its evolution, paleogeography, paleoenvironment, paleoecology and the responses to the recovery of the Triassic biosphere.
- Workshop of NSFC Major International Joint Research Project 40920124002: "Radiation bio-event sequence of marine reptile faunas and global migratory-evolutionary pattern within the course from early recovery to radiated reconstruction of Early-Middle Triassic ecosystem after the end-Permian Mass Extinction".

1.2 Academic sessions

The symposium will include platform presentations and poster presentations. Leading authorities will be invited to be the conveners (chairs) for the following academic sessions:

1. "The diversity evolution and paleogeography on the Triassic and later marine reptiles".

Conveners: Olivier Rieppel, Ryosuke Motani, WU Xiao-chun

 "The evolution and paleogeography of Triassic fishes and invertebrates". Conveners: Andrea Tintori, JIN Fan, SUN Yuan-lin

LUO Yong-ming, HU Shi-xue

 "Roundtable Forum on research of Triassic marine vertebrate faunas in China" Conveners: SUN Yuan-lin, LI Chun

1.3 Important Dates and sites

- Registration: August 27, 2010, 8:00 am 18:00 pm Shaoyuan Hotel of Peking University, Beijing
- Academic sessions: August 28-29, 2010

Yifu Building No 2 (New Geoscience Building) Peking University

Yiheyuan Street 5#, Haidian District, Beijing 100871

1.4 Program of Academic sessions

• August 28, 2010

8:30-9:00, OPENING CEREMONY

Moderator: Prof. PAN Mao, Prof. HAO Wei-cheng

Prof. CHANG Mee-mann, address

Dr. CAI Hua-wei, representative of Prof. YANG Qun (President of Palaeontological Society of China) Mayor of Guanling County

Mayor of Meride and Presideng of Monte San Giorgio Foundation, Switzerland

9:00-11:00, SYMPOSIUM KEYNOTE SPEECHES Moderator: Prof. CHANG Mee-mann

- 9:00-9:30, Olivier Rieppel: Triassic Marine reptiles (Sauropterygia, Protorosauria, Thalattosauria) from the Eastern and Western Tethyan Faunal Provinces
- 9:30-10:00, WU Xiao-chun: Reproductive patterns of the Mesozoic aquatic reptiles
- 10:00-10:30, Andrea Tintori, Sun Zuoyu, Cristina Lombardo: How fast was the recovery after the Permo/Triassic crisis? The answer from the actinopterygian fishes
- 10:30-11:00, SUN Yuan-lin: Stratigraphy and sequence of Triassic marine vertebrate faunas of south China
- 11:00-11:30, Ryosuke Motani: Triassic Ichthyopterygian fossils from China and their unique significance

11:30-12:00, photograph, in front of the Yifu Building No 2 12:00-13:00, lunch, on site packet food

13:00-16:00, ACADEMIC SESSIONS I-1: THE DIVERSITY EVOLUTION AND PALEOGEOGRAPHY ON THE TRIASSIC AND LATER MARINE REPTILES

Moderator: Olivier Rieppel, Ryosuke Motani, WU Xiao-chun

- 13:00-13:20, Marta S. Fernández, Zulma Gasparini, Yanina Herrera: Tithonian Marine Herpeto Faunas from the Neuquen Basin (Northwest Patagonia, Argentina)
- 13:20-13:40, Neil Kelley, Ryosuke Motani, Da-yong Jiang, Olivier Rieppel: Strontium Isotopes Corroborate Sea Level Fluctuation as a Mechanism for Ecologically Selective Extinction among Early Mesozoic Marine Reptiles
- 13:40-14:00, F. Robin O'Keefe: New plesiosaur discoveries from the Jurassic Sundance Formation: novel body morphologies and inferences of prey selection
- 14:00-14:20, Nicholas C. Fraser, Olivier Rieppel, Da-yong JIANG, Amy Smith: The Tanystropheidae and their global distribution
- 14:20-14:40, Heinz Furrer: Palaeogeography, palaeoecology and taphonomy of Middle Triassic vertebrate fossil lagerstaetten in the Swiss Alps
- 14:40-15:00, Jun LIU, Da-yong JIANG, Olivier Rieppel, Ryosuke Motani, Michael J. Benton, Jonathan C. Aitchison, Shi-xue HU, Qi-yue ZHANG, Chang-yong ZHOU: A preliminary review of the diversity of marine reptiles from Luoping Fauna
- 15:00-15:20, Long CHENG, Xiaohong CHEN and ZHANG Baomin: Anshunsaurus huangnihensis, Cheng (Reptilia: Thalattosauria) from the Middle Triassic of Guizhou, China: A transitional node in Askeptosauridae ingroup
- 15:20-15:40, Tamaki Sato and Xiao-Chun Wu: Late Cretaceous plesiosaurian fauna of Manitoba Escarpment, Canada

- 15:40-16:00, Torsten M. Scheyer and James M. Neenan: evolution and paleobiology of marine reptiles: using placodontia as a case study for integrating osteological and 3d imaging, developmental, and paleohistological data
- 16:00-17:00, Exhibition in Geological Museum of Peking University Poster and free discussion

17:00-18:00, Symposium Banquet

• August 29, 2010

8:00-9:40, ACADEMIC SESSIONS I-2: THE DIVERSITY EVOLUTION AND PALEOGEOGRAPHY ON THE TRIASSIC AND LATER MARINE REPTILES

Moderator: Olivier Rieppel, Ryosuke Motani, WU Xiao-chun

- 8:00-8:20, Leslie Francis Noe: Mary Anning, Thomas Hawkins and plesiosaurs across the Triassic-Jurassic Boundary, with Special reference to southern England.
- 8:20-8:40, Cheng JI: True Tailbend Occurred in Triassic Evidence from the Triassic Ichthyousaur Skeletons of South China
- 8:40-9:00, Jun LIU, Da-yong JIANG, Ryosuke Motani, Olivier Rieppel, Jonathan C. Aitchison, Shi-xue HU, Qi-yue ZHANG, Chang-yong ZHOU: A review of Chinese mixosaurids
- 9:00-9:20, Le-tian MA: The Restudy of the "Dingxiaosaurus luyinensis" from Guizhou, China
- 9:20-9:40, Peng-fei YANG and Wen-qi CHEN: Morphological study on *Mixosaurus panxianensis* from the Middle Triassic of Guizhou, China

9:40-11:20, ACADEMIC SESSIONS II: THE EVOLUTION AND PALEOGEOGRAPHY OF TRIASSIC FISHES AND INVERTEBRATES

Moderator: Andrea Tintori, JIN Fan, SUN Yuan-lin, LUO Yong-ming, HU Shi-xue

- 9:40-10:00, Fei-xiang WU and Yuan-lin SUN: New saurichthyids (Actinopterygii, Saurichthyidae) from the Middle Triassic (Pelsonian, Anisian) of Southwest China
- 10:00-10:20, Wan-lu FU, George D.F. Wilson, Da-yong JIANG, Yuan-lin SUN, Wei-cheng HAO and Zuo-yu SUN: New taxon of Phreatoicidea (Crustacea, Isopoda) from Luoping Fauna (Middle Triassic) and Its Significance of Paleogeography
- 10:20-10:40, Tomaž Hitij, Andrea Tintori, Jure Žalohar, Silvio Renesto: New Fossil Sites with Triassic Vertebrate Fauna from the Kamnik-Savinja Alps, Slovenia
- 10:40-11:00, Hun-qin LIN, Zuo-yu SUN, Tintori Andrea, Wei-cheng HAO, Da-yong JIANG: New insights on *Habroichthys* Brough, 1939 (Actinopterygii: Habroichthyidae): the material from the Middle Triassic of Yunnan Province, South China
- 11:00-11:20, Wen WEN: A new Triassic Actinopterygian fishes from Luoping, Yunnan Province
- 11:20-11:40, Andrea Tintori and Cristina Lombardo: The Dolomiti Garden: which crisis for the fishes?

11:40-13:00, lunch, on site packet food

13:00-17:00, ACADEMIC SESSIONS III: Roundtable Forum on research of Triassic marine vertebrate faunas in China

Moderator: SUN Yuan-lin, LI Chun

Speakers:

LI Chun: free talk, from *Qianosuchus* to *Odontochelys* SHANG Qing-hua: Nothosaurs in China JIANG Da-yong: free talk on Mixosaurs SUN Zuo-yu: Middle Triassic fishes from Luoping

17:00-18:30, Symposium Banquet

1.5 Post-symposium trip

The post-symposium field trip, will visit the fossil sites, excavation exposures, stratigraphic sections and field museums in Guanling County, Xingyi City, Panxian County of Guizhou Province, Luoping County of Yunnan Province, and Chaohu City of Anhui Province.

During the stay in Guanling, from August 30 to September 1, we may attend the social activities of the symposium such as the forum on the development of Geological park, construction of field museum on site, fossil protection and exchange.

The preliminary schedule is as following:

• August 30:

5:30 am, take a university bus leave the Shaoyuan Hotel, to the Beijing Capital International Airport.

7:50 am - 11:20 am, CA 1461, early morning flight from Beijing to Guiyang.

12:00 noon – 13:00 pm, lunch at Guiyang.

13:00 pm – 18:00 pm, tour bus to visit Huangguoshu Waterfall.

Arrive at Guanling in the evening.

- Stay in the Qianling Hotel for the nights from August 30 to September 1
- August 31:

Visit stratigraphic sequence from Lower Triassic Yongningzhen Formation, Middle Triassic Guanling Formation, Yangliujing Formation, and Middle/Upper Triassic Zhuganpo Member of Falang Formation, Upper Triassic Wayao Member of Falang Formation.

Visit the Guanling National Geological Park and field museum.

• September 1:

Attend the Guanling forum, the social part of the symposium, and visit local village of minor nationality in the mountain.

• September 2:

Take bus from Guanling to Xingyi (3 hours).

Visit the fossil site and *Keichousaurus* Museum at Dingxiao (Xingyi).

Visit Malinghe gorge.

Arrive at Xingyi City in the evening.

Stay in the Panjiang Hotel for the night, two guests share one

standard room.

• September 3:

Visit the fossil sites at Wusha of Xingyi, stratigraphic sequence of later Ladinian Zhuganpo Member of Falang Formation, and excavation exposure.

Visit Wanfenglin (the famous karstland site).

Stay in the Panjiang Hotel for the night, two guests share one standard room.

• September 4:

Visit the fossil site at Yangjuan, Xinmin of Panxian, stratigraphic sequence of Anisian Guanling Formation, excavation exposures.

Go to Luoping of Yunnan in the evening.

Stay in the Xinyuan Hotel for the night, two guests share one standard room.

- September 5:
 - Visit the fossil site at Luoping of Yunnan Province, stratigraphic sequence of Anisian Guanling Formation, and excavation exposures.
 - Stay in the Xinyuan Hotel for the night, two guests share one standard room.

• September 6:

Take bus go to Guiyang, meet the Provincial officials in the late afternoon.

• September 7:

13:00pm – 14:45pm, CZ6430, take noon flight from Guiyang to Hefei of Anhui Province.

Take bus transferring to Chaohu City.

Stay night in Chaohu.

• September 8:

Visit the fossil site of *Chaohusaurus* at Chaohu, stratigraphic sequence of Lower Triassic Yinkeng Formation, Helongshan Formation Nanlinghu Formation, and the excavation exposure.

Go to Hefei in the noon.

Visit the Anhui Geological Museum.

End the trip, and stay night in Hefei..

• September 9:

8:00am – 9:30am, CA 1846, part of attendees back to Beijing

2 Organization

2.1 Sponsors:

- School of Earth and Space Sciences, Peking University
- Key Laboratory of Evolutionary Systematics of Vertebrates, Chinese Academy of Sciences

Co-sponsors

- Palaeontological Society of China
- Department of Earth Science, National Natural Science Foundation of China
- Chengdu Centre of Chinese Geological Survey
- Office of Geological Environment, Department of Land and Resources, Guizhou Provincial Government
- Guanling County Government, Guizhou Province

2.2 Executive Unit:

• Geological Museum, and Department of Geology, Peking University

Co-executive units:

- Paleozoological Museum of China, IVPP
- Zhejiang Museum of Natural History

2.5 Hosts

(1) Honorary Chair:

• CHANG Mee-mann, Peking University and Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences

Co-chairs of Organization Committee:

- PAN Mao, Dean of SESS, Peking University
- HAO Wei-cheng, Director of Geological Museum, Peking University
- ZHU Min, Director of Key Laboratory of Evolutionary Systematics of

Vertebrates, Chinese Academy of Sciences

- Olivier RIEPPEL, The Field Museum, Chicago, USA
- Andrea TINTORI, Milano University, Italy
- **Ryosuke MOTANI**, University of California (Davis), USA

(2) Members of Organization Committee:

WU Xiao-chun Canadian Museum of Nature, Ottawa, Canada

YANG Qun Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science

YAO Jianxin Institute of Geology Chinese Academy of Geological Sciences

- TONG Jinnan China University of Geosciences, Wuhan
- **WANG Yangeng** Bureau of Geology and Mineral Exploration and Development of Guizhou Province
- WANG Liting Bureau of Geology and Mineral Exploration and Development of Guizhou Province
- **LUO Yongming** Bureau of Geology and Mineral Exploration and Development of Guizhou Province

ZHANG Qiyue Chengdu Centre of Chinese Geological Survey, Sichuan Province

ZHAO Lijun Zhejiang Museum of Natural History

- WANG Yuan Paleozoological Museum of China, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences
- LIU Jun Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences
- LI Chun Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences

ZHANG Lifei School of Earth and Space Sciences, Peking University

WU Chaodong Office of Scientific Research, Peking University

- **BAI Zhiqiang** Institute of Paleontology and Paleoenvironment, School of Earth and Space Sciences, Peking University
- MA Xueping Institute of Paleontology and Paleoenvironment, School of Earth

and Space Sciences, Peking University

- SUN Yuanlin Institute of Paleontology and Paleoenvironment, Department of Geology and Geological Museum, School of Earth and Space Sciences, Peking University
- LIU Jianbo Institute of Paleontology and Paleoenvironment, School of Earth and Space Sciences, Peking University
- JIANG Da-yong Institute of Paleontology and Paleoenvironment, Department of Geology and Geological Museum, School of Earth and Space Sciences, Peking University

(3) Secretary-General: JIANG Da-yong, LI Chun

(4) Offices of Committee

• Administrative Office:

Member: Qin Jianghong, Yin Chao, Ma Letian, Sun Jicai, Li Meizheng Zou Xiaodong, Lin Hunqin, Huang Jiwei, Chen Wenqi

Duty: registration on site, symposium materials, gifts, meeting-rooms organizing, accommodation and ground transportation

• Academic Office:

Member: Sun Zuoyu, Wu Feixiang, Ji Cheng, Yang Pengfei, Fu Wanlu

Duty: pre-registration, organization of presentations and thematic meetings, editing abstracts, arrangement of post-symposium trips, special issue of publication

3 Travel Information in Beijing

Peking University is the top university in China. The campus, known as "Yan Yuan" (the garden of Yan), is situated at Yiheyuan Street 5#, Haidian District in Beijing, near to the Yuanmingyuan Garden and the Summer Palace.

• Transportation from Beijing Capital International Airport to Peking University:

Shuttle Bus: The airport is linked to central Beijing by Airport Express buses

from 8:30 am to 9:30 pm. Bus ticket price is RMB 16 and the two-way shuttle interval is about 30 minutes. Airport Express buses Route 5 has arrival terminal at Zhongguancun (the 4th bridge). Then walk 150m east, at Baofusi bridge west bus station, take bus route 696 or 498 after two stops and get off at Zhongguanyuan bus station, Peking University east gate arrival.

- Taxi: It takes about 60 minutes by taxi to get to Peking University from airport. The taxi station is located just outside the airport terminal.
- Subway: First take Subway Airport Line to Sanyuanqiao Station, transfer to Subway Line 10 and get off at Haidianhuangzhuang Station. Then transfer to Subway Line 4 and get off at the east gate arrival.

To get more information of the airport, go to the web site of Beijing Capital International Airport, http://en.bcia.com.cn/index.shtml.

The host will try to arrange to pick you up at the airport, if you require.

• Hotels in the campus of Peking University:

• Shaoyuan Hotel: near the west gate of the campus

Tel: +86-10-62752218, +86-10-62752200

Website: http://162.105.113.240/index.aspx

The host has made room pre-reservation for the attendees who prefer to stay in the Shaoyuan Hotel, and negotiated to get the best discount from the Hotel. For standard two-bed room, the basic fare is about 380 Yuan/per room (including breakfast).

♦ Lake View Hotel ★★★★★:

Tel: +86-10-82689999

Website: http://www.thelakeviewhotel.com.cn/index_en.html The standard room fare is expensive, around 1000 Yuan/per room. If you prefer to stay in this hotel, you may contact the hotel directly, OR the host may



help you to make the reservation if you ask before the 20th of July.

• Weather in Beijing

The climate in Beijing is of the continental type. The end of August is coming into the Autumn, the best season with good weather, not too hot with cool night. In autumn, jeans and a sweater are usually enough. Rain gear is necessary.

4 Fees of registration and post-symposium field trip

Registration fee will be ¥800 (RMB Yuan) for regular participants, ¥500 for students. The registration fee will cover the symposium documents, drinks and meals in the Campus refectory during the symposium in PKU.

The fee of the entire post-symposium field trip, including the inland flights (Beijing to Guiyang, Guiyang to Hefei, and Hefei to Beijing or your destination), hotels, tour bus and insurance, will basically be the charge of the attendees. The Guanling County Government promises to cover the accommodation and regional travel cost during the stay in Guanling area from August 30 to September 1. And the host will provide part of fund for the meals. In this case, we estimate the amount

¥9000 (RMB Yuan) for the field trip. The host will arrange the trip and accommodation for the attendees, who must pay for the trip when registration.

6 Important Dates:

Third Circular: July 1, 2010 Registration: August 27, 2010 Academic sessions: August 28 to 29, 2010 Post-symposium field trip: August 30 to September 8, 2010 Please regularly check the website for information update.

Abstract

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Anshunsaurus huangnihensis, Cheng (Reptilia: Thalattosauria) from the Middle Triassic of Guizhou, China: A transitional node in Askeptosauridae ingroup

CHENG LONG^{*} CHEN XIAOHONG AND ZHANG BAOMIN Wuhan Institute of Geology and Mineral Resources, Wuhan 430223, China, ycclong2001@yahoo.com.cn

Thalattosaurs are a monophyletic clade of early to late Triassic marine reptiles (Nicholls, 1999). They can be subdivided to two taxa - Askeptosauroidea and Thalattosauroidea (Nicholls, 1999; Müller, 2002; Müller, 2005; Liu and Rieppel, 2005). The former is distinguished from the later distinctly by longer neck (>10 cervical vertebrae) and larger body (Müller, 2005; Liu and Rieppel, 2005). However, Askeptosauroidea only includes *Askeptosaurus italicus* from the Middle Triassic and *Endennasaurus acutirostris* from the Norrian of the Late Triassic of Monte San Giorgio (Kuhn-Schnyder E., 1952; Renesto, 1992; Müller, 2002; Müller et al., 2005). *Anshunsaurus huangguoshensis* Liu, 1999, first record of thlattosaur from China (Liu, 1999; Rieppel and Liu, 2000), indicated that askeptosaur radiated to east Tethys ocean in Triassic. Recently, *Anshunsaurus wushaensis* Rieppel, 2006, and *Anshunsaurus huangnihensis* Cheng, 2007, were reported from the Middle Triassic Zhuganpo Formation, and *Miodentosaurus brevis* Cheng, 2006, was reported from the Upper Triassic Xiaowa Formation, successively (Rieppel et al., 2006; Cheng et al., 2007; Cheng et al., 2007). They all belong to Askeptosauroidea. Hitherto, Askeptosauroidea includes 4 gena and 6 species.

When Anshunsaurus huangnihensis was reported, some scholars were doubtful that it was the synonym of Anshunsaurus wushaensis from the same layers (Xingyi Fauna) (Zhao et al., 2008). For examining the validity of Anshunsaurus huangnihensis, one of us (Cheng L.) prepared the dorsal side of the skull and the right side of the proximal cervical vertebrae of the holotype (YIGM V 30017). The postcranial skeleton was described in 2007 when the species was reported (Cheng et al., 2007), so, we only described the skull in this paper.We found that the skull was not only distinctly different from other species of Anshunsaurus, but also had some important transitional characters between Askeptosaurus and Anshunsaurus.

Systematic paleontology

DIAPSIDA Osborn, 1903 THALATTOSAURIA Merriam, 1904 ASKEPTOSAUROIDEA Kuhn-Schnyder, 1952 Anshunaurus Liu, 1999

Anshunaurus huangnihensis Cheng, 2007. (Fig.1)

Holotype: Wuhan Institute of Geology and Mineral Resources (Yichang Institute of Geology and Mineral Resources), YIGM V 30017.

Locality and horizon: Xiemi of Wusha village, Xinyi County, Guizhou Province, southwestern China; Zhuganpo Formation, Middle Triassic.

Diagnosis(revised): Middle to large thalattosaur, with more than 2m total length; 17 cervical vertebrae and 21 dorsal vertebrae; external naris restricted posteriorly; postorbital lunular, restricted at postodorsal orbit; the anterolateral process of frontal shorter than anteromedial process; the posterior process of frontal overlapping the anterior part of parietal; the ventral process of squamosal short; the parietal suture serrated; the anterior part of supratemporal not contacting the posterior process of the postfrontal; the posterior part of supratemporal exceeding the end of the parietal; splenial being the longest bone in mandible; the anterior part of coracoid extending anteriorly and the posterior part concave; seven ossified carpal elements and six ossified tarsal elements; the formula of toe: 2-3-4-5-4.

The former researching results indicated that *Endennasaurus acutirostris* was the most outgroup taxon in Askeptosauroidea and that *Anshunsaurus* was closely related to *Askeptosaurus* which formed

Askeptosauridae (Nicholls, 1999; Rieppel et al., 2000; Liu and Rieppel, 2005; Müller, 2002; 2005; Wu et al., 2009). In the postcranial skeleton, the coracoid of *Anshunsaurus huangnihensis* is distinctly different to that of *Anshunsaurus huangguoshuensis* and *Anshunsaurus wushaensis*, but, is very similar to that of *Askeptosaurus italicus* and *Endennasaurus acutirostris* (Cheng et al., 2007). So, it indicates that *Anshunsaurus huangguoshuensis*. However, the skull is the most primary for identifying in tetropod vertebrates.

Compared the skull of *Anshunsaurus huangnihensis* to that of *Anshunsaurus huangguoshuensis*, the differentiation is distinct. The nasal of the former extends anteriorly and forms the anterior margin of external naris, however, that of the latter is restricted at the posterior margin of external naris. The most distinct differentiation between *Anshunsaurus huangnihensis* and *Anshunsaurus huangguoshuensis* is the following: (a) although the postfrontal is very small, it does not fuse to the postorbital in the former, whereas the postfrontal and the postorbital fuse to postorbitofrontal in the latter; (b) the slender posterolateral process overlaps the parietal and extends posteriorly to the level of the middle portion of the pineal foramen in the former, whereas it extends posteriorly behind the level of the posterior margin of the pineal foramen between the postorbitofrontal and parietal; (c) the posterior process of the jugal in the former extends posteriorly to the level of the lower temporal fenestra, whereas that in the latter closely approaching the quadrate in the articulated skull (Liu and Rieppel, 2005).

The skull of the holotype (IVPP V 13782) of Anshunsaurus wushaensis was exposed laterally, so the sutures of skull roof can not be showed. Rieppel et al. were not sure whether there was posterolateral process of frontal (Rieppel et al., 2006). There should be a slender posterolateral process after we reexamined the holotype of Anshunsaurus wushaensis. However, it is distinct that the postfrontal and postorbital fuse to one bone as Anshunsaurus huangguoshuensis. It is the most distinct differentiation between Anshunsaurus huangnihensis and Anshunsaurus wushaensis. According to above comparison, it is reasonable that the huangnihensis is the third species of Anshunsaurus, although it was yielded in the same layer to Anshunsaurus wushaensis.

It is easy to distinguish *Anshunsaurus huangnihensis* to *Miodentosaurus brevis* located in early Canian (Upper Triassic). However, some characters are similar in these two taxa. Cheng et al. considered that there was not posterolateral process of frontal in *Miodentosaurus brevis* (Cheng et al., 2007). Wu et al. restudied the holotype (NMNS-004727/F003960) of *Miodentosaurus brevis*, they identified that the posterolateral process of the frontal overlapped the parietal as *Anshunsaurus huangnihensis* and the pineal foramen located between parietal and frontal instead in parietal (Wu et al., 2009).

Hitherto, *Askeptosaurus italicus*, from the Middle Triassic Grenzbitumenzone (Anisian/Ladinian) in Monte San Giorgio, was the oldest record of Askeptosauridae. Some characters of the skull of *Anshunsaurus huangnihensis* are similar to that of *Askeptosaurus italicus*: postfrontal not fusing to postorbital; the posterior process of the jugal short. But, the upper temporal fenestra does not close and the frontal has no posterolateral process in *Askeptosaurus italicus* (Müller, 2002; 2005). These are plesiomorphic characters in Askeptosauridae. So, *Askeptosaurus italicus* represents primitive taxon in Askeptosauridae. The coracoid is similar among *Askeptosaurus italicus, Anshunsaurus huangnihensis* and *Endennasaurus acutirostris*. It indicates that this character should be another one plesiomorphic character in Askeptosauridae. So, *Anshunsaurus huangnihensis* should be the important transitional node in Askeptosauridae evolution.

In tetrapod vertebrates, the skull generally grows negatively allometric (Rieppel et al., 2006). The skeletal ratios not only help identifying genus and species of Askeptosauridae but also are used to analyzing the skeletal evolutional direction in their water adaptation. Most ratios are almost equal between *Anshunsaurus huangnihensis* and *Anshunsaurus wushaensis* (Table 1). And, the ratios of them are just between those of *Askeptosaurus italicus* and *Anshunsaurus huangguoshuensis*. That result corresponds to the age of them. So, it indicates that the evolutional direction should be from *Askeptosaurus italicus* to *Anshunsaurus huangguoshuensis*. In evolutional progress, the rostrum and skull increase gradually related to the body (Table 1, Fig.2). Those more benefit preying. Limbs scarcely change related to the body in evolutional progress, but the distal width of the humerus

becomes more expanded which can supply more power for swimming in ocean. The ratios of *Miodentosaurus brevis* are much different to other taxa of Askeptosauridae. It indicates *Miodentosaurus brevis* is one peculiar taxon in Askeptosauroidea. Keywords: Thalattosaur, Anshunsaurus, Triassic, Guizhou

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TITHONIAN MARINE HERPETOFAUNAS FROM THE NEUQUEN BASIN (NORTHWEST PATAGONIA, ARGENTINA)

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RH: FERNÁNDEZ ET AL.—TITHONIAN MARINE REPTILES FROM PATAGONIA, ARGENTINA

Marine reptiles from the Neuquén Basin represent the best record of Jurassic marine reptiles from Gondwana. The Neuquén Basin is located on the eastern side of the Andes in Argentina and central Chile, between 32° and 40°S latitude. Of particular interest are Tithonian (Late Jurassic) marine reptiles that have been found in transgressive offshore facies of the Vaca Muerta Formation. This Tithonian record is outstanding for two main reasons: first, it documents a complete succession of early, middle, and late Tithonian-Berrasian marine reptile faunas dominated by off-shore predators; second, in at least four localities, natural casts of internal cavities of metriorhynchid skulls have been found. Tithonian marine assemblages of the Neuquén Basin include ichthyosaurs (Caypullisaurus bonapartei, Aegirosaurus sp. and another ophthalmosaurid); marine testudinata (Neusticemys neuquina and Notoemys laticentralis); pliosaurids (Pliosaurus sp.), and metriorhynchids (Cricosaurus araucanensis and Dakosaurus and intensis). Although metriorhynchids in the Neuquén Basin are represented only by two nominated taxa, C. araucanensis and D. andiniensis, they represent both extremes of the morphological diversity of the clade. Another peculiarity of metriorhynchid records is that skull materials are three-dimensioned preserved contrasting with most flattened metriorhynchids recovered from European basins. On the other hand, natural casts of C. araucanensis from the Vaca Muerta Fm. provide exceptional information allowing the reconstruction of soft organs housed in the snout of these metriorhynchids. Soft organs reconstructed include exocrine glands (salt glands), and the paranasal sinus system. Recent finding of a natural cast of D. andiniensis snout, including salt gland casts, is reported.

INTRODUCTION

Marine reptiles from the Neuquén Basin represent the best record, both quantitative and qualitative, of Late Jurassic marine reptiles from Gondwana. Since the XIX century, the Jurassic of the Neuquén Basin has been known to yield marine reptiles (Burmeister and Giebel, 1861; Dames, 1893; Phillipi, 1895). Rusconi (1948a, 1948b, 1949, 1967) described and named Jurassic ichthyosaurs and plesiosaurs from Mendoza province (Argentina). However most of the names he proposed are of

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doubtful application and must be regarded as nomina dubia. In the seventies, as part of a research program of Mesozoic marine reptiles of South America, the paleontological prospection of marine rock formations in the Neuquén Basin from which vertebrate fossils have been reported by Rusconi, and anecdotally by local people, resulted in a rich collection of marine reptiles including ichthyosaurs, pliosaurs, metriorhynchid crocodyliforms, and turtles. Most of the specimens are held in the Museo de La Plata (La Plata, Argentina) and Museo Olsacher (Zapala, Neuquén, Argentina). Of particular interest are those specimens found in transgressive offshore marine sediments of the Tithonian Vaca Muerta Formation. The base of this formation was deposited by a rapid transgressive event biostratigraphically dated as Tithonian–Valanginian that extended over a large part of the basin.

Tithonian deposits of the Vaca Muerta Fm. show features of restricted marine circulation and deep-water anoxia, resulting from the combination of a long term rise in sea level, the gulf–like palaeogeography of the basin, and its partial isolation from the proto–Pacific ocean by the growing Andean magmatic arc (Spalletti et al., 2000; Veiga et al., 2005). Several Tithonian localities throughout the Neuquén Basin have traditionally been known to be fossiliferous (Fig. 1). Gasparini and Fernández (1997) published a synthesis of Tithonian marine reptile assemblages from Neuquén. Since then, new findings and the re–examination of previously exhumed material increased our knowledge of these rich assemblages. In particular, the discoveries in the last decade of exceptionally well–preserved natural casts of the internal cavities of metriorrhynchid skulls allowed for exploration of their soft anatomy and brought important insights into the key innovations leading to the unparalleled marine specialization of metriorhynchids among archosaurs. Within this context, the purpose of the present contribution is to present an up–date synthesis of Tithonian marine reptile assemblages from the Neuquén Basin.

MARINE REPTILE–BEARING LOCALITIES FROM THE TITHONIAN OF THE NEUQUÉN BASIN

The marine Tithonian is represented by rich, organic dark shales with calcareous nodules of the Vaca Muerta Formation which is widely distributed in the entire basin. Tithonian deposits show a gradual passage from shallow marine to deeper areas without a significant slope break. A depositional ramp model has been proposed (Mitchum and Uliana, 1985; Legarreta and Uliana, 1991). Spalletti et al. (1999, 2000) recognized four environments for the Vaca Muerta Fm.: basinal, outer, middle and inner ramp, and marine reptiles were found in basinal and outer ramp anoxic facies.

To characterize Tithonian marine reptiles from the Neuquén Basin, we have selected three of the richest fossiliferous localities of this basin: Cerro Lotena (39°11'S, 69°40'W) which is the closest to the coast; Los Catutos (38°49'S, 70°12'W), and Yesera del Tromen-Pampa Tril (37°17'S, 69°53'W) (Fig. 1).

Localities

Cerro Lotena—Most specimens in the collection of the Museo de La Plata and Museo Olzacher were collected in this locality. The ammonite association belonging to the *Virgatosphinctes mendozanus* Zone corresponds to the early Tithonian (Leanza, 1980, 1981; Riccardi, 1984; Aguirre-Urreta, 2001). The middle section of the Vaca Muerta Formation is composed of light green calcareous shales interspersed with light gray concretional limestones up to 1 m thick. The vertebrates, quite well preserved, were found in the lower part of this section. At Cerro Lotena, the palaeoenvironment of the early Tithonian has been interpreted as temperate–warm shallow waters

(Leanza, 1980, 1993).

The most abundant marine reptiles from this locality are ichthyosaurs. All the diagnostic remains can be referred to *Caypullisaurus bonapartei*, being its holotype one of the most complete ichthyosaurs from the Neuquén Basin (Fernández, 1997, 2007). Metriorhynchid crocodyliforms are represented by several specimens of *Cricosaurus araucanensis* (= *Geosaurus araucanensis*), including the holotype (Gasparini and Dellape, 1976; Herrera et al., 2009) (Fig. 2A). Metriorhynchid record from Cerro Lotena is outstanding for two reasons: first, contrary to the European records, all the skulls recovered are three-dimensioned preserved; second, in at least one specimen (MLP 86-XI-10-6), the natural casts of salt glands have been exceptionally preserved (Fernández and Gasparini, 2000, 2008). Two Testudinata occur in this localiy: the cryptodira *Neusticemys neuquina*, including the holotype; and the pleurodira *Notoemys laticentralis*. Plesiosaurs are represented only by a mandible of *Pliosaurus* (= *Liopleurodon*) sp.

Los Catutos—Most of the marine reptiles from Los Catutos Area were found in the lithographic limestones of the type locality of the Los Catutos Member, the fossiliferous quarry called 'El Ministerio' (Cione et al., 1987; Leanza and Zeiss, 1990, 1992, 1994). Sedimentological and structural analyses suggest that these limestones were deposited in a shallow sea (10–30 m) no more than 100 km from the eastern coast of the Neuquén Basin (Leanza and Zeiss, 1990; Scasso et al., 2002). The Los Catutos Member belongs to the middle–late Tithonian *Windhauseniceras internispinosum* ammonite zone (Leanza and Zeiss, 1990, 1992, 1994). This age is also confirmed by the association of calcareous nannofossils, particularly *Polycostella beckmanii* (Scasso and Concheyro, 1999). Before 1990, marine reptiles were recovered by geological and paleontological expeditions. Later on, 'El Ministerio' and other quarries have been privately exploited, and paleontological expeditions are, since then, not authorized. However, and despite the uneven collecting efforts during these years, the marine reptile assemblage from Los Catutos is significant due to the preservation quality and diversity.

Marine reptiles include flattened and articulated remains of ichthyosaurs, turtles, metriorhynchid crocodyliforms, and a disarticulated pterodactyloid. Turtles are the most commonly remains found. As in Cerro Lotena, the two major clades of Testudinata, Cryptodira and Pleurodira, are represented by Neusticemys neuguina and Notoemys laticentralis respectively. Articulated skeletons of both taxa recovered from Los Catutos (Fig. 2B-D) do not indicate long post-mortem transport, and suggest that as early as the Tithonian pleurodires and cryptodires were adapted to life in marine environments. A peculiar testudinata material from Los Catutos is an articulated hindlimb of Neusticemys neuquina that depict a very unusual pattern of limb morphology characterized by the elongation of the post-axial digit achieved through the elongation of the bones, as well as a moderate hyperphalangy (four phalanges in the pedal digit V) (de la Fuente and Fernández, 2010). Ichthyosaurs are represented by several remains but two juvenile articulated specimens are of particular interest: one of them is an almost complete specimen identified as Aegirosaurus sp. based on the forefin morphology, being the first occurrence of this taxon out of the western Tethys. The other, currently under revision, is a new Ophthalmosauridae formerly identified as Ophthalmosaurus monocharactus (= O. icenicus) by Gasparini (1988). Later on, Maisch and Matzke (2000) in their revision of Ichthyosauria referred it to the genus Aegirosaurus. However, no evidence supports its assignation neither to Ophthalmosaurus nor to Aegirosaurus (Fernández, 2007). Metriorhynchid remains include a complete skull of an undescribed Cricosaurus. Only few isolated teeth can be referred to a plesiosauroid. A nearly complete postcranial skeleton of a pterodactyloid represents the most complete Jurassic pterosaur so far known from South America (Codorniú et al., 2006).

Yesera del Tromen-Pampa Tril—This marine reptile-bearing locality is situated in the central Neuquén Basin. Marine reptiles were collected from the deposit of a basinal to outer ramp environment of the lower portion of the Vaca Muerta Formation, composed of thick intervals of black shales associated with black marls, thin packstone–wackestone beds and fine–grained pyroclastic fall deposits. According to Spalletti et al. (1999) the age of this locality is late Tithonian-Berriasian. Marine reptiles recovered include *Dakosaurus andiniensis* (Fig. 2E), *Caypullisaurus bonapartei* (Fig. 2F), *Cricosaurus araucanensis*, and undescribed pliosaurs including one specimen with a mandibular length up to 2.4 m. Up to date no Testudinata remains have been recovered. The most conspicuous feature of marine reptiles from this locality is that most of them are large, exceeding 4 m in total length.

UNUSUAL PRESERVATIONS OF NATURAL INTERNAL CASTS OF METRIORHYNCHID SKULLS

In 2000, Fernández and Gasparini indentified for the first time, the casts of salt glands in the skull of two specimens of *C. araucanensis* exhumed from Tithonian levels of the Vaca Muerta Fm. outcropping in Cerro Lotena (39°11'S, 69°40'W) and Sierra de Reyes (36°40'S, 69°20'W). Later on, we found in the collections of the Museo de La Plata three other specimens from Sierra de Reyes, Cerro Granito (39°09'S, 69°34'W) and a locality in Cerro Lotena area, Bosque Petrificado (39°12'S, 69°42'W), in which these same structures can also be identified (Fernández and Gasparini, 2008). The specimens from Sierra de Reyes have also preserved a large portion of the snout including paired diverticula associated to the nasal capsule that forms part of the paranasal sinus system (Fernández and Herrera, 2009) (Fig. 3A). New field trips carried on in Pampa Tril area yielded three natural snout casts of *C. araucanensis* (Fig. 3B). But the most exciting finding is an undescribed specimen of *Dakosaurus andiniensis* found in Mallin Quemado locality (38°35'S, 70°04'W) which also preserves the casts of enlarged salt glands (Fig. 3C).

DISCUSSION

The Tithonian marine reptile record of the Neuquén Basin is outstanding for two main reasons. First, the succession of early-middle and late Tithonian-Berrasian marine reptile faunas of the Vaca Muerta Fm. is one of the most complete worldwide. By the Late Jurassic the sea level in the European basin dropped, resulting in less attractive habitats for large offshore predators, and thus, the tithonian record is abundant in costal forms (Bardet, 1994). However, in the Neuquén Basin, transgressive marine sediments of the Vaca Muerta Formation yielded a great amount of well-articulated specimens of off-shore predators, some of them (e.g., Cricosaurus araucanensis or Aegirosaurus sp.) could be considered as intermediate species in a food-web, while others (e.g., Pliosaurus sp., Dakosaurus andiniensis) were top-predators. Excepting for Notoemys laticentralis, the rest of the Tithonian marine reptiles from the Neuquén Basin correspond to offshore predators. In the sourthern area of the basin, in Cerro Lotena and Los Catutos, the reptile bearing horizons are also characterized by rich invertebrate faunas, principally ammonites (Leanza, 1980, 1981; Riccardi, 1984; Riccardi et al. 2000; Aguirre–Urreta, 2001). In the early Tithonian of Cerro Lotena, interpreted as a palaeoenvironment characterized by temperate-warm shallow waters, turtle remains, and in particular Notoemys laticentralis, are more abundant. Large off-shore predators are represented by Caypullisarus bonapartei, and Pliosaurus. In the middle-late Tithonian of Los Catutos, also interpreted as a shallow

sea paleoenvironment, marine reptile remains are small or middle-sized. In the deeper parts of the basin, in Yesera del Tromen–Pampa Tril, the reptile bearing horizons are largely devoid of invertebrates; and the marine reptile assemblage is dominated by large size off-shore predators. Most of the remains exhumed exceed 4 m in total length.

The second outstanding characteristic of the Tithonian record of the Neuquén Basin is that in several Tithonian localities, like Cerro Lotena, Bosque Petrificado, Yesera del Tromen-Pampa Tril, and Sierra de Reyes, exceptionally preserved natural casts of cranial cavities of metriorhynchid skulls have been found. The soft organs that could be reconstructed upon them include enlarged salt glands, and diverticula associated to the nasal capsule corresponding to the pneumatic paranasal sinus system. These fossils provide exceptional information about the key innovations leading to the unparalleled marine specialization of metriorhynchids among crocodyliforms. The integration of fossil information with those of extant marine reptiles (Hazard, 2001, 2004; Dunson and Mazzotti, 1989; Jackson et al.,1996) indicates that C. araucanensis salt glands had high secretory capacity, both in volume and concentration of the secreted fluid, and implies that this metriorhynchid could ingest osmoconforming preys (e.g., cephalopods) (Fernández and Gasparini, 2008). Noteworthy, belemnites have been reported as an important item in this metriorhynchid diet (Martill, 1986). However, the presence of enlarged salt glands was also significant for the top predator metriorhynchid-like Dakosaurus, whose diet could include mainly osmoregulator preys. Enlarged salt glands (i.e., glands with high secretory capacity) are also related to the capacity of drinking seawater (e.g., extant sea turtles). Extant crocodylids (even estuarine populations) have small salt glands of low secretory capacity and drink only fresh water (Jackson et al., 1996), so dispersal capacities of these forms are limited. On the other hand, the presence of enlarged salt glands in metriorhynchids indicates that, at least once in the evolutionary history of crocodyliforms, the capability of drinking seawater was achieved allowing trans-oceanic dispersal. The capability of transoceanic dispersal as a factor to explain the distribution of different crocodyliforms lineages has been traditionally pointed out (e.g., Jackson et al., 1996; Vélez-Juarbe et al., 2007; Taplin et al., 1999), and evidences like those of the metriorhynchids bring new insight into this topic.

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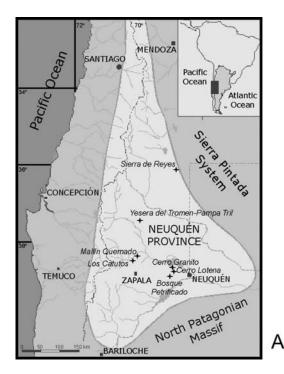
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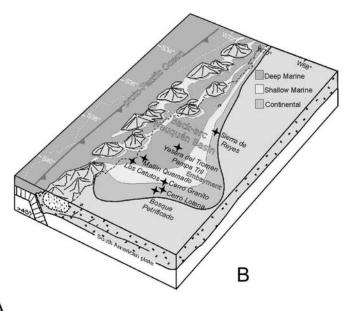
FIGURE CAPTIONS.

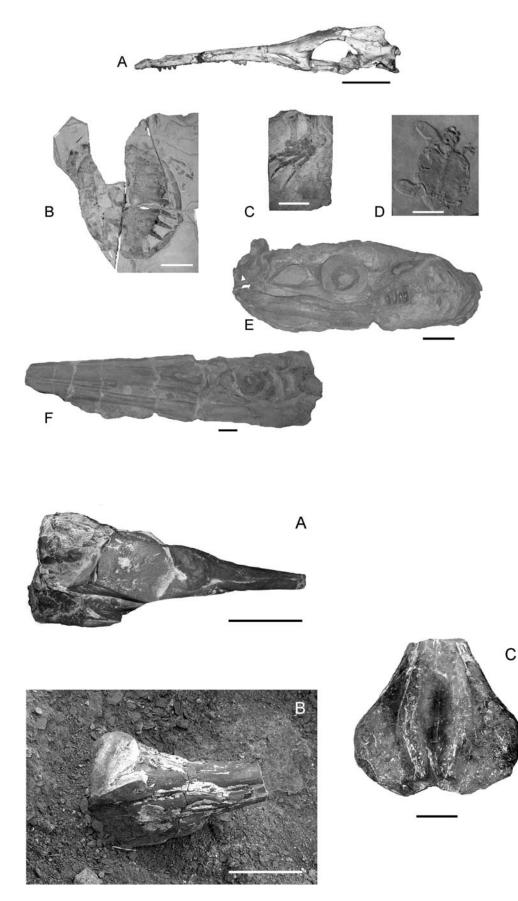
FIGURE 1. Location map of marine reptiles bearing localities (A) and reconstruction of the Neuquén Basin(B). Modified from Veiga et al., 2005

FIGURE 2. Tithonian marine reptiles from the Neuquen Basin. **A**, holotype of *Cricosaurus araucanensis* (MLP 72-IV-7-1); **B**, *Neusticemys neuquina* (MLP 92-IV-10-1); **C**, *Neusticemys neuquina* (MPCA 6769) hindlimb and pes; **D**, *Notoemys laticentralis* (MOZ 4040); **E**, *Dakosaurus andiniensis* (MOZ 6146); **F**, *Caypullisarus bonapartei* (MOZ 6139). Scale bar 10 cm. [planned for page width].

FIGURE 3. **A**, Natural cast of *Cricosaurus araucanensis* (MLP 76-XI-19-1) in right lateral view; **B**, natural cast of part of the snout of *C. araucanensis* of a new specimen recovered form Pampa Tril area; **C**, natural cast of *Dakosaurus andiniensis* in dorsal view. Scale bar 5 cm. [planned for page width].







THE TANYSTROPHEIDAE AND THEIR GLOBAL DISTRIBUTION.

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The protorosaurs constitute a little known but diverse and important radiation of Permian and Triassic reptiles. The group includes lizard-like terrestrial forms, chameleon-like arboreal forms, and marine representatives with extreme neck elongation. *Protorosaurus* from the early Late Permian (*Kupferschiefer*) of Germany is considered to be the oldest representative of the group, while the tanystropheids were the last representatives of the clade, and went extinct in the Late Triassic.

The best known tanystropheid is *Tanystropheus* (Fig. 1) from Middle Triassic marine sediments in Central and Alpine Europe (Wild, 1973; Nosotti, 2007), the Middle East (Rieppel, 2001), and China (Li, 2007; Rieppel et al., 2010). With a neck over half the length of the entire animal, *Tanystropheus* was a bizarre reptile that may have been almost entirely restricted to water as an adult. Closely related to *Tanystropheus* is *Tanytrachelos ahynis*, a freshwater form from the Late Triassic of eastern North America (Olsen, 1979) known from numerous complete specimens (Fraser et al., 1996; Casey et al., 2007). Most recently, Fraser and Rieppel (2006) also referred *Amotosaurus* from the Black Forest to the Tanystropheidae. One of the key characteristics of the group is the metatarsal-like form of the proximal phalanx of digit V of the tarsus. Based on the presence of this feature together with the elongated cervical series, *Langobardisaurus* from the Norian of Italy (Renesto 1994) is almost certainly a member of the same clade. The sister-group to all these taxa is *Macrocnemus* from Middle Triassic marine deposits of the Southern Alps (Peyer, 1937) and China (Li et al., 2007).

Tanystropheus longobardicus was originally described on the basis of a number of specimens with an extensive size range that originated from the Grenzbitumenzone (Anisian/ Ladinian) of Monte San Giorgio. Wild (1973) described in detail marked difference in the dentition that are clearly present between the smallest specimens and the largest individuals. All the large examples exhibit a marginal dentition comprising large acutely conical teeth, while the smaller specimens have a heterodont dentition with tricuspid marginal teeth lining the posterior half of each jaw quadrant. Wild postulated that the smaller specimens were the juveniles and that they at least were partially terrestrial in their habit and were insectivorous. By contrast he considered the larger adults to be piscivores that were largely confined to the sea.

A second species, *T. meridensis* was described on the basis of a single specimen from slightly younger (Lower ladinian) strata (Wild 1980a). This specimen also bears tricuspid teeth. Fraser et al (2004) were unable to find any characters to distinguish *T. meridensis* from the putative juveniles of *T. longobardicus*, and these authors suggested that all instances of small individuals with the heterodont dentition might represent a separate species distinct from *T. longobardicus*.

A third species was recognized by Ortlam (1967) and Wild (1980b) from the Black Forest, and was referred to as *Tanystropheus antiquus*. However, Fraser and Rieppel (2006) referred it to a new genus *Amotosaurus* recognizing, among other differences, that it had only eight cervical vertebrae

rather than twelve as recognized at the time in Tanystropheus, (but see below).

A recently described specimen of *Tanystropheus* from the upper part of the Zhuganpo Member of the Falang Formation is consistent with *T. longobardicus* (Rieppel et al., 2010). However, since it lacks a skull it cannot be unequivocally assigned to the same species at the present time. This specimen also demonstrated for the first time that there are 13 cervicals in *Tanystropheus* possesses rather than 12 as described by Wild (1973). A condition that has been confirmed upon re-examination of the original *Tanystropheus* material from the Grenzbitumenzone.

With the exception of *Tanytrachelos* in Eastern North America (and possibly also from isolated remains), the distribution of tanystropheids within the Eastern (China) and Western (Middle East, Europe) Tethyan Faunal Province closely mirrors that of some Triassic sauropterygians and thalattosaurs. *Tanytrachelos* is also unusual in being the only member of the group not known from marine deposits. Moreover, it occurs in the interior of Pangaea prompting intriguing questions concerning the distribution and radiation of the group. A recent study of the depositional environment of sediments yielding *Tanystrachelos* (Liutkus et al., 2010) may offer some important insights.

Tanytrachelos (Fig. 2) is known almost exclusively from the Newark Supergroup, although isolated fragmentary cervical ribs and vertebrae from the Chinle Formation of the American Southwest (Kaye and Padian, 1994) might conceivably be attributed to the same genus. Most occurrences of *Tanytrachelos* are at the Solite Quarry on the Virginia-North Carolina State line where several hundred specimens have been collected. Olsen (1979) described it as having 12 cervicals, although examination of new material particularly using CT scan data indicates that it too possessed 13 cervicals. Growing up to 30 cm it is considerably smaller than *Tanystropheus* and the neck while markedly elongate, does not attain quite the disproportionate length seen in *Tanystropheus*.

A recent study of the Solite sediments (Liutkus et al, in press) suggests that *Tanytrachelos* inhabited a rather inhospitable paleoenvironment. Contrary to the generally held view that *Tanytrachelos* lived in and around relatively deep lakes, new evidence suggest that *Tanytrachelos* may have habitually lived in and around the margins of rather toxic alkaline, saline and shallow lake systems. Such conditions would require very special adaptations in *Tanytrachelos*, but possibly ones that were not inconsistent with its marine origins.

ACKNOWLEDGMENTS

We are grateful to Heinz Furrer and Heinz Lanz for access to the *Tanystropheus* and *Macrocnemus* material in the collections of the Paläontologisches Institut und Museum der Universität Zürich. Mary Ann Turner kindly loaned material of *Tanytrachelos* housed in the collections of the Yale Peabody Museum. NCF and OR especially want to thank Stefania Nosotti for the many fruitful discussions on tanystropheids.

Institutional abbreviations — **GMPKU**, Geological Museum of Peking University, Beijing; **YPM**, Yale Peabody Museum.

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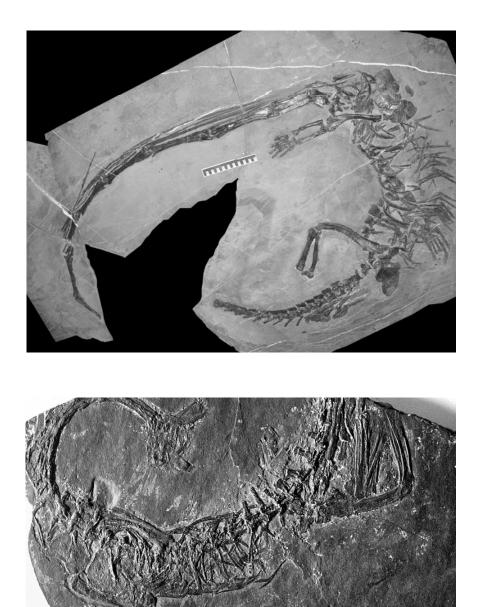
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FIGURE CAPTIONS

FIG. 1. *Tanystropheus* cf. *T. Longobardicus*, GMPKU-P-1527, from the Zhunganpo member of the Falang Formation of Guizhou Province, PRC.

FIG 2 The holotype of Tanytrachelos ahynis, YPM 7496, from the Virginia Solite Quarry, Virginia, USA.



NEW TAXON OF PHREATOICIDEA (CRUSTACEA, ISOPODA) FROM LUOPING FAUNA (MIDDLE TRIASSIC) AND ITS SIGNIFICANCE OF PALEOGEOGRAPHY

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INTRODUCTION

The suborder Phreatoicidea, the first isopod group to appear in the Paleozoic fossil record (Wilson and Edgecombe, 2003), is an important taxon for the phylogeny of isopod. Till now, all of the Mesozoic phreatoicidean fossil records were found in Gondwanan terranes and in fresh water. However, the new specimens of Phreatoicidea which show an implication of Australian paleogeographic affinity were newly collected from the Upper Member of the Guanling Formation at Dawazi Village, Luoping County, Yunnan Province, southwestern China. This recently-discovered site holds abundant Middle Triassic marine reptiles and fishes, and was described as the Marine Luoping Fauna (Zhang et al., 2008; Sun et al., 2009). Herein we provide a detailed description on the fossils and discuss the implications of this first marine record of the crown group Phreatoicidea outside of Gondwana.

GEOLOGICAL SETTING

The complete phreatoicidean isopod fossils were excavated from the upper vertebtate horizons (UVH) in the Upper Member of the Guanling Formation with the age of Pelsonian, Anisian, Middle Triassic at Dawazi Village, Yunnan Province, southwestern China (Fig. 1). The upper vertebtate horizons (UVH), which contains abundant marine reptile fossils (e.g.: Mixosaurus, Placodus, Nothosaurus and Lariosaurus), mainly consist of thin-bedded marly limestone. The lithology and coexisted other invertebrate fossils (e.g.: crustaceans, echinoderms, gastropods) suggest the fossil site situated in a near-shore rather than pelagic sedimentary setting during the Anisian of the Middle Triassic.

SYSTEMATIC PALAEONTOLOGY

Order ISOPODA Latreille, 1802

Suborder PHREATOICIDEA Stebbing, 1893

Family AMPHISOPIDAE Nicholls, 1943

Genus PROTAMPHISOPUS Nicholls, 1943

Type species: Phreatoicus wianamattensis Chilton, 1918, from Rouse Hill Siltstone Member, Ashfield Shale (Middle Triassic, Anisian) at former brick clay pits, St. Peters, New South Wales, Australia; by monotypy.

Diagnosis (revised from Wilson and Edgecombe, 2003): Head dorsal surface lateral profile smoothly curved; tubercles absent. Eyes present, large, projecting anteriorly, approximately round. Mouth field adjacent to posterior margin of head and anterior margin of pereonite 1. Pereon with transverse ridges. Pereopod I and IV not sexually dimorphic. All pereopodal bases with dorsal ridges and lateral face ridges; ischia especially short, less than third length of bases, but still fully articulated. Pleon in lateral view much deeper than pereonites with basal region of pleopods not visible. Pleotelson vaulted with vertical lateral fields, dorsal surface in lateral view evenly curving, smooth; posterolateral margin uninterrupted; posterior apex visible in lateral view; distal tip not elaborated or substantially modified. Uropod protopod not reaching pleotelson apex, dorsomedial ridge produced, plate-like, margin smooth, in lateral view approximately straight.

DESCRIPTION Fig. 2

Head: Lateral profile of dorsal surface smoothly curved; surface pitted; tubercles absent; setae unknown. Eyes projecting anteriorly; approximately round. Cervical groove straight, extending over dorsal margin of head and connecting medially. Mandibular notch present. Clypeal notch present. Antennal notch deep. Antennula length 0.09 body length, with 9-10 articles. Antenna length 0.24 body length; flagellum with 11–13 articles. Maxilliped epipod distal tip broadly pointed. Pereon: Transverse ridges present. Pereopods I-VII coxae not laterally projecting; not sexually dimorphic; basis dorsal ridge in cross-section, forming distinct plate, lateral face central ridge present, lateral face ventral ridge present; propodus articular plate present. Pereopod I subchelate; dactylus shorter than palm; propodal palm convex weakly. Percopod IV not prehensile. Pleon: Pleonites much deeper than perconites in lateral view, with large pleurae, basal region of pleopods not visible; pleonite 1 pleura distinctly shallower than pleurae of pleonites 2-5. Pleotelson: Lateral profile vaulted. Dorsal surface in lateral view evenly curving, smooth, median ridge present, setae present (assumed from setal sockets), lateral ridges continuous with posterior apex. Ventral surface anterior to uropods strongly concave, with single row of simple robust setae; postanal ventral surface present; lateral uropodal ridge curving strongly and extending posteriorly from uropods on pleotelson margin with a few robust setae . Posterolateral margin uninterrupted. Posterior apex projecting in dorsal view; visible in lateral view; free. Uropod protopod not reaching pleotelson apex, plate-like, margin smooth; endopod subequal to protopod length, longer than exopod, dorsal margin straight; ventral margin convex.

DISCUSSION

Habitat classification: This new record is thought to site in a near-shore setting and comparably preserved in low density, whether it imply a marine habitat or a secondary introduction into marine waters needs a detailed taphonomic and sedimentary investigation to convince.

Significance of Paleogeography: This new phreatoicidean taxon are an important member of the Middle Triassic Panxian-Luoping Fauna, which is one of the best preserved Triassic marine vertebrate faunas in the world. It is a representative marker of the rapid evolutionary radiation of biota in the Middle Triassic with the global sea level maximum on both stage and period scale (Jiang et al., 2009). As it is reported, the marine reptile and fish of the Panxian-Luoping fauna show a strong western Tethyan paleobiogeographic affinity between Southwestern China and Europe, indicated by cogenera of

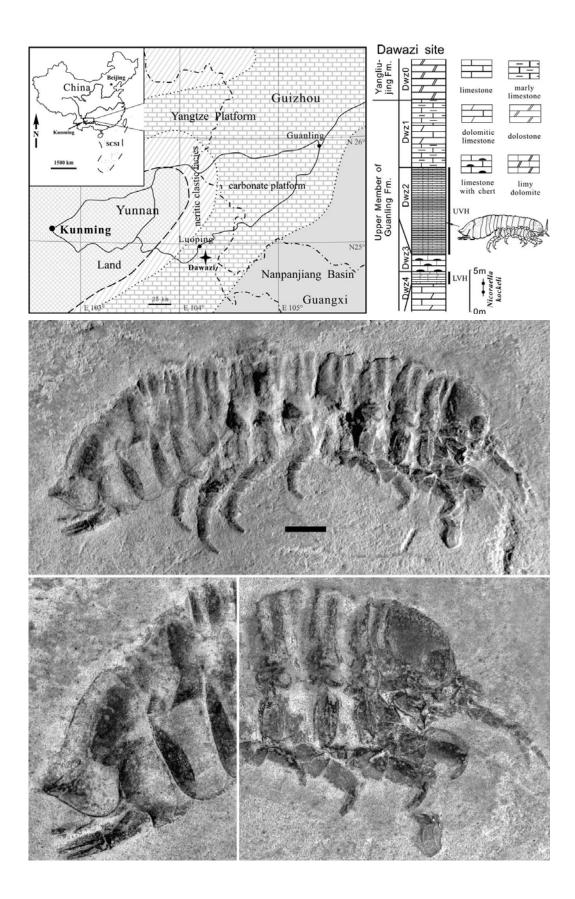
the *Mixosaurus*, the *Placodus*, the *Nothosaurus*, and the *Lariosaurus*. However, the new isopod taxon shows an implication of Australian paleogeographic affinity. These findings hint a Middle Triassic fauna distributed along the northern coastline of the Paleotethys. This requires further discussion of the paleogeographic history of South China Terrane (Fu et al., 2010).

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FIGURE CAPTIONS

Figure 1. (A) Middle Triassic paleogeographic map of eastern Yunnan and western Guizhou, South China, from Fu et al., 2010; (B) The stratigraphic column showing position of the layers bearing Protamphisopus at Dawazi site, from Fu et al., 2010. Abbreviated characters: UVH, upper vertebrate horizons; LVH, lower vertebrate horizons. Figure 2. photographs of *Protamphisopus* sp. in lateral view. Scale bar 1 mm.



PALAEOGEOGRAPHY, PALAEOECOLOGY AND TAPHONOMY OF MIDDLE TRIASSIC VERTEBRATE FOSSIL LAGERSTAETTEN IN THE SWISS ALPS

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The Monte San Giorgio in the Southern Alps (Ticino) and the Ducan mountain chain in the Eastern Alps (Grisons) yield two well studied vertebrate fossil lagerstaetten in the marine Middle Triassic of Switzerland (Fig. 1). The Monte San Giorgio area, situated at the border between Southern Switzerland and Northern Italy, is a truly unique locality renowned for it's importance as a UNESCO World Heritage site. Approximately 80 fish and 20 reptile taxa, and numerous invertebrates and plants have been excavated in its five vertebrate beds from the late Anisian to late Ladinian age since 1850 (Besano and Meride Formations, Furrer, 2003). Systematic excavations in the Ducan mountain chain near Davos started in 1992 and unearthed 5 reptile, 30 fish, a number of invertebrate and plant taxa (Furrer, 2009). Precise U-Pb age determinations from two volcaniclastic layers indicate a radiometric age of 241 Ma for the richest fossil beds in the uppermost Prosanto Formation, suggesting an early Ladinian age, compared to the Global boundary Stratotype Section and Point (GSSP) for the base of the Ladinian at Bagolino in Northern Italy (Brack et al., 2005; Furrer et al., 2008).

All these vertebrate beds were deposited in similar environments consisting of small restricted basins situated on a wide shallow marine carbonate platform at the Western end of the Tethys.

The outstanding quality of preservation of many articulated skeletons in bituminuous shales, laminated limestones and dolomites can be explained by deposition of the dead pelagic organisms in fine grained sediments at the bottom of these restricted basins amongst dysoxic to anoxic conditions (Fig. 2). Thin, often lenticular, accumulations of benthic calcareous algae, foraminifers and ostracods, bivalves and gastropods, and thin bedded calciturbidites suggest transport of benthic organisms and resedimentation of carbonate sand and mud from the rims of the basins and shallow water platforms. Wood and other terrestrial plant remains, rare terrestrial reptiles and insects document the existence of neighbouring islands or coastal plains.

The association and number of various fossils in the studied sections together with exciting specimens of five different species of *Saurichthys*, yielding not fully digested prey in the mouth, throat or stomach, allowed the reconstruction of a simplified food web of the Middle Triassic seas (Fig. 3). The relationships between prey and predators are illustrated by arrows.

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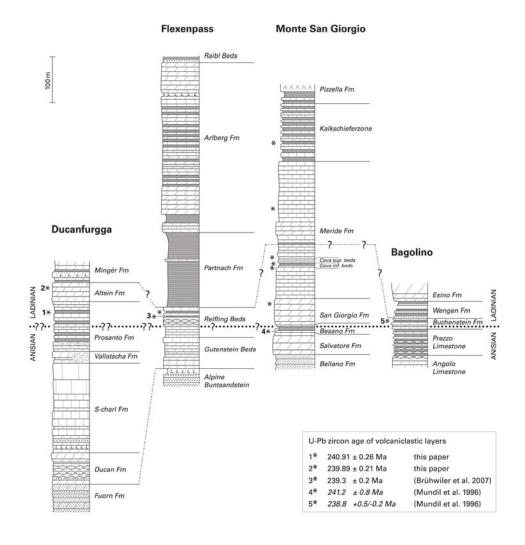
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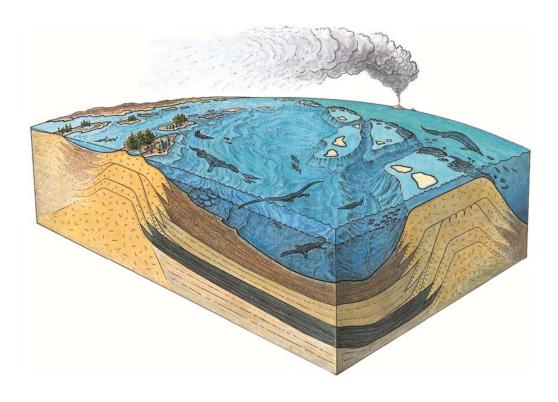
FIGURE CAPTIONS

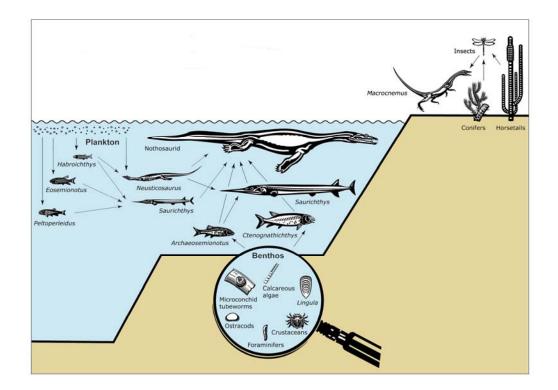
FIGURE 1. Correlation of the Middle Triassic section at Ducanfurgga (Eastern Switzerland, Upper Austroalpine Silvretta nappe) with sections at Flexenpass (Western Austria, Upper Austroalpine Lechtal nappe), at Monte San Giorgio (Southern Switzerland, western Southern Alps), and the GSSP-section for the base of the Ladinian stage at Bagolino (Northern Italy, Southern Alps) (after Furrer et al., 2008).

FIGURE 2. Diagram of a restricted basin in the early Ladinian carbonate platform at the western end of Tethys (not to scale, modified from Furrer, 2003).

FIGURE 3. A simplified food web of the Middle Triassic seas. The relationships between prey and predators are marked by arrows (modified from Furrer, 2009).







NEW FOSSIL SITES WITH TRIASSIC VERTEBRATE FAUNA FROM THE KAMNIK-SAVINJA ALPS, SLOVENIA

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INTRODUCTION

After the winter of 2006, several samples of Triassic dark bituminous marlstone and laminated limestone were collected loose in the scree in the Kamniška Bistrica valley in the Kamnik-Savinja Alps, northern part of the Central Slovenia (Fig. 1). The site was then more precisely investigated and during the field excursion in September 2006 the first fish remain was found on a fragment of dark bituminous marlstone. Afterwards, several surveys were carried out in search for the original outcrop, which was discovered at the end of September 2006. In the following years the broader area of the Kamnik-Savinja Alps was investigated in more detail. As a result of this work, several new sites with mostly very well preserved Early and Middle Triassic plant, mollusk, decapod, brachiopod, echinoid, ophiuroid, crinoid, amphibian, fish, and reptile remains were found. In this article, new sites and collected fossil material is described. Here we describe the Middle Triassic Velika planina Horizon and Strelovec Formation and their fossil content.

VELIKA PLANINA HORIZON AND ITS FOSSIL CONTENT

An approximately 200 m thick succession of dark laminated to thick bedded bituminous limestone of the vertebrate-bearing Velika planina horizon is best exposed in a broad area of the Velika planina Mountain (Fig 1.). This horizon could represent lateral equivalent of the Lower Anisian dolomite in the lower part and of the slightly younger, probably Middle Anisian, Strelovec Formation in the upper part (Fig. 2). Unfortunately, relatively extensive conodont sampling gave no results. Therefore, the exact

age is questionable.

Among frequent coprolites and isolated reptile remains, the fish specimens are rare. Most of the fish specimens were slightly distorted before fossilization, therefore their determination is difficult. Among the fish specimens genus *Eosemionotus* (Pl. 1a), *Placopleurus*, and *Saurichthys* were indentified so far. More common are isolated reptile bones. Additionally, two fragmentary reptile specimens have been collected, while there are not yet enough elements for a detailed description. A quick survey of the specimen T-882 allows to identify a sacral vertebral series and a partial vertebral series with long bones, which all most probably belong to a pachypleurosaurid sauropterygian (Pl. 1b).

Mollusks and brachiopods are rare and appear only in few levels. Among rare echinoderms, one well preserved almost complete crinoid was found, which cannot be easily ascribed to any existing genus. No plant fossils were found in the Velika planina Horizon.

Among the fish specimens, the number of disarticulated specimens exceeds the number of the articulated ones, pointing to the predominantly disaerobic environment. There are also specimens showing clear unimodal dispersal with correlated position of similar elements indicating occasional current transport. However, we can also find completely articulated specimens. The different colour and texture of the sediment covering completely articulated specimens might indicate episodes of fast burial and anoxic conditions. The conditions at the sediment/water interface probably depended on the current action and might have had seasonal character. After the currents ceased, all the oxygen on the bottom was consumed and anoxic environment was established.

THE STRELOVEC FORMATION AND ITS FOSSIL CONTENT

Strelovec Formation represents a very distinct stratigraphic and/or lithologic reference in the investigated area (Fig. 2). It can be observed in a wide area of the Kamniška Bistrica Valley, Robanov kot, Logarska dolina Valley, and Matkov kot (Fig 1). The Strelovec Formation is represented by up to 60 meters thick succession of dark laminated bituminous limestone and bright laminated to thin bedded limestone and dolomite. The conodont analyses were negative. However, based on the stratigraphic position above the Lower Anisian carbonates and below the Upper Anisian Contrin Formation, it could be of the Middle Anisian, probably Pelsonian age.

Among fish specimens the most abundant is the genus *Eosemionotus*, followed by *Habroichthys* (Pl. 1c), *Placopleurus* (Pl. 1d), *Saurichthys* (Pl. 1e), and the early neopterigians probably close to semionotiform Locally, *Eosemionotus* specimens can be found in large numbers on single bedding planes (possibly mass mortality events). The fish fauna found in the dark laminated bituminous limestone differs from that found in the bright laminated to thin bedded dolomite. In the dark laminated to thin bedded dolomite it is not so common. In these latter beds the other neopterigians are quite common, but so far they have not been recovered from the dark laminated bituminous limestone.

The reptile remains are locally very common. Isolated vertebra, ribs, and unidentifiable fragmented bones predominate, among them a small fragment of placodont armour and 7 vertebrae belonging to an ichthyosaur (Pl. 1 f). So far, only two specimens have been found representing parts of articulated reptile individuals, which can be identified as belonging to pachypleurosaur sauropterygians. Specimen T-801 (Pl. 1 g) represents an incomplete caudal series, of a sauropterygian, and the change in the angle of orientation of the ribs shaft, along with the shift of the articulation of the ribs indicates that the preserved series belonged to the cranialmost portion of the tail. The low neural spines, along with

small size and the broad and stout zygapophyses suggest that they may have belonged to a pachypleurosaur.

Beside vertebrate fossils a variety of other animal fossils were found. Among crustaceans a *Schimperella* specimen, Isopods, a crab belonging to Erymidae, a Xiphosura and several thylacocephalans were found. The finds of echinoderms are rare; however, the ophiuroids of the genus *Aspidurella* are locally very common. Brachiopods, approximately 8 mm in diameter with hyaline shell, are one of the most characteristic fossils. The bivalves are rare. However, in the upper part of the Strelovec Formation up to 15 m thick succession can be observed, where shell-beds with *Gervillia* remains appear in several beds. The gastropods are rare; however, they can occur locally in large numbers. Plant remains are almost absent. Only a few poorly preserved '*Voltzia*' remains were found.

The majority of the fish specimens from the Strelovška Formation sites is complete and articulated pointing to predominantly anoxic environment. There are no indications of the current action and no indications of the seasonal character in deposition of the sediments. Synsedimentary structures (slump-folds, micro-faults, resedimented blocks) are common, indicating an inclined depositional surface or irregular sedimentation rate and/or subsidence. However, in the ~5 m thick layers in the lower part of the Strelovec formation on the Slatinski plaz site thin pyritic patinas on fish bones can be found suggesting a rapid burial in organic-rich sulfidic muds and a disaerobic environment. These layers might indicate the gradual shift of the aerobic environment to the completely anoxic one. Above them lies a bright laminated to thin bedded dolomite where complete and articulated fish specimens were found. These beds were probably deposited in waters with an anoxic bottom and a low productivity of the surrounding areas. Above them lies dark laminated bituminous limestone, which forms the largest part of the Strelovška formation. Here, also a large number of complete and articulated fish specimens were found. Dark laminated bituminous limestone was probably deposited in waters with a totally anoxic bottom and a high productivity of the surrounding areas. In this dark laminated bituminous limestone no evidence of pyritization on fossils has been detected, while in certain layers abundant framboidal pyrite is disseminated in the sediment which is typical for anaerobic environments). In the layers of dark laminated bituminous limestone up to 3 cm long celestine crystals can be found. The presence of celestine in these beds might be explained as being a consequence of evaporation of the sea water in the coastal marine settings. As the brines refluxed into underlying or laterally adjacent sediments, they leached substantial amounts of strontium when attempting to achieve chemical equilibrium with their host sediments. In between the dark laminated bituminous limestones, several, up to 4 m thick sequences of the light thick-bedded limestone, can be observed. Here, isolated reptile bones were found. These beds might indicate temporarily more open marine conditions with oxygenated bottom. In the upper part of the succession of the Strelovec formation in the Kamniška bistrica Valley, dark laminated bituminous limestone can be observed containing several dark bivalve shell-beds. Among the shells isolated reptile and fish bones can be found. These beds indicate well oxygenated bottom and high productivity of the surrounding areas.

CONCLUSION

The Tethydean Middle Triassic basins yield several sites which are very rich in marine vertebrates. The majority of localities are concentrated in the Southern Alps mainly in Lombardy (Italy), Canton Ticino and Graubunden (Switzerland), and in Southern China (Guizhou and Yunnan Provinces). The recently discovered sites from Slovenia lie in between these two regions. The fossiliferous areas show different paleoenvironmental setting. In the Southern Alps several intraplatform basin existed in the deeper parts of the carbonate-evaporite carbonate platforms. In Slovenia, their formation was related to the extensional tectonics in the Anisian and Ladinian. The basins were small and sedimentological and paleoenvironmental conditions were strongly influenced by local tectonic and paleotopographic settings. In Southern China, each single Middle Triassic fossiliferous level is known sometimes from hundred of square kilometers being furthermore quite homogeneous in environmental conditions. Some fish genera were very widespread and were also found on the new Slovenian sites: *Eosemionotus, Habroichthys, Placopleurus* are among the very small fishes that are frequently found all along the Alps as well in Southern China. However, as each area has also its own endemic genera such as *Felberia* or *Dipteronotus* for the Central Alps sites or several new genera under description from the Southern China area, therefore, it can be expected that also in the Slovenian sites there will be new interesting finds with the ongoing field works.

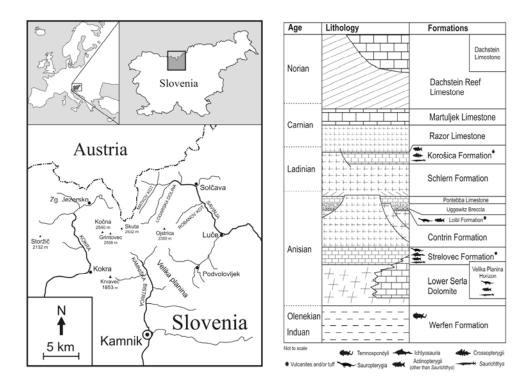
The new fossil sites from the Kamnik-Savinja Alps, Slovenia, yielded to date the most abundant Triassic fish and reptilian fauna found in Slovenia. Despite difficult terrain, which was probably the cause that these sites were not discovered earlier, very well preserved specimens, large variety of species and large still not well investigated area give hope for the discovery of new interesting finds and fossil sites in the future.

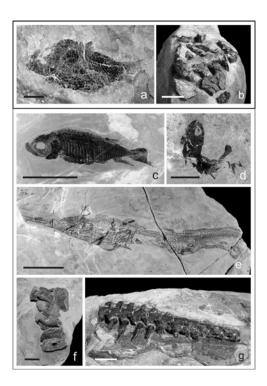
FIGURE CAPTIONS

FIGURE 1. Simplified geographic map of the investigated area, Kamnik-Savinja Alps, Slovenia.

FIGURE 2. Simplified stratigraphic column, showing (1) the stratigraphical development of the Triassic beds in the central part of the Kamnik-Savinja Alps and (2) the position of the vertebrate-rich horizons.

PLATE 1. *a*) T-949: scale bar = 1 cm; *b*) T-882: sacral part of Pachypleurosaur sauropterygian, scale bar = 2 cm. Both specimens T-949 and T-882 are form Velika planina horizon form fossil site Velika planina. This horizon could represent lateral equivalent of the Lower Anisian dolomite in the lower part and of the Middle Anisan Strelovec Formation in the upper part. *c*) T-899: *Habroichthys* sp. from location Slatinski plaz; *d*) T-994: *Placopleurus* sp. from location Slatinski plaz, scale bars = 1 cm; *e*) T-1013: *Saurichthys* sp. with a recently eaten young *Eosemionotus* sp. in its belly, location Čemaževka, scale bar = 20 mm; *f*) T-1014: vertebrae belonging to an ichthyosaur, scale bar 1 cm; *g*) T-801: an incomplete caudal series from the cranialmost portion of the tail of a Pachypleurosaur sauropterygian from location Čemaževka, scale bar = 2 cm. The specimens T-899, T-994, T-1013, T-1014, and T-801 are from the Strelovec Formation. The age of Strelovec Formation could be of the Middle Anisan, probably Pelsonian.





OSTEOLOGY OF A JUVENILE INDIVIDUAL OF *GUANLINGSAURUS* (ICHTHYOSAURIA) FROM SOUTHWESTERN CHINA

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INTRODUCTION

During the last decade, the Guanling Biota has yielded abundant well preserved Late Triassic fossils notably marine reptiles and crinoids, and especially the first Chinese thalattosaurs and placodonts and complete articulated ichthyosaur skeletons of 1 arge size up to more than 10 m. *Guanlingsaurus liangae*, a large-bodied ichthyosaur, was established by Yin et al. (2000) with the foundation of *Guanlingsaurus* and Guanlingsauridae based on some postcranial characters. This species can be clearly separated from the other large-bodied ichthyosaur preserved in the same locality in having a shorter snout, large presacral number and toothless, etc. However, the authors did not give detailed description because it is barely prepared.

Here a new material of *Guanlingsaurus* from Guanling Biota is described from dark grey limestone of Wayao Member, Falang Formation (Lower Carnian, Upper Triassic)(Sun et al., 200) in Guanling County, Guizhou Province which is probably the same location with the holotype specimen and it officially belongs to the Guanling National Geopark.

Institutional Abbreviations-dq, Guanling National Geologic Park

SYSTEMATIC PALAEONTOLOGY ICHTHYOPTERYGIA Owen, 1860 GUANLINGSAURIDAE YIN, 2000 *GUANLINGSAURUS* YIN, 2000

Type Species—Guanlingsaurus liangae Yin, 2000

Diagnosis: Short snout, the skull is wide triangular. The presacral number is about 80, which is the biggest number in all ichthyosaurs so far. The scapula is small with a long neck and a fan-blade. Humerus is near round, wider than longer. The radius is not more than 1.2 times of the ulna. The pubis foramen is almost entirely open and pubis is about the same size of the ischium, both plate-like; the femur and tibia are both thick styloidal, slightly longer than wider, expanded proximally and distally and slightly constricted medially; the fibula is semi-circular, concaved postaxially.

DISCRIPTION

It is almost complete with most of the skull and postcranial skeleton, missing the anterior part of the snout and part of the digits and toes. It is prepared in the ventral view and the skull is prepared in both dorsal and ventral view. The total length is 3.76m, including the skull 0.52m and the tail 1.83m (about 48.7% of the total length).

SKULL

The skull is wide triangular in dorsal view and the right cheek is preserved and prepared, so part of the right orbit and sclerotic plated are visible. The total length of the skull is 52cm lacking the anterior part of the snout and the maximum of the width is 21.5cm, with a ratio of about 5:2.

Premaxilla—Only the posterior part of the premaxilla is preserved because of the lacking the anterior part of the snout. It is tongue-shaped and extends posteriorly, ending at the level of the anterior narial margin and forming part of the anterior margin of the external naris. There is no distinct dorsal lamina that extends posteodorsally and no ventral lamina visible possibly because of the overlapping of the maxilla. Therefore, the premaxilla does not contact the prefrontal externally. It extends anteriorly along a long suture with maxilla until the breakage so there is no accurate evidence where the anterior tip of the premaxilla starts.

Maxilla—The maxilla is long triangular and extends anteriorly, which is further than the anterior of the nasal. Because of the missing of the tip of the snout, it is not known where the maxilla extends anteriorly. It almost forms the entire ventral margin of the external naris. The dorsal lamina of maxilla overlaps the nasal and extends posteriorly forming in a short contact with prefrontal. The dorsal lamina of maxilla which also forms the posterior margin of the naris is longer than the ventral lamina, which contacts the lacrimal along arc-shaped suture. The maxilla is separated from the anterior margin of orbit by the lacrimal.

Nasal—The nasal is completely preserved, nearly elongated triangular in dorsal view. The antetior branches over the naris are overlapped by the premalla and distinctly become narrower anteriorly. Posterolaterally, the nasal ends in a lanceolate process that is pinched in between the prefrontal and postfrontal laterally and the frontal medially. The nasal contacts the frontal posteriorly along a wide serrated suture, which is the maximum of the nasal's width and at about one third of the level of the orbit. It contacts the prefrontal and postfrontal ventrally and forms the dorsal margin of the external naris. The external naris is oriented dorsal-lateral, relatively small and almost triangular. It is situated nearly in the middle of the longitudinal line of the nasal. Posterior to the naris, the nasal contacts processus postnarialis of the maxilla which it underlaps.

Prefrontal—The prefrontal is relatively small compared with the postfrontal, nearly rectangular, forming a fractin of the anterodorsal margin of the orbit. It is convex possibly because of the preservation. The prefrontal contacts the lacrimal anteriorly and extends into the orbit ventrally. Consequently, they form the anterior terrace of the orbit together. Dorsally the prefrontal contacts the dorsal lamina of the maxilla anteriorly and the nasal posteriorly with relative straight suture. The suture between the prefrontal and postfrontal is not clear on the right side of the skull because of the poor preservation while the prefrontal clearly overlaps the postfrontal on the left side.

Postfrontal—The postfrontal is a long item extending anterodorsally—posteroventrally, forming almost the entire dorsal margin of the orbit. It meets the prefrontal anteriorly and nasal, frontal and supratemporal dorsally, the sutures with each taking up the postfrontal about one third of the dorsal margin. Posterodorsally, the postfrontal contacts the frontal with relatively long and straight suture and is overlapped by the postorbital posteriorly. The postfrontal does not take part in the formation of the upper temporal fenestra. On the left side, the postfrontal possibly takes part in forming the anterior terrace of the upper temporal fenestra while on the right side there is no clear evidence because of the preservation.

Frontal—The frontal is smaller than the nasal, extending almost to the level of the anterior margin of the orbit, about half of the length of the orbit. Anteriorly it meets the nasal along the serrated

suture and becoming wider posteriorly. On the right side, the frontal overlaps the parietal posteriorly and forms an oblique suture near the medial line and an arc-shaped line posteriorly, forming a "W"-shaped suture on the skull. The frontal meets the supratemporal dorsal-laterally and the postfrontal laterally along an oblique line, forming the maximum of the width of the frontal at the most lateral suture. The frontal does not take part in forming the margin of the upper temporal fenestra but forming part of the anterior margin of the small anterior terrace of the former. It is excluded from the margin of the parietal foreman and extends to the level of less than one fifth of the upper temporal fenestra.

Parietal—The parietals are preserved almost complete and are in the middle of two upper temporal fenestra. The two parietals have three branches extending anteriorly, of which the middle one is formed by both parietals and gets narrower anteriorly and is possibly overlapped by the frontals along serrated suture line. The other two branches run in below the frontals, contributing the formation of most of the anterior terrace of the upper temporal fenestra. Nevertheless, the anterior part of this branch is broken so it is hard to decide whether the frontals have taken part in the formation of the upper temporal fenestra. The parietal foreman is in between the two parietals and is nearly at the one third of the length of the upper temporal fenestra. Posteriorly the parietals form a sagittal crest together and form the medial margin of the upper temporal fenestra. Then they extend posterolaterally and contact with supratemporal, forming a parietal shelf posteriorly and half of the posterior margin of the UTF.

Supratemporal—The supratemporal extends laterally to the upper temporal fenestra and form the lateral and part of the anterior margin of the latter. It also contributes to the lateral anterior terrace of the UTF. It is expanded and convex laterally and posteriorly, forming a strong border. The left supratemporal contacts the parietal in posterior to the UTF and forming a prominence extending posteriorly. It contacts frontal along the anterior terrace anteriorly and the postfrontal, postorbital and squamosal ventrally. Posteroventrally, the supratemporal meets the quadrate while the latter is poorly preserved.

Squamosal—The right squamosal is nearly complete while the left one is partly preserved. The squamosal lies lateral under the supratemporal and is plate-like, nearly rectangular. It contacts the jugal anteroventrally and the postorbital anteriorly. The quadratojugal is not preserved so the relation between the jugal and quadratojugal is not known. The squamosal is excluded from the bordering the UTF by supratemporal. The suture between the squamosal and postorbital is not clear probably resulted from the preservation.

Jugal—Only a small part of the right jugal is preserved. It is ventral to the squamosal and postorbital, mostly contacts the former.

Quadrate—Only part of the right quadrate is preserved. The exposed part is expanded proximally and distally and constricted medially. The quadrate is strong and contacts supratemporal and squamosal anterodorsally.

Lacrimal—The lacrimal is lunate, forming the anterior margin and anterior terrace of the orbit. It is convex laterally and forming a slightly crest along the anterior terrace of the orbit, with the ventral processus markedly longer than the dorsal processus. Anterodorsally the lacrimal overlaps the maxilla and is excluded from bordering the external naris by the dorsal lamina of maxilla. It forms the anterior terrace of the orbit together with the prefrontal. The only preserved right orbit is dorsal-ventral compressed during preservation so it is elliptical, longer remarkably than wider and only the dorsal part of the orbit is visible. About eight sclerotic rings are preserved, radicalized in the orbit.

Vertebrates

The presacral number is 77 in this individual while it is 80 in the holotype. There are about 9 cervical vertebrae and about 111 caudal vertebrae, biconcave, height/length ratio about 2.3 in dorsal vertebrae. The tailbend exists in this individual, forming an angle of about 10° (Ji et al., 2010).

Pectoral Girdle

The pectoral girdle in this specimen is not preserved completely, only part of the left scapula and coracoids visible (Fig. 2). The left scapula is strongly distorted and it has a fan-shape blade and probably has a long neck which is similar to *Besanosaurus*. Its coracoid and humerus facets are not visible because of the preservation. Both coracoids have lost the anterior part and the left one is flattened. The posterior margins of the coracoids are slightly concaved without a fan-shaped blade extending posteriorly.

Forelimb

Both humeri and ulna and the right radius are preserved. The right humerus is 9cm wide and 7.3cm long, nearly elliptical and wider than longer. The anterior margin is concaved slightly and the glenoid facet is almost triangular in the ventral view. The deltopectoral crest and deltopectoral ridge are visible and the latter extends from the glenoid facet to about half of the humerus. The articular facets for ulna and radius are not clear probably because the humerus is slightly compressed.

The right radius is nearly complete, missing the anterior about one fourth of the whole element. Both the radius and the ulna are almost round. There is a small crest near the articular facet with the humerus in the radius and the posterior margin is arc-shaped, without a notch. According to the preservation, unlike *Guizhouichthyosaurus*, the radius cannot be as much as 1.5 time wider than the ulna. The right radius is 4.9cm long and less than 5.2cm wide while the right ulna is 4.3cm long and 4.6cm wide. There is a pronounced crest in the middle of the ulna possibly because of preservation.

Pelvic Girdle

The left pubis, ischium and both iliac are completely preserved but not articulated. The pubis is 3.5cm wide proximally, 5.2cm distally and 5.4cm long. It is near fan-shaped, with the obturator foramen mostly open, similar to that of *Californosaurus* (Motani, 1999). The anterior margin is emarginated and distal margin is remarkably larger than the proximal margin. The ischium is about the same size of the pubis, near semi-circular, posterior end emarginated which is not completely ossified and the ossification core is still visible. The left ilium is preserved from the ventral view while the right one is from the posterior view. It is expanded proximally more than distally and slightly constricted medially, the length/width about 2.0. The proximal facet is not parallel to the distal facet, forming an angle of about 25° .

Pelvic Fin

Both femur are preserved nearly from the ventral view. The femur is a strong ; the femur and tibia are both thick and short styloidal, slightly longer than wider, expanded proximally and distally and slightly constricted medially. The right femur is 7cm long, 4.8cm wide proximally and 5.5cm distally while the left femur is 6.8cm long, 4.7cm wide proximally and 6.5cm distally. The right tibia is 5.4cm long, 5.4cm wide proximally and 5.4cm distally while the left tibia is 5.2cm long, 3.8cm wide proximally and 3.7cm distally. The fibula is semi-circular, concaved postaxially. It is ossified only in the core and preserved the impression of the unossified cartilage, which is about the same size of the tibia.

DISCUSSION

The specimen is probably a juvenile individual according to the following characters: 1. The total vertebrae number is 197 with 77 presacral vertebrae while the whole length is only 3.76m. The total length of the holotype specimen is 6.44m. 2. The fibula and ischium is not completely ossified, preserving only the core and the impression of the bone. 3. The articulations among the pubis, tibia and fibula and the ones between digits are not tight, leaving spaces which may not be exist when it is an adult.

Guanlingsaurus shows some unique features that have never been reported from the other species. The prelimitary analysis of *Guanlingsaurus* using a published data (Motani, 1999) shows this taxon has a close relationship with some derived Jurassic types as *Stenopterygius* which has never been seen in Triassic ichthyosaurs. This may indicate that within the new taxons from China, the phylogeny of ichthyopterygia may largely change and the South China might be the key to discuss the pathway of the immigration of ichthyosaurs and the connection between Triassic and Post-Triassic types.

FIGURE CAPTIONS

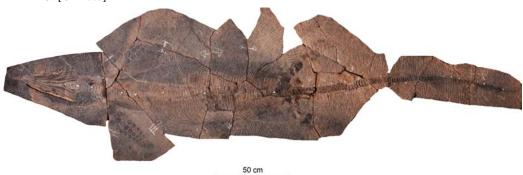
FIG 1. A juvenile individual of *Guanlingsaurus* (dp-50) from Guanling Biota from the ventral view. FIG 2. Left: Line Drawing of the skull of *Guanlingsaurus* (dq-50) from the dorsal view. Right: The left FIG 3. The pelvic girdle and pelvic fin of *Guanlingsaurus* (dq-50) from the ventral view. Left: the right pelvic fin; right: the left pelvic girdle and pelvic fin.

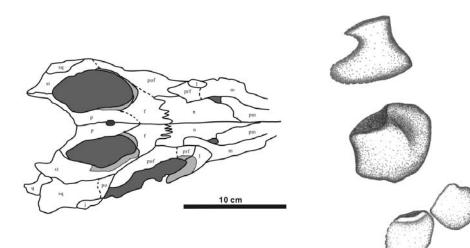
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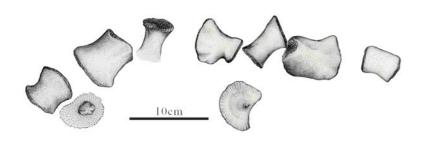
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CRETACEOUS ICHTHYOSAURS: CURRENT PERSPECTIVES ON DIVERSITY, RELATIONSHIPS AND PALAEOBIOLOGY

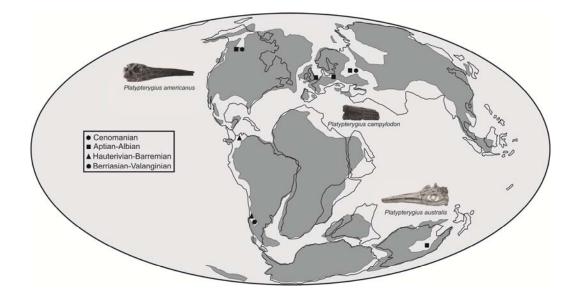
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Ichthyosaurs (Ichthyopterygia) were a group of secondarily marine amniotes whose fossil record extends from the Lower Triassic (Spathian) through to the Upper Cretaceous (uppermost Cenomanian). Their radiation peaked during the Triassic and Early Jurassic, but by the Cretaceous, they had dwindled to only a few closely related (all belonging to the family Ophthalmosauridae), and geographically widely dispersed taxa. Current classifications have recognized up to four genera: the monospecific Caypullisaurus (Berriasian: Argentina) and Maiaspondylus (lower Albian: boreal Canada), **Brachypterygius** (lower Albian: England), and the cosmopolitan **Platypterygius** (Hauterivian-Cenomanian: England, Germany, Russia, North and South America, and Australia) - the latter comprising a complex of between five to ten species. Unfortunately, many of the presently described remains comprise single, often fragmentary skeletons or isolated elements a situation contributing to ambiguous diagnostic characters, and most critically, a lack of consensus on species-level diversity within Platypterygius. In an attempt to address these issues, recent studies have re-examined key specimens from Europe, North America, and Australia and rationalized phylogenetically important traits to distinguish regional morphotypes. Preliminary results from this research indicate that Caypullisaurus, Maiaspondylus, and Platypterygius are indeed valid Cretaceous ichthyosaurs but that intraspecific variability, especially in humeral morphology, might eventually render some palaeobiogeographically disparate *Platypterygius* spp. as synomymous. The recovery of exceptionally preserved remans from Australia has also provided insights onto the palaeobiology of *Platypterygius*, including the possible utilization of underwater olfaction and a dermal sensory system (e.g. electroreceptors), dietary preference for both small and large vertebrate prey (indicated by gut contents and bite marks), and even a potential example of combat between conspecific individuals over mates and/or food.

FIGURE CAPTIONS

FIGURE 1. Map showing distribution of Cretaceous ichthyosaur taxa: Berriasian–Valanginian (\bullet), *Caypullisaurus bonapartei* (Argentina); Hauterivian–Barremian (\blacktriangle), *Platypterygius hauthali* (Argentina), *P. sachicarum* (Colombia), *P. birjukovi* (Russia) and *P. bedengensis* (Russia); Aptian–Albian (\blacksquare), *Maiaspondylus lindoei* (Canada), '*Brachypterygius*' cantabridgensis (England) *P. platydactylus* (Germany) *P. hercynicus* (Germany) *P. campylodon* (England, France, Russia), *P. americanus* (U.S.A.) and *P. australis* (Australia); Cenomanian (\bullet), *P. campylodon* (England) and *P. ochevi* (Russia).



Strontium Isotopes Corroborate Sea Level Fluctuation as a Mechanism for Ecologically Selective Extinction among Early Mesozoic Marine Reptiles.

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Early Mesozoic marine geochemical records exhibit trends and excursions thought to reflect major physical changes in the oceans, including transitions in seawater chemistry, circulation, productivity and sea level. Many of these geochemical patterns correlate temporally, and perhaps causally, with extinction events and ecological shifts among marine invertebrates. However potential correlations between geochemical records of regional or global change and changes in the ecological and taxonomic diversity of early Mesozoic marine reptiles have yet to be fully explored.

We compiled a comprehensive sub-stage resolution diversity database from published sources encompassing a total of 180 named marine reptile species spanning the Spathian (Olenekian, Early Triassic) through the Late Toarcian (Early Jurassic), a time interval of approximately 70 million years. Our compilation includes both relatively diverse and well-studied groups including ichthyopterygians and sauropterygians as well as relatively more obscure or marginal groups including thalattosaurs, aquatic protorosaurs, hupehsuchians and aquatic archosaurs. When then classified species according to two characteristics: the presence of crushing dentition (durophagy), and the development of modified locomotory systems consistent with cruising ability, hypothesized as indicators of near-shore vs. open-water habits respectively.

We then examined the proportional diversity of these two ecological subsets relative to total marine reptile diversity within each substage to look for evidence of ecologically selective extinctions through time. We compared the total diversity, proportion of durophagous and proportion of pelagic species to changes in seawater ⁸⁷Sr/⁸⁶Sr from published sources. ⁸⁷Sr/⁸⁶Sr of seawater reflects the balance of inputs from more radiogenic strontium sources (primarily continental weathering and runoff) and less radiogenic sources (mid-ocean ridge activity and erosion of island arcs). ⁸⁷Sr/⁸⁶Sr has a long residence time in the ocean (~5 million years) and thus serves as an index of long-term changes in continental weathering and sea-floor spreading and tracks sea level change via changes in continental exposure, base level and mid-ocean ridge volume. ⁸⁷Sr/⁸⁶Sr values were averaged by substage and a LOWESS regression curve (smoothing factor (f) = 0.05) was fit to the raw data to model the long-term trend in ^{87/86}Sr.

Overall there is a good correspondence between seawater strontium isotopes, major transgression-regression trends and marine reptile diversity. Intervals of elevated marine reptile diversity occur during times of maximum sea level and also correlate with minima in the ⁸⁷Sr/⁸⁶Sr

record. Conversely, reduced marine reptile diversity during the Norian and Rhaetian correspondences to a time of lower eustatic sea level and an ⁸⁷Sr/⁸⁶Sr peak. This may partly reflect a preservational bias as major marine reptile Lagerstätten are restricted to high sea level, low ⁸⁷Sr/⁸⁶Sr times.

More importantly, using linear regression we found a good correlation between the proportion of marine reptiles with crushing dentition within a substage and change in strontium isotopes expressed both as slope during that substage and differences of mean ⁸⁷Sr/⁸⁶Sr from the previous substage. This is consistent with the hypothesis that marine regression in the Late Triassic disproportionately affected near-shore adapted groups, and culminated in the successive extinction of multiple durophagous lineages that were successful through the Middle Triassic and the Carnian. It is interesting that some of the last surviving representatives of near shore marine reptile groups that were successful in the Middle Triassic and Carnian (e.g. placodonts, thalattosaurs) are found in lagoonal or restricted platform settings suggesting that these habitats might have served as refugia during this time of marine regression.

Interestingly we did not recover a strong correlation between proportion of pelagic species and strontium isotopes across substages. This might partly be explained be the fact that for the majority of the Early Jurassic substages, all known species possessed highly modified limbs consistent with a fully marine existence therefore the proportion remained static at "1" despite a steady declining trend in seawater strontium isotopic ratio. It is noteworthy that only pelagic marine reptile lineages survived across the Triassic/Jurassic boundary, while new lineages of reptiles invaded the oceans (e.g. thalattosuchians, palaeopleurosaurs) during the Early Jurassic, an interval of steadily declining seawater ⁸⁷Sr/⁸⁶Sr and a long-term transgression.

NEW INSIGHTS ON *HABROICHTHYS* BROUGH, 1939 (ACTINOPTERYGII: HABROICHTHYIDAE): THE MATERIAL FROM THE MIDDLE TRIASSIC OF YUNNAN PROVINCE, SOUTH CHINA

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INTRODUCTION

Habroichthys, a highly distinctive genus of Triassic actinoptrygian fishes characterized by a single longitudinal row of greatly deepened flank scales terminated caudally in a broad semicircular scale, was initially named by Brough (1939), who first described the type species *Habroichthys minimus* based on an incomplete specimen (lacking snout, cheek-region, jaws and the paired fins) from the Middle Triassic of Besano (Lombardy, Italy). Griffith (1977) later described a new species *H. gregarious* from the Upper Triassic of Polzberg bei Lunz (Austria), which, however, should either be included within the genus *Peltopleurus* or placed in a new genus of its own in the view of Bürgin (1992), who, meanwhile, referred several additional specimens to this species and described *Habroichthys griffithi* as a new species based on material from the fossilferous layers of the Monte San Giorgio (Canton Tessin, Switzerland).

Brough (1939) tentatively attributed *Habroichthys* to the family Peltopleuridae as information on *Habroichthys* was scare and their diagnosis was based on few characters from a poorly preserved fossil fish. Consequently, Gardiner (1967) recognized the similarity and difference of *Habroichthys* to the genus *Peltopleurus* and erected the family Habroichthyidae to accommodate *Habroichthys* and, also, distinguished it from Peltopleuridae.

Even though Bürgin (1992) provided a further detailed description of the gill cover, the fins and the squamation of *Habroichthys*, the skull region still remains practically unknown, particularly the taxonomically important gill-cover and jaws, which left substantial details open to question. Here we report new finds of *Habroichthys* based on nine well-preserved specimens from Luoping (Yunnan, China) which allow to give much better information regarding both skull and body anatomy, but also to extend the stratigraphical and geographical range of the genus.

GEOLOGICAL SETTING

The fossil fishes are collected from a more than 10-m thick, vertebrate fossiliferous interval near the top of the Guanling Formation (Pelsonian, Anisian, Middle Triassic) exposed around Dawazi village (Fig. 1A), Guishan area of southeastern Luoping, Yunnan Province.

The fossil-bearing level (Fig. 1B) is in the Upper Member of the Guanling Formation, 10 m below the overlying Yangliujing Formation. It comprises two horizons, namely lower and upper vertebrate horizons (LVH and UVH, respectively). LVH is 1.8 m thick, consisting of black medium-bedded limestone, whereas UVH is represented by light grey laminated marly shales 10.5 m thick. Between LVH and UVH exists a 1.8 m thick interval of grey marly limestones with chert concretions, where few fossils have been found. Along with marine reptiles (e.g. protorosaurs, ichthyosaurs, pachypleurosaurs etc.), thousands of well-preserved fossil fishes were produced.

PALEONTOLOGICAL DESCRIPTION

Class Osteichthyes Huxley, 1880 Subclass Actinopterygii Cope, 1887 Order Peltopleuriformes Gardiner, 1967 Family Habroichthyidae Gardiner, 1967 Genus *Habroichthys* Brough, 1939

Diagnosis (Emended from Bürgin, 1992): Very small fusiform fishes. Single very deep scale-row, bearing the lateral line, occupying all the flank and ending with a large semicircular scale. Frontals, parietals and dermopterotics fused in a single shield-like bone with sinuous supraorbital sensory canal. Suspensorium vertical. No teeth. Opercular much larger than subopercular. Fringing fulcra abstent from all the fins.

Type species: Habroichthys minimus Brough, 1939

Geographical and stratigraphical distribution: the genus *Habroichthys* has so far a Tethys distribution, from the Alps (Italy, Switzerland, Slovenia) to the South China (Guizhou and Yunnan Provinces, with its known range being from the Pelsonian (Middle Anisian) to the latest Ladinian.

Habroichthys sp. Fig. 2

They are small fusiform fishes, not longer than 30 mm in standard length (SL). The ratio of skullto standard-length is more or less 30%. The body-depth/body-length varies from 38-44%. The dorsal fin is narrow and posteriorly located, extending for four scale rows. The anal fin is situated midway between the pelvic fins and the caudal fin.

The skull roof is formed by a large rectangular bony plate, interpreted to be the fusion of at least the frontals, parietals, and dermopterotics. The exposed surface of the skull roof is smooth and flat. The course of the supraorbital sensory canal goes closely similar to that of *Habroichthys griffithi*.

Circumorbital elements are not well preserved. The dermosphenotic is a triangular bone. The suborbital and supraorbital is not present. A rectangular bone located in the middle of the orbit is interpreted as the parasphenoid. Below the parasphenoid, a markedly enlarged plate is interpreted as palatoquadrate herein. It possibly comprises the metopterygoid, the ectopterygoid, the entopterygoid, and the quadrate.

The upper jaw is somewhat shorter than the lower jaw. The maxilla is an elongate and wedge-shaped element. The mandible is much stouter. It appears to be wedge-shaped and pointed anteriorly, with a prominent medial process at the anterior end.

The opercular series comprises the preopercle, opercle and subopercle. The preopercle appears to be a gentle 'L'-shape. The opercle is a broad, shield-like bone, about twice deeper than long, with a

rounded dorsal margin and a straight ventral one. Its size is about 2.5 times of the semicircular subopercle which is longer than deep. The element beneath the subopercle is interpreted as the first branchiostegal.

The pectoral girdle consists of the paired shield-like posttemporals separating each other by a series of scales, a squarish supracleithrum and a large, lunate-shaped cleithrum. The pectoral fin is broad-based, with a series of at least 10 segmented fin rays.

The pelvic fins are partially preserved and overlap each other, with about 5 segmented fin rays. They start at scale row 11-12.

The dorsal fin begins at scale row 18-20, located much closer to the tail than those of *H. minimus* and *H. griffithi*. The anal fin, positioned opposite to the dorsal one, comprises 6-8 unsegmented and only distally branched fin rays. The caudal fin is externally symmetrical and moderately forked. There are not trace of fringing fulcra on any of the fins.

The squamation consists of 29-32 vertical scale rows of highly deepened flank scales. Between the leaf-like scute and the terminal flank scale, there are 5-6 small scales which are arranged in two rows, covering the dorsal base of the caudal fin rays, and 3-4 smaller scales on the pelvic margin in one row. The course of the lateral line usually runs dorsally within the flank scales in the anterior part of the body and then descends gradually to the midlength of the terminal semicircular flank scale. The thick scales are covered by ganoine, with a smooth surface and posterior margin.

CONCLUSIONS

The new specimens we described herein is attributed to the genus *Habroichthys* based on its being small, fusiform fishes with an unique deepened scale-row, occupying all the flank and ending with a large semicircular scale, the shield-like skull-roof (frontals, parietals and dermopterotics fused) with sinuous supraorbital sensory canal, orbital large, suspensorium vertical, operculum more than twice as deep as the suboperculum, fringing fulcra absent. The body length and the number of deepened flank scales of *Habroichthys* sp. show an intermediate morphology between *H. minimus* and *H. griffithi*, but the proportions of the gill-cover elements is the biggest and the shape of skull-roof is like that of *H. griffithi*. The main characters it different from *H. minimus* and *H. griffithi* are that its dorsal fin starting at scale row 18-20, posteriorly located and the course of the lateral line running dorsally within the flank scales in the anterior part of the body and then descending gradually to the mid-length of the terminal semicircular flank scale, instead of a more ventral position. So *Habroichthys* sp. should be regarded as a new species.

With the new discovery, especially these from the Middle Anisian of Yunnan Province, the diagnosis of this still little-known genus, due to poor preservation, was greatly improved. The short and free maxilla, narrow and gentle curved preoprecular are usually considered as typical structures of neopterygian one, together with the lobe of tail reduced, somewhat indicating that *Habroichthys*, though belonging to subholosteans, is much closer to neopterygian than paleopterygian. Regarding no interoperculum and teeth present, these changes can be seen as a biomechanical specialization related to trophism and the feeding apparatus may be the sucking type of dentition. Also, the tail is slightly asymmetrical, with a very small body lobe supporting few epaxial rays. In addition, other characteristics are also distinctive: few branchiostegal rays (usually one); suborbitals absent as probably the case for supraorbitals; very large triangular dermosphenotic; infraorbitals, if present, tube-like; fringing fulcra abstent from all the fins.

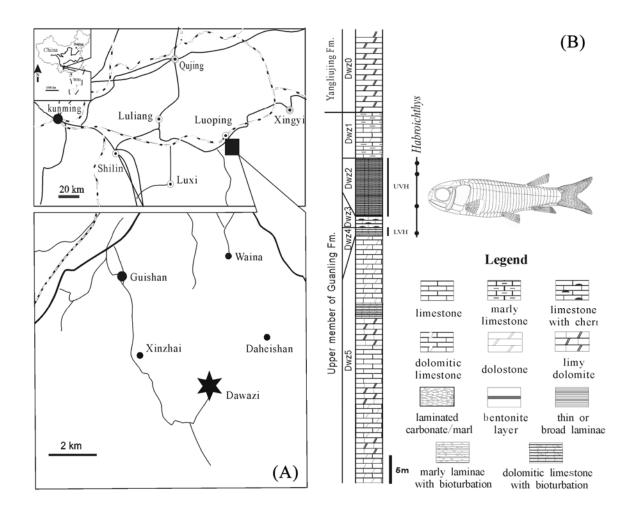
The fossil fishes, from Luoping Yunnan Province, furtherly ascertained that Habroichthys is a

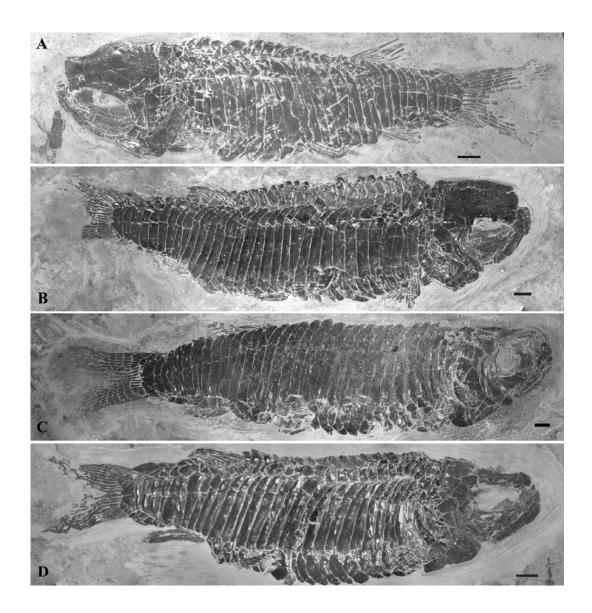
typical Middle Triassic taxon, ranging from Pelsonian to latest Ladinian, with a restricted Tethydian distribution from the Alps (Italy, Switzerland, Slovenia) to the South China (Guizhou and Yunnan Provinces). In the Alps *Habroichthys* is quite common around the Anisian/Ladinian boundary, while in Southwestern China it ranges from the Middle Anisian to the latest Ladinian. The oldest record is not surprising as many Late Anisian western Tethys genera of actinopterygians are now considered as migrated from East during the Middle Anisian; more interesting is the upward extension as the genus has never been found in the Late Ladinian sites of western Tethys.

FIGURE CAPTIONS

Fig. 1. (A), Map showing locality (Dawazi site) where fossil fishes were collected. (B), The stratigraphic section bearing the fossilferous layers.

Fig. 2. *Habroichthys* sp. A, GMPKU-P-1463 in left lateral view. B, GMPKU-P-1492 in right lateral view. C, GMPKU-P-1491 in right lateral view. D, GMPKU-P-1462 in right lateral view. Scale bars equal 1mm.





A PRELIMINARY REVIEW OF THE DIVERSITY OF MARINE REPTILES FROM LUOPING FAUNA

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The Luoping Fauna is a Middle Triassic marine Lagerstätte discovered during the 1:50000 geological mapping in the Luoping area of eastern Yunnan Province by the Chengdu Center of China Geological Survey (CCCGS) at the end of 2007. Abundant well-preserved fish fossils, associated with articulated marine reptiles, macro invertebrates, and plant fossils have been found in the Member 2 of the Guanling Formation. Detailed conodont analyses suggest a Pelsonian age for this Lagerstätte, which is also supported by our unpublished SHRIMP zircon U-Pb age from interbedded tuff. The Luoping Fauna represents a nearly complete Middle Triassic marine ecosystem and provides us a window to understand the ancient life in the Middle Triassic oceans. To date, three new species from this Lagerstätte including one anthropod and two fishes have been reported. Here we provide a preliminary review of the reptile diversity of this marine Lagerstätte.

Several main lineages of marine reptiles have all been recorded in Luoping Fauna based on the paleontological collections of Chengdu Center of China Geological Survey and Geological Museum of Peking University. Ichthyosaurs are exclusively composed of mixosaurids, which are the most abundant reptiles in this fauna. Two morphotypes have been recognized. Sauropterygians include one placodont and several pachypleurosaurs and nothosauroids. The only placodont is tentatively identified as *Placodus* sp. One of pachypleurosaurs has been described and classified within the Keichousauridae. Others need more preparation and further study. Nothosauroids include *Lariosaurus* sp., *Nothosaurus* sp., *Nothosaurus* cf. *giganteus*, and other undeterminated taxa. Protosaurs are composed of two morphotypes. One of them is identified as *Dinocephalosaurus orientalis*. The other has much thinner cervical vertebrae and is tentatively identified as cf. *Dinocephalosaurus*. Other reptiles in our collections include one possible thalattosaur and several archosaur teeth.

Our preliminary review of the reptile diversity of Luoping Fauna shows that the top predators of this Lagerstätte have already been highly diversified. It supports the hypothesis that the Luoping Fauna is one of the earliest records that mark the full recovery of the marine ecosystem from the P/T mass extinction.

A REVIEW OF CHINESE MIXOSAURIDS

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The first report of a Chinese mixosaurid, which is also the first report of an ichthyosaur occurrence in China, was rendered by C.C. Young in 1960 who named the taxon as Mixosaurus maotaiensis in 1965. This taxon has been considered a nomen dubum recently because the holotype is not diagnostic at the species level. Except for this specimen, all other known mixosaurids are from the Panxian Fauna and Luoping Fauna, and constitute the most abundant reptile group in both faunas. Two mixosaurid species has been reported from the Panxian Fauna. They are Mixosaurus panxianensis and Phalarodon cf. fraasi, respectively, and different from each other mainly by the tooth implantation and narial structure. Two morphotypes are also recognized in the Luoping Fauna. Type A from the Luoping Fauna shares a unique synapomorphy with Mixosaurus panxianensis among mixosaurid ichthyosaurs, i.e., two notches in the leading edge of the radius, but has consistent differences with Mixosaurus panxianensis in the region of the posterior dentition and the leading edge of the forefin. Type A is either a new species that is closely related to Mixosaurus panxianensis or a population of Mixosaurus panxianensis that presents consistent anatomical differences. The so-called Mixosaurus kuhnschnyderi has also been reported from the Luoping Fauna. After our personal examination of the specimen, we think the alternation of conical and mound-shaped teeth in the posterior jaw of this specimen to be a taphonomic alteration, rather than a natural situation. This specimen can be classified into Type A with the retention of two notches in the leading edge of radius. Type B from the Luoping Fauna is different from Type A with a smoothly concave leading edge of radius, which is also seen in all other mixosaurid species. Phylogenetic relationships of all Chinese mixosaurids and their implication for the origin of ichthyosaurs will be discussed.

THE RESTUDY OF THE "*DINGXIAOSAURUS LUYINENSIS*" FROM GUIZHOU, CHINA

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The specimen was collected in Dingxiao, Xingyi City of Guizhou Province, Southwest China, consisting of incomplete forelimbs, scattered ribs and vertebrae. It comes from the Middle Triassic Yangliujing Formation (Ladinian). The primitive description considered it as an isolated form of the early marine reptiles, which shows closer affinity with the primitive ichthysaurs and remoter affinity with the earliest plesiosaurs, and propose for it a new family Dingxiaosauridae (Liu et al.,2002). Others considered it as a pistosauroid(Cheng et al.,2006) which had too few characterization to report a new genus. In short, the taxonomic position of this specimen is still controversial. We describe and compare the forelimbs which have been renovated in detail to define its taxonomy. The detail study shows some characters suggesting it is possibly an incomplete specimen of superfamily Pistosauridea.

SYSTEMATIC PALEONTOLOGY

SAUROPTERYGIA Owen, 1860 EOSAUROPTERYGIA Rieppel, 1994 PISTOSAUROIDEA Rieppel, 1998

Type Species- "*Dingxiaosaurus luyinensis* sp. nov." **Distribution-** Middle Triassic of China.

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Morphological Description

Most of the humerus have been badly damaged during subsequent preparation, so that I found almost nothing worthy of comment. There is only a part of distal end(Fig. 1A) with a low-ridge. As in other sauropterygians, the distal end of the humerus is dorsoventrally flattened. It lies in front of the proximal head of the radius.

The ulnas and radius are preserved in natural articulation. The total length of the unla is 117.3mm, somewhat longer than the radius, which is 105.5mm in length (Fig. 1).

The ulna is flattened, especially near the distal end, whose width is 48.2mm, wider than that in proximal head(39.6mm). The ratio of the widths of the distal and proximal ends is 1.2. It's posterior margin, with an unobserved inner fovea on the 3/4 proximal end, is less curved than the anterior one.

The radius are also dorsoventrally flattened bones with constricted shafts, with a proximal width 51.5mm, a distal width 43.0mm, minimal width 29.1mm. The thickness of distal end is similar to that of proximal head, and both of them are slightly thicker than middle position. Its proximal head is expanded and is 1.2 times as wide as the distal head.

Seven ossified carpals are present as subrounded bones in two rows. There are two in the proximal

(intermedium and ulnare) and five in the distal row. As preserved, the intermedium is between the distal ends of the radius and unla, 41.2mm in long diameter and 34.9 in short diameter. Due to preservation, we believe ulnare of the proximal row is dislocated distal to the intermedium, without clear articulated surface, comparing to others in situ conservation(Fig.1). It's short diameter is approximately 14.2mm, its long diameter 17.5mm. In the row of distal carpals, two of the five bones are identified as distal carpal 4 and 5 .The general outline of distal carpal 5 is oval, with a width of 18.7mm, and a length of 31mm, being located distal to the ulnare. Three margins of distal carpal 4 have slightly concave articular surfaces to articulates with the ulnare, two other distal carpals, respectively(Fig.1). Unfortunately, the three smaller carpals are dislocated and hardly to be distinguished.

The metacarpals and phalanges are elongate bones, whose number has neither increased nor decreased from the usual count of five in Pistosoriod. The first and last one is positioned upper than others.

Among the metacarpals, the first one is the shortest(36.0mm in length), whose margin is straighter than others', comparing to 50+mm in others (Table 1). In addition, the fifth's distal end doesn't expand so strongly as others. The third and forth metacarpals are the longest, 62.8mm and 63.0mm, respectively(Table 1). II -IV are dumbbell-shaped with articulation surfaces on only the two ends. The last one is wider relative to its length than all the others. Most of the digits are reserved and show the phalangeal formula of 3-7-8-8-5, corresponding to the hyperphalangy character of Pistosauroids(Cheng et al., 2006).

	I			II			III			IV			V							
Forelimb	Leng	th	width		Leng	th	width		Lengt	h	width		Length		width		Length	v	vidth	
		Pro	Mini	Dist		Pro	Mini	Dist		Pro	Mini	Dist		Pro	Mini	Dist		Pro	Mini	Dist
mc	36.0	17.8	13.8	16.5	55.0	20.3	14.8	19.9	62.8	21.2	12.2	22.0	63.0	20.2	14.5	23.8	53.1	26.8	18.9	29.7
phalanx 1	25.7	14.1	10.5	13.3	38.6	19.1	13.0	19.2	46.9	19.0	12.9	22.2	46.5	21.0	13.0	21.9	45.4	29.0	16.4	27.4
phalanx 2	22.5	9.5	6.4	9.9	27.3	16.2	12.0	15.6	34.0	18.0	10.5	16.5	37.0	19.1	12.9	21.3	36.4	24.0	13.6	22.3
phalanx 3	14.2	5.7	3.8	4.1	20.1	12.2	8.8	13.0	26.9	16.1	9.3	16.9	29.8	19.8	11.5	19.2	27.0	18.9	9.5	15.5
phalanx 4					18.8	9.8	5.9	9.8	23.0	13.8	9.0	14.9	26.0	16.4	10.0	17.5				
phalanx 5					18.2	8.1	5.5	8.5	24.9	14.2	8.1	14.8	21.7	15.0	10.0	16.2				
phalanx 6					15.4	5.8	4.9	6.4	20.8	12.9	7.6	12.9	18.3	13.2	10.1	12.1				
phalanx 7					11.7	5.0	3.7	5.0	19.1	12.3	8.0	12.3	14.5	11.7	7.0	9.9				
phalanx 8									15.4	11.0	7.0		8.7	7.3	5.1	5.6				

Table 1. Selected skeletal measurements in mm of the forelimb.

All non-terminal phalanges are dumbbell-shaped, while some of the terminal ones are not completely preserved. Similar to the situation of III and IV metacarpals, the third and forth digits are the longest. The ratio of the length and median width of the metacarpals and phalanges are located in Table 2 and Fig. 2.

Discussion

The dorsoventrally flattened humerus with constricted sharft indicates the sauropterygian affinities of

the specimen. The seven carpals and hyperphalangy (Cheng et al., 2006), it's allowed to consider this specimen as a member of superfamily Pistosauroidea. Unfortunately, it is too incomplete to diagnose the genus and species on the basis of preservation of two forelimbs.

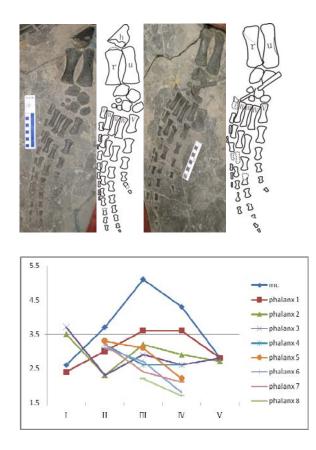
	Ι	II	III	IV	V
mc	2.6	3.7	5.1	4.3	2.8
phalanx 1	2.4	3.0	3.6	3.6	2.8
phalanx 2	3.5	2.3	3.2	2.9	2.7
phalanx 3	3.7	2.3	2.9	2.6	2.8
phalanx 4		3.2	2.6	2.6	
phalanx 5		3.3	3.1	2.2	
phalanx 6		3.1	2.7	1.8	
phalanx 7		3.2	2.4	2.1	
phalanx 8			2.2	1.7	

Table 2. The ratio of the length and median width of metacarpals and phalanges (in mm)

FIGURE CAPTIONS

FIGURE 1. The Forelimbs.

FIGURE 2. The ratio of the length and median width of metacarpals and phalanges



TRIASSIC ICHTHYOPTERYGIAN FOSSILS FROM CHINA AND THEIR UNIQUE SIGNIFICANCE

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Ichthyopterygian paleontology has a long history dating back to the early 19th Century in England. The first scientific description of an ichthyopterygian was given in 1814, and the genus *Ichthyosaurus* was named in 1821. The ichthyopterygian study soon spread to the continental Europe, where it remained active until mid 20th Century. On the contrary, no ichthyopterygian was known from East Asia until 1960, when Young C. C. reported a fragmentary skeleton that he later named *Mixosaurus maotaiensis*. Despite of such a late start, it is impossible to discuss the evolution of ichthyopterygians without references to several important Chinese fossils.

Ichthyopterygians are noted for tuna-shaped body profiles that witness their aquatic adaptation as large cruisers. The earliest ichthyopterygian to be discovered were all from the Jurassic, by which time they had adapted to the cruising lifestyle. Ichthyopterygian paleontology in 19th to mid 20th Centuries largely focused on these forms. However, as expected for a group of reptiles that originated on land and invaded the sea, early ichthyopterygians could not have been tuna-shaped. Yet, our knowledge of body designs in early ichthyopterygians that marked the evolutionary transition from land to water was limited until Chinese fossils were unearthed. Notably, there were three body designs of Triassic ichthyopterygians known from more than a century ago, namely of *Mixosaurus*, *Cymbospondylus*, and *Californosaurus*. John Merriam was clearly aware of the importance of the evolutionary transition that these genera exhibited yet limited attention was paid by the others after he left his research career.

The discovery of the Early Triassic ichthyopterygians *Chaohusaurus* Young and Dong 1972 and *Utatsusaurus* Shikama, Kamei, et Murata 1978 from East Asia re-ignited interests in Triassic ichthyopterygians. A series of studies by Jean-Michel Mazin, Judy Massare, and Jack Callaway tried to illuminate the evolution of ichthyopterygians during the Triassic. However, most Triassic specimens were fragmentary at the time, making it difficult to clarify the evolutionary transition.

In 1991, Yu Hailu, then a Master student at IVPP, reported a complete skeleton of *Chaohusaurus* from the Lower Triassic (Olenekian) of Wuwei, Anhui (Fig. 1) in his thesis. It was the first Early Triassic ichthyopterygian to show the body design, which may be casually described as "a lizard with flippers" (Fig. 2B). This fossil was the precursor to the "Gold Rush" of ichthyopterygian discoveries from China. Before the turn of the Century, Li Chun reported *Qianichthyosaurus* from the Upper Triassic (Carnian) of Guanling, Guizhou. This genus shows for the first time the body design of Toretocnemidae (Fig. 2F), which had been known only from fragmentary fossils. The genus exhibits the most derived body designs of all Chinese Triassic ichthyopterygians. Additional discoveries from Guanling, reported by Yin Gongzheng and his colleagues, further improved our knowledge. *Guizhouichthyosaurus* exhibited an extreme design within Shastasauridae (Fig. 2E).

After the localities in Guanling were reported, new fossil quarries in western Guizhou and eastern Yunnan started to yield Middle Triassic ichthyopterygians. Many of them are mixosaruids (Fig. 2D) from the Anisian, of which *Mixosaurus panxianensis* reported by Jiang Dayong and his colleagues was the first to be named. Jiang and his colleagues also described *Xinminosaurus*, a hitherto unknown type of ichthyopterygian that fed on hard-shelled prey. Ichthyopterygian fossils are also known from the Ladinian of Wusha, Xingyi, Guizhou.

All Chinese genera listed above are known from nearly complete skeletons. They therefore drastically improved our knowledge of how the body design in ichthyopterygians evolved during the Triassic (Fig. 2) Most importantly, the evolutionary transition of the tail structure is now evident. Tuna-shaped ichthyosaurs are known to have the tailbend, which is a downturn of the vertebral column at the anterior end of the caudal fluke that allows the column to continue into the lower lobe of the fluke (Fig. 3). It is now clear that this structure is associated with at least seven anatomical features, two of which were already present in the earliest ichthyopterygians. The rest of the features were acquired step by step during the Triassic, eventually giving rise to the semi-symmetrical flukes seen in tuna-shaped ichthyopterygians.

Future discovery of additional ichthyopterygian specimens is expected from the Triassic of China. Given that most specimens have been articulated, such additional specimens should largely improve our understanding of ichthyopterygian evolution. Further efforts to collect and preserve ichthyopterygian specimens are crucial.

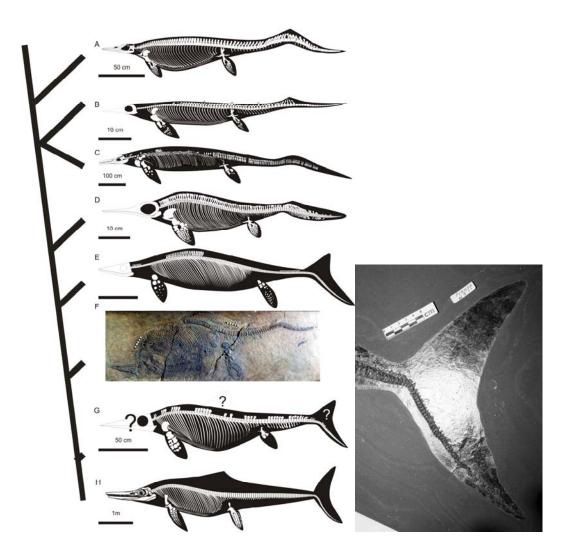
FIGURE CAPTIONS

Figure 1. Seven major ichthyopterygian localities in China. a, Chaohu; b, Wuwei; c, Guanling; d, Panxian; e, Xingyi; f, Luoping; g, Fuyuan. The provinces that contain these localities (outline by thick real line) are, from northeast to southwest, Anhui, Guizhou, and Yunnan.

Figure 2. Body form evolution of Ichthyopterygia. A, Utatsusauridae; B, Grippidae; C, Cymbospondylidae; D, Mixosauridae; E, Shastasauridae; F, Toretocnemidae; G, Californosauridae; E, Temnodontosauridae (Parvipelvia). The Families B-F are known from China.

Figure 3. Tailbend structure of Stenopterygius, a typical tuna-shaped ichthyopterygian from the Jurassic.





MARY ANNING, THOMAS HAWKINS AND PLESIOSAURS ACROSS THE TRIASSIC-JURASSIC BOUNDARY, WITH SPECIAL REFERENCE TO SOUTHERN ENGLAND

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The traditional view of the sauropterygian fossil record suggests an extinction at the end of the Triassic, after which the plesiosaurs suddenly appeared, fully formed, to explosively radiate into Jurassic seas. However, analysis of latest Triassic and earliest Jurassic plesiosaur faunas from southern England, and elsewhere, indicates a much more complex history. In all likelihood plesiosaurs invaded the seas sometime during the Triassic, but remained in deeper waters, to suddenly 'appear' in the fossil record due to transgression onto areas which had previous been land, with a major radiation continuing well into the Jurassic.

Plesiosaurs were first recognised just less than 200 years ago on the south coast of England. The early finds, initially consisting of isolated bones but shortly afterwards of complete skeletons, amazed the men of science of the day and rapidly captured the public imagination. These first plesiosaurs were principally found by two very different collectors: Mary Anning of Lyme Regis in Dorset, and Thomas Hawkins of Street in Somerset. Mary Anning was a poor, but self-taught, working class woman who found and sold fossils to keep herself and her family. Thomas Hawkins was wealthy and aspired to be a gentleman. He purchased specimens from local quarry owners and prepared them from their limestone matrix. He sold his early collection to the British Museum (now the Natural History Museum, London) and later made donations to the universities of Oxford and Cambridge.

Many of these early plesiosaurs were recovered from rocks close to the Triassic-Jurassic boundary. Today, this critical boundary is recognised as one of the five largest mass extinction events in the history of the Phanerozoic, yet there has been much uncertainty as to where the boundary lies; and there is still no consensus as to exactly where it should be placed. This uncertainty, together with an apparent difference in the timing of extinctions for land and sea based taxa, is hindered by poor provenance data for many early plesiosaur specimens. In addition, difficulties in correlating time units (chronostratigraphy) with the southern English lithostratigraphic record (the 'White Lias', '*Ostrea*', 'pre-*Planorbis*', and '*Planorbis*' beds) is confounded by widespread marine transgression related to the opening of the Central Atlantic Magmatic Provence. Hence understanding the early evolution, diversity and radiation plesiosaurs across the T-J boundary remains a complex challenge.

NEW PLESIOSAUR DISCOVERIES FROM THE JURASSIC SUNDANCE FORMATION: NOVEL BODY MORPHOLOGIES AND INFERENCES OF PREY SELECTION.

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The upper Sundance Formation (Oxfordian) is a shallow, heterogeneous marine facies exposed over large areas of the American west. The formation was produced by the Sundance Seaway, an intracontinental incursion of the Pacific, and records its final transgressive -regressive cycle. This incursion was cut off by the rising Rocky Mountains to the west, and this orogeny provided a sediment source filling the basin and ultimately producing the terrestrial Morrison Formation. In consequence, the Sundance Formation is a shallow-water facies; a heterogeneous, glaucanitic shale with abundant invertebrate fossils. Ichthyosaurs are relatively common in the formation, while plesiosaurs are more rare. Several years of field work in Sundance outcrops in the Bighorn Basin of Wyoming have produced significant plesiosaur fossils, including two partial skeletons. One is referable to Pantosaurus striatus, a taxon known previously from the juvenile holotype only. The partial skeleton consists of 15 articulated vertebrae spanning the mid-dorsal, sacral, and proximal caudal regions, along with ribs, gastralia, and the complete pelvic girdle. Characters of the skeleton establish that Pantosaurus is a valid taxon, differing significantly from taxa from the well-known Oxford Clay (Callovian) of the United Kingdom. The skeleton is pathological in several details, and also contains a mass of stomach contents. This mass contains a few gastroliths, a large sand fraction, fish scales, and an ichthyosaur embryo. The embryo is the first known from the Upper Jurassic, and documents the consumption of carrion by plesiosaurs. The second partial skeleton is referable to Tatenectes laraminensis, and comprises a complete vertebral dorsal series, the scarum, and first two caudals, many ribs and gastralia, and a complete pelvic girdle. The morphology of this skeleton is unique; the thorax is extremely dorso-ventrally compressed, unlike that of any other plesiosaur. This compression is produced by novel characters of the vertebrae, the pelvis, and the ribs and gastralia. Additionally, the gastralia show a novel type of pachyostosis resulting in a heavy, keel-like mass of bone along the ventral midline. Taken together, these features indicate the *Tatenectes* was a shallow-water animal, with a body adapted for stability on or near the surface. This inference accords with the shallow, sediment-choked paleoenvironment in which the animal was found.

TRIASSIC MARINE REPTILES (SAUROPTERYGIA, PROTOROSAURIA, THALATTOSAURIA) FROM THE EASTERN AND WESTERN TETHYAN FAUNAL PROVINCES.

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During the Triassic, after the end-Permian extinction, a rapid diversification of marine reptiles took place in the eastern and western Tethyan realms. Remarkably close affinities can be recognized among the sauropterygian and protorosaur taxa of these two faunal provinces. The diversification of marine reptiles in the western Tethys correlated with a marine transgression across central Europe that began in the late Early Triassic, and proceeded from East to West. This provided an opportunity for the colonization of the central European Muschelkalk basin by sauropterygians and protorosaurs. The opening of a southern gateway allowed sauropterygians and protorosaurs to disperse and further diversity into intraplatform basins that formed along the northwestern shore of the Western Tethys. Invertebrates, such as ammonites and crinoids, suggest the colonization of the Muschelkalk basin from the East. The same seems to be indicated by sauropterygians. Pachypleurosaurs from China, for example, are the sister-taxa to European pachypleurosaurs; amongst the latter, the Muschelkalk pachypleurosaurs are the sister-taxa of those from the Alpine Triassic. Cladistic relationships of pachypleurosaurs thus indicate a diversification from the eastern Tethyan Faunal Province into the western Tethys. On the other hand, very close systematic affinities of some placodonts, as also of protorosaurs and thalattosaurs, indicate the possibility of a faunal interchange along the northern coastline of the Tethys between the Eastern and Western Tethyan realm throughout the Triassic.

LATE CRETACEOUS PLESIOSAURIAN FAUNA OF MANITOBA ESCARPMENT, CANADA

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Cretaceous vertebrates of the Western Interior Seaway of North America have been studied since the 19th century, and they have been the major source of information for our understanding of Mesozoic marine reptiles, including the popularized images of the long-necked plesiosaurs and savage mosasaurs (see Everhart (2005) and references therein). Much of our knowledge on the Western Interior Seaway has, however, come from the southern one-third in US, and relatively few vertebrate taxa are known from the rest of the seaway in Canada (e.g., Bardack, 1968). Interestingly, previous studies have noted the reptilian faunas in northern parts of seaway differ from those of the south; for example, Nicholls and Russell (1990) compared the early Campanian vertebrate faunas in four localities within the seaway from Alabama to the Arctic, and noted the variation in the relative abundance of reptilian taxa. It is obvious that further collection and studies of Canadian material is necessary to give a more complete picture of the vertebrate fauna of the seaway.

The current contribution is a preliminary report of our on-going project since 2008 in which we explore the plesiosaurian fauna in the eastern margin of the Western Interior Seaway in Canada. Our focus is in the stratigraphic distribution and taxonomy of the material from the Manitoba Escarpment (Figure 1). The research includes an examination of a number of undescribed museum specimens, as well as the new material obtained by our fieldwork. The Manitoba Escarpment consists of a series of hills and mountains, i.e., Pasquia Hills, Porcupine Hills, Duck Mountain, Riding Mountain, and Pembina Mountain (or Pembina Hills) from north to south. The escarpment stretches over several hundred kilometers from the eastern Saskatchewan to northern North Dakota across the southern Manitoba.

The Cretaceous marine sediments of the Manitoba Escarpment represent nearly continuous sequence from the Albian to Maastrichtian (McNeil and Caldwell, 1981). Vast majority of the fossil vertebrates from the escarpment which were reported to the scientific community came from the Campanian Pembina Member of Pierre Shale in the vicinity of Morden in southern Manitoba (e.g., Nicholls, 1989). On the other hand, geology and paleontology of the Cenomanian-Turonian strata in the northern area of the escarpment saw significant progress recently (e.g., Cumbaa and Tokaryk, 1999; Wu et al, 2001; Schröder-Adams et al., 2001). Information on vertebrate fossils from other horizons, however, is conspicuously poor. In the following, we give a brief summary of the result of our project, with a review of previous works on vertebrate fossils from the Cretaceous sequence in the escarpment.

The lowermost Cretaceous unit in the Manitoba Escarpment is the Swan River Formation. This unit has yielded little macro- or microfossils commonly used for the dating of Cretaceous marine sediments, and its Albian age is suggested by palynology (Playford, 1971). To our knowledge, no vertebrate remains have been reported from this formation. Our fieldwork confirmed only the abundance of carbonized plant material and trace fossils at the type locality as noted by earlier workers

such as Wickerden (1945) and McNeil and Caldwell (1981).

A number of vertebrate taxa (selachians, teleosts, reptiles, and birds) have been reported from the Cenomanian Ashville and Cenomanian-Turonian Favel formations in the Pasquia Hills. Most of the vertebrate fossils came from bonebeds or bioclastic lenses in shale (Cumbaa et al., 1993; Tokaryk et al., 1997; Wu et al., 2001; Cumbaa and Bryant, 2001). The Ashville Formation is the lowermost section from which plesiosaurian fossils are known in the Manitoba Escarpment. Numerous vertebrate remains have been collected from the Ashville exposed at Carrot River in Pasquia Hills by a local resident over years (Cumbaa and Bryant, 2001), and they are now housed in the Royal Saskatchewan Museum in Regina. The RSM collection includes dozens of plesiosaurian elements, and most of them are isolated vertebrae of polycotylid and elasmosaurid plesiosaurs. These bones are disarticulated, relatively robust, more or less damaged, and of similar size, suggesting the effect of sorting before the final deposition. Therefore it is difficult to estimate the number of individuals in this collection. Our fieldwork in 2009 found polycotylid remains from an approximately same stratigraphic level in the Ashville Formation exposed along Little Woody River in the Porcupine Hills.

The overlying Favel Formation in Treherne in southern Manitoba has yielded the type specimen of *Trinacromerum kirki* Russell 1935, and this is the only published account on plesiosaurs from this formation. Nevertheless, occurrences of nearly complete skeletons of fish and associated skeleton of a marine crocodile in the Favel Formation in Pasquia Hills (Schröder-Adams et al., 2001; Wu et al., 2001) imply a high possibility of producing well-preserved specimens, so does our fieldwork in Porcupine Hills and Riding Mountain where isolated vertebrate fossils such as plesiosaurian vertebrae were encountered. The Morden Shale (Turonian) overlies the Favel, but very few macrofossils have ever been reported from this unit (McNeil and Caldwell, 1981). We have not sufficiently searched this unit yet.

McNeil and Caldwell (1981) divided the Niobrara Formation of the escarpment into two informal members, i.e., the calcareous shale and the chalky members in ascending order. They dated the entire formation as largely Santonian, but the uppermost section might be Early Campanian and the lowermost portion as old as Late Turonian. In contrast to the famous diversity and abundance of marine vertebrates of the Niobrara Formation in Kansas, USA, surprisingly few fossil vertebrates have ever been reported from this formation in Manitoba (Bardack, 1968). The paucity of vertebrate fossils should not be taken literally because of the obvious difference in the intensity of research activities specifically aiming at collection of vertebrates, but it is also true that previous geological or paleontological studies of Canadian Niobrara rarely noted vertebrate remains when compared with invertebrate macrofossils or vertebrates in other sections of the escarpment (e.g., Wickenden, 1945; McNeil and Caldwell, 1981).

ROM 29010 (Royal Ontario Museum, Toronto, Canada) is a partial skeleton of a polycotylid plesiosaur collected in 1974, and the collection record and our fieldwork indicate the specimen came from the Chalky Member of the Niobrara Formation near Thornhill in Pembina Mountain. The specimen consists of associated skull elements including braincase, incomplete vertebral series, girdles, and limb bones. In addition to the stratigraphic and biogeographic significance as the first marine reptile from this formation in Manitoba with reasonably preserved skeleton, the braincase of this specimen is in an excellent condition with little deformation, permitting a detailed anatomical study and a digital three-dimensional reconstruction of the plesiosaurian braincase for the first time. Description of the ROM specimen and braincase reconstruction is presented elsewhere (Sato and Wu, submitted).

The Pierre Shale (Campanian-Maastrichtian) in the escarpment is divided into five members, i.e., Gammon Ferruginous, Pembina, Millwood, Odanah, and Coulter Members. The Early Campanian Pembina Member is by far the most productive of vertebrate fossils in the Cretaceous sequence of the escarpment. Fossil bones from the Pembina Member usually suffer from gypsum intrusion that obscures the boundary between the bone and matrix, often causing difficulties in identification at lower taxonomic level. Yet hundreds of vertebrate specimens came from the bentonite quarries in Morden area in Pembina Hills over years, and Canadian Fossil Discovery Centre (CFDC, formerly Morden District Museum) has been actively collecting and curating specimens. Through descriptions of the Pembina vertebrate fauna by Nicholls and her colleagues (Nicholls, 1987, 1989; Nicholls and Russell, 1990; Nicholls et al., 1990) have documented a diverse marine vertebrate fauna including turtles, mosasaurs, plesiosaurs, and birds. In addition to the documentation of taxonomic diversity, their studies demonstrated that the relative abundance of vertebrate fauna in Pembina differs from the contemporaneous strata in other areas of the Western Interior Seaway, and recognized the presence of two faunal subprovinces within the seaway for marine vertebrates. Later studies such as Cuthbertson et al. (2007) and Konishi and Caldwell (2009) continue to add new information on the Pembina mosasaurids.

Plesiosaurian specimens are less common than other vertebrates such as mosasaurs and birds in the Pembina fauna, but about 100 specimens have been registered to CFDC (Hatcher, 2009). Nicholls (1989) noted the abundance of polycotylids relative to elasmosaurids, and the ratio differs from those in more southern faunas at approximately same age (Nicholls and Russell, 1990) and the slightly later fauna of the Bearpaw Formation (Late Campanian to Maastirchtian) on the western side of the seaway at similar latitude (Sato, 2003, 2005). Recent discoveries of new plesiosaurian material from the Pembina Member include a polycotylid specimen with stomach contents (Janzic, 2007).

Ammonites and bivalves were reported in the Millwood and Odanah Members in previous studies (McNeil and Caldwell, 1981), but there are virtually no published records on the vertebrate fossils from these units. CFDC collection includes fragmentary fish, bird, and mosasaur remains from the Millwood Member, but no plesiosaurian remains have been obtained so far. Our brief fieldwork found ammonite *Baculites* and a possible vertebrate bone at an outcrop of the Odanah Member in south of Morden; these fossils were found on relatively fresh surface of a hard shale, but poorly preserved, suggesting the diagenesis/weathering well into the shale. We are not aware of published accounts on vertebrate fossils from the rest of the Pierre Shale and the overlying Bossevain Formation (Maastrichtian), and our search has not covered these units.

In summary, the Cretaceous marine sediments of the Manitoba Escarpment has a great potential to yield vertebrate fossils that contribute to the further understanding of the vertebrate fauna of the Western Interior Seaway by filling the stratigraphical and geographical gaps in the record. In addition to the Campanian Pembina Member of Pierre Shale that has produced a large number and diversity of fossil vertebrates, other units such as Ashville, Favel, and Niobrara formations are promising. Previous findings in the Pasquia Hills area and our discoveries of vertebrate fossils in Porcupine Hills and Riding Mountain suggest the wide extent of the fossiliferous layers in the Cenomanian-Turonian sequence. The Niobrara Formation in the escarpment may not be as productive as the equivalent in south in terms of the number of specimens, but the exquisite condition of the braincase of the ROM plesiosaur from the Niobrara Formation in Pembina Mountain area contributes to the anatomical knowledge of the Polycotylidae in general and not just for the characterization of the local fauna. Meanwhile, upper strata of the sequence, i.e., Millwood and Odanah Members of the Pierre Shale,

remain admittedly undersearched; the known few fossils are bright sign, but further field study is necessary to evaluate their potential.

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FIGURE CAPTION

FIGURE 1. Schematic map of Manitoba Escarpment in Canada. Close-up view after McNeil and Caldwell (1981).

EVOLUTION AND PALEOBIOLOGY OF MARINE REPTILES: USING PLACODONTIA AS A CASE STUDY FOR INTEGRATING OSTEOLOGICAL AND 3D IMAGING, DEVELOPMENTAL, AND PALEOHISTOLOGICAL DATA

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Because of the large-scale faunal change from amphibian-dominated Paleozoic to reptilian-dominated Mesozoic vertebrate communities, the Triassic (251-201 Ma; GSA Geological Timescale, 2009) is one of the most significant periods in vertebrate evolution. Both land and sea life suffered from a major set-back of diversity at the most severe mass extinction event in Earth history at the end of the Permian (e.g., Benton et al., 2004; Erwin, 2008, and references therein). Following this event, especially the early Triassic is characterized as a period of imbalance as well as a period of recovery (e.g., Payne, 2004). It is not until the Middle Triassic that marine invertebrate communities and ecosystem complexity fully recover; however, instead of a gradual diversity increase, several drastic turnover and rapid radiation events appear to be responsible for the increase of diversity in the marine realm (e.g., Brayard et al., 2009).

During the Paleozoic, reptiles largely exploited terrestrial and semi-aquatic freshwater habitats, and only a single lineage of Permian parareptiles, the mesosaurs, were apparently well adapted to an aquatic marine lifestyle. The Triassic on the other hand constitutes the period in which several lineages of reptiles, including placodonts and the remaining eosauropterygians, thalattosaurs, and ichthyosaurs, for the first time independently re-invaded the aquatic realm (e.g., Motani, 2009). The vertebrate community of the Triassic period thus ultimately reveals some of the major evolutionary trends in tetrapod evolution. Just two of the questions that might be asked in this respect are: 'Why did so many reptile lineages return to the marine environment during the Triassic?' and 'what were the environmental, developmental and structural constraints, which act on an organism returning to a marine lifestyle?'

Sauropterygia, including placodonts (e.g., Rieppel, 2000), and Ichthyopterygia (e.g., McGowan and Motani, 2003) are globally well represented from numerous localities, whereas the Thalattosauria were, prior to the recent findings in China (e.g., Rieppel et al. 2000; Wang et al., 2008; Cheng et al., 2009, and references therein), only well known from the Middle Triassic UNESCO world heritage site of Mt. San Giorgio, Ticino, Switzerland (Rieppel, 1987; Müller, 2005). Because all these groups lack modern descendants, it is sometimes difficult to interpret the paleoecology or lifestyle of these animals.

Herein, we would like to focus on the placodonts, a rather heterogeneous group of marine reptiles characterized by a pronounced crushing dentition, which are the sistergroup to all remaining Eosauropterygia (Rieppel, 2000). After briefly introducing the group and the spatiotemporal distribution of the European Placodontia (Fig. 1), novel results and interpretation of the postcranial skeleton of *Cyamodus hildegardis* Peyer, 1931 from the Besano Formation (Anisian-Ladinian boundary) from Monte San Giorgio, Switzerland and northern Italy, the bone histology and microanatomy of

placodont armor, as well as new preliminary data on placodont skulls are presented.

Cyamodus hildegardis belongs to the Cyamodontoidea, which are characterized by more "bean"-shaped crushing dentition and extensive postcranial armor (i.e., dorsal carapaces and also, in some cases, plastra; see Rieppel, 2002), superficially resembling turtles. As was recently shown in a broad-based study of vertebral numbers among Amniota cyamodontoids, similar to other amniote taxa carrying extensive armor, shells, or modified thoracic ribs, generally possess low presacral counts (Müller, 2010). The trunk of *C. hildegardis*, covered by a larger main carapace and separate, smaller hip shield, is now reconstructed more rounded and less laterally expanded than previously hypothesized (Scheyer, in press). Both shields carry a series of enlarged tubercular armor plates laterally. The pelvic shield mainly protects the pelvic girdle as well as the base of the tail. The tail is further protected by four series of armor plates: a dorsal, a left and right lateral, and a ventral row.

A study of the bone microstructures and microanatomy of a sample of placodont armor plates (Scheyer, 2007) revealed the unique presence of a fibro-cartilaginous tissue not known from other dermal ossifications in Amniota (i.e., osteoderms). This 'postcranial fibro-cartilaginous bone' tissue lead to the assumption that different developmental pathways are active in placodont plate armor than in other tetrapod osteoderms, indicating that these armor structures are not homologous. Furthermore, a detailed comparison (Scheyer, 2008) of armor plates and turtle shell bones showed that the purportedly oldest piece of turtle shell, *Priscochelys hegnabrunnensis* Karl, 2005, from the Middle Triassic of southwestern Germany, which would have predated even the newly described *Odontochelys semitestacea* from China (Li et al, 2008), did not belong to a turtle, but instead is a placodont armor fragment. As such it was similar or closely-related to *Psephosaurus suevicus*, an armor-only taxon known from the Muschelkalk.

In an ongoing project supported by the Swiss National Science Foundation (31003A_127053 / 1) the phylogenetic relationships of placodont reptiles is studied. Previously described placodont taxa will be re-examined in the light of novel morphological/osteological data (Fig. 2), acquired mainly though means of CT scanning and 3D reconstruction of crania. For the first time, these data will then be combined with bone histological and developmental data (i.e., data on limb development) in a comparative study.

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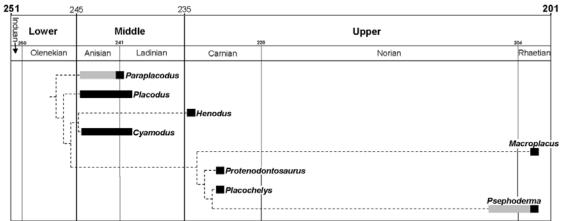
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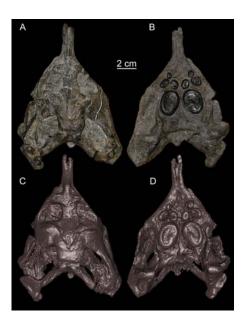
FIGURE CAPTION

FIGURE 1. Time-calibrated phylogenetic hypothesis of European placodont genera (time scale in Ma), based mainly on Rieppel (2000), with additions from Diedrich (2010). Black bars indicate well supported occurrences; grey bars indicate less diagnostic or possible occurrences.

FIGURE 2. New and yet undescribed skull of *Psephoderma alpinum* Meyer, 1858 from the Kössen Formation (late Norian - early Rhaetian, Upper Triassic) of the Schesaplana mountain, Swiss-Austrian border. **A**, **B**, skull in dorsal and ventral view. **C**, **D**, preliminary 3D surface model of skull.



TRIASSIC



STRATIGRAPHY AND SEQUENCE OF TRIASSIC MARINE VERTEBRATE FAUNAS OF SOUTH CHINA

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Until the end of last century, there was only a few isolated records of Triassic marine vertebrates in China. However, this situation changed quickly in the last decade with discoveries of several important Lagersttätte-type Triassic marine vertebrate faunas in Lower Yangtze area and Guizhou-Yunnan area of southern China, including the Olenikian Chaohu-Jurong Fauna, the Anisian Panxian-Luoping Fauna, the Ladinian Xingyi-Luoping-Fuyuan Fauna and the Carnian Guanling Fauna. The new findings provide good chance for scientists to approach the processes and patterns of the biotic recovery and radiation in the marine ecosystem after the P/T mass extinction. In this paper we will present a brief summary about the sequence of these faunas.

Lower Triassic Olenikian Chaohu-Jurong Fauna

This is the oldest Triassic Lagersttätte-type marine vertebrate fauna so far discovered in sourthern China, represented by two localities in the lower Yangtze area: Chaohu of Anhui Province and Jurong of Jiangsu Province. The fossils are yielded in the Lower Triassic Nanlinghu Formation. The biostratigraphic work on the Lower Triassic sequence in Chaohu area indicates that the Nanlinghu Formation belongs to the mid-late Olenikian in age (Tong et al., 2001). The vertebrates from this fauna are dominated with actinopterygian fishes. The only record of the reptiles from this fauna is *Chaohusaurus geishanensis* from Chaohu (Young and Dong, 1972).

Several publications dealt with the fishes of the fauna (Qian et al., 1997; Liu et al., 2002; Jin et al., 2003; Tong et al., 2006) from the two sites, mainly including *Plesioperleidus yangtzensis* (Su, 1981), *P. dayeensis, P. jiangsuensis* (Qian et al., 1997), *Lepidotes jurongensis, Zhangina cylindrica, Stensiönotus dongchangensis, Jurongia fusiformis, Qingshania cercida, Suius brevis, S. cf. S. brevis* and coelacancanthid *Chaohuichthys majiashanensis*. The fauna is characteristic with relatively abundant perleidids and a few parasemionotids and coelacancanthids. Similar perleidids were also found in several other places of southern China, suggesting such fish fauna had been widely distributed there. Relatively monotonous and endemic feature of the fauna might reflect a slow recovery of the marine biota in the Early Triassic.

Middle Triassic Anisian Panxian-Luoping Fauna

The Anisian fauna was mainly found in two sites, around Yangjuan Village of Panxian, Guizhou, and Dawazi of Luoping, Yunnan. All the fossils from the two sites are recovered from the Upper member of the Guanling Formation. The conodont analysis on the type sections of the two sites indicated that the fossils from two sites occur in the same conodont zone, *Nicoraella kockeli* Zone, suggesting a middle Anisian in age (Sun et al., 2006; Zhang et al., 2009; Huang et al., 2010). Researches from Peking University (Beijing) and Geologic Survey of Southwestern China (Chengdu,

Sichuan) had made extensive excavation on the two sites, respectively. Both the reptiles and fishes show a very high taxonomic diversification, suggesting a rapid radiation after the P/T mass extinction.

Ten taxa of marine reptiles have so far been described from the fauna (Jiang et al., 2003, 2005b, c, 2006a-c, 2007, 2008a-d; Li, 2003; Li et al., 2004, 2006; Shang, 2006), showing very high taxonomic diversification, including: ichthyopterygians *Mixosaurus*, *Phalarodon* and *Xinminosaurus*; sauropterygians *Placodus*, *Keichousaurus*, *Nothosaurus* and *Lariosaurus*; eosauropterygian *Wumengosaurus*; protorosaur *Dinocephalosaurus* and archosaur *Qinosuchus*.

Mixosaurus, *Phalarodon* and *Xinminosaurus* from this fauna represent an early differentiation of the ichthyopterygians. *Mixosaurus* is a typical form for the reptiles in the fauna. The reptile fauna shows a strong similarity to the younger Monte San Giorgio Fauna in the West Tethys by the co-occurrence of several genera of the marine reptiles, such as *Mixosaurus*, *Placodus*, *Nothosaurus*, *Lariosaurus*, occurring in the course of the global sea level rising to the top both on the stage-scale and the period-scale. They represent a rapid biotic radiation and the quick westward establishment of a new vertebrate ecosystem with concurrent marine paleoenvironmental stabilization along the northern coastline of the Paleotethys.

Nearly 30 types fishes were excavated from the fauna but so far only a few were described (Tintori et al., 2008; Sun et al., 2008, 2009; Wu et al., 2009; Zhang et al., 2010), including *Colobodus baii* from Panxian, *Marcopoloichthys ani, Luopingichthys bergi, Saurichthys dawaziensis*, and *S. yunnanensis* from Luoping (Sun et al., 2009). Preliminary observation reveals that the fish fauna is characterized with much diversified saurichthyids (at least 4 generic forms) and neopterygians, shared many generic taxa with West Tethys, such as *Saurichthys, Birgeria, Peltopleurus, Placopleurus, Sangiorgioichthys, Eosemionotus, Habroichthys*, and *Perleidus*, suggesting a tight biogeographic relationship between west and east Tethys. However, the radiation of the neopterygians in the East Tethys seems much earlier than in West Tethys.

Middle Triassic Ladinian Xingyi-Luoping-Fuyuan Fauna

The strata contains fossils of this fauna is widely distributed in Xingyi-Luoping-Fuyuan area, near the Yunnan-Guizhou bordering area. The fossils of the fauna are richening in the lower part of the Zhuganpo Formation. The conodont and ammonite biostratigraphic work indicates an age of late Ladinian. Researchers from Institute of Vertebrate Paleontology and Paleoanthrology (IVPP, Beijing) and Peking University (Beijing) made field excavation in some places. This fauna contains abundant reptiles and fishes.

The following reptiles had been recorded in the fauna (Young, 1958; Li et al., 2002; Li and Jin, 2003; Li and Rieppel, 2004; Rieppel et al., 2003 and Cheng et al., 2004; 2006; 2007): sauropterygians: *Keichowsaurus*, *Nothosaurus and Lariosaurus*; **thalattosaur**: *Anshunsaurus*; **ichthyosaur**: *Guizhouichthyosaurus* or *Shastasaurus*; and **pisttosaur**: *Yunguisaurus*.

It shares the sauropterygian (*Keichowsaurus*, *Nothosaurus and Larisaurus*) with the preceding Anisian Panxian-Luoping fauna but lacks the mixosaur ichthyosaur. Meanwhile the presence of the thalattosaur (*Anshunsaurus*) and large ichthyosaur (*Guizhouichthyosaurus* or *Shastasaurus*) also suggests a close relationship with the succeeding Carnian Guanling Fauna.

Part of the fishes from this fauna were described by Su (1959), Jin (2001), Liu et al. (2002, 2003), and Tintori et al. (2008), including *Peltopleurus*, *Asialepidotus*, *Sinoeugnathus*, *Birgeria*, *Guizhouamia*, *Guizhouniscus*, *Guizhoubrachysomus*, and *Xingyia gracilis* and *Marcopoloichthys ani*, reflecting a fish

fauna dominated with the 'subholosteans'.

Late Triassic Guanling Fauna

The fossils were excavated from the lower part of Wayao Formation exposed around Xinpu Town, about 40 km west to Guanling County. The coexisted conodonts and ammonites suggested an age of the Carnian of the Late Triassic. This fauna is featured with thalattosaurs and large ichthyosaurs(Li, 1999, 2000; Liu, 1999, 2001; Rieppel et al., 2000; Yin et al., 2000; Li and Rieppel, 2002; Li and You, 2002; Luo and Yu, 2002; Nicholls et al., 2002; Cheng, 2003; Chen and Cheng, 2003; Liu and Rieppel, 2001, 2005; Rieppel and Liu, 2006; Jiang et al., 2004, 2005; Maisch et al., 2006; Pan et al., 2006), with body size varying from 5 m to more than 10 m long..

ichthyosaurs The nominated large including Guizhouichthyosaurus tangae, Typicusichthyosaurus tsaihuae, Guanlingsaurus liangae, Cymbospondylus asiaticus, Panjiangsaurus epicharis, and Callawayia wolonggangensis. Although some nominated taxa are questionable, the discovery of abundant specimens of large ichthyosaurs strongly suggests that the marine reptiles began to reach its dawn of the flourish. Anshunsaurus and Xinpusaurus are the typical thalattosaurs of the fauna. Phylogenetic analysis indicates the former closes to the Middle Triassic Askeptosaurus from the West Tethys while the latter closes to the Late Triassic Nectosaurus from North American (Liu and Rieppel, 2001; Jiang et al., 2004; Müller, 2005). The placodonts are represented by Sinocyamodus xinpuensis and Psephochelys polyosteoderma (Li, 2000; Li and Rieppel, 2002), suggesting a tight biogeographic relationship with the fauna from the West Tethys. Discovery of Odontochelys semitestacea provided important clue about origin and formation of the turtle shell (Li et al., 2008).

Fishes is relatively few in the fauna compared to that in the Middle Triassic ones, but characteristic with the large fishes such as *Birgeria* and *Guizhoueugnathus* (Liu et al., 2006). Other fishes recorded in the fauna including two actinopterygians *Pholidopleurus* and *Peltopleurus*, and a coelacancanthid *Guizhoucoelacanthus*.

THE DOLOMITI GARDEN: WHICH CRISIS FOR THE FISHES?

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A few fish remains have been found in the latest Permian/ earliest Triassic rocks (Bellerophon Formation/Werfen Formation) in the Dolomiti area around the half of the last century. A revision of the material gives a quite surprising result as we can prove that two, probably three, fish taxa went through the P/Tr boundary, namely Bobasatrania antiqua (Accordi 1955), the hybodont shark Palaeobates and possibly Achaeolepidotus leonardii (a Parasemionotiformes, not a semionotids as proposed by Accordi 1955). The Dolomiti area is famous for the uppermost Permian fauna, dominated by the large brachiopods Comelicania together with other brachiopod, molluscs, especially the gastropods Bellerophon, and calcareous algae. The very rich Late Permian benthic fauna appear very much reduced in the basal Triassic beds, as everywhere, even if very small gastropods and bivalvs where still rather common. We focused especially on Bobasatrania, a highly specialized suction feeder that could reach over half a meter in length already in the latest Permian, being then widespread all over the world (except South China!!) during the Early Triassic and the Anisian. Bobasatrania preyed possibly on small/thin molluscs that was grinded by the pharyngeal tooth plates, while Palaeobates had a more powerful crushing dentition. Hybodont sharks are very widespread during late Paleozoic and Mesozoic, but both Bobasatrania and the parasemionotids have been considered typical of the 'Early Triassic' fish faunas: however, they appear already in the latest Permian. Taphonomy of the beds yielding these remains point to a strong mechanical selection so that only stout teeth could survive and be included in the sediment: this means that we may expect to find more 'Triassic' fishes in the Late Permian rocks.

HOW FAST WAS THE RECOVERY AFTER THE PERMO/TRIASSIC CRISIS? THE ANSWER FROM THE ACTINOPTERYGIAN FISHES

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The massive Permo-Triassic crisis engendered the extinction of as much as 90% of the living organisms on the entire Earth; the recovery of life after such a dramatic event has always been thought to have proceeded by slow steps.

Though, recent researches carried out on new Chinese marine vertebrate faunas of early Middle Triassic age seem to suggest much faster developments. On the other hand, only a few years ago our knowledge was almost entirely based on the European faunas contained in the Formazione di Besano on Monte San Giorgio (Late Anisian-Early Ladinian) and, only occasionally, in the Muschelkalk of Central Europe. Sparse finds also come from North America, most of all from Nevada. These western Tethys focused data show a well differentiated fauna starting from Late Anisian. The latest data recorded in China are remarkably changing the picture: southern China appears as the main centre of the radiation, whose beginning proves to be older and older as the research progresses. The Pelsonian faunas from Panxian and Luoping (Southern China) undoubtedly support this hypothesis: fishes as well as marine reptiles were already well differentiated in the Middle Anisian. The Chinese excavations have yielded a striking amount of specimens, dug up in a very wide area, often incredibly well preserved, allowing extremely detailed studies. Likely, some groups (among both fishes and reptiles) that have always been considered as endemic of western Tethys have actually first appeared in the easternmost part of the ancient oceanic gulf, later migrating westwards. As a consequence, the major Late Anisian radiation witnessed by the rocks of Monte San Giorgio exclusively concerns the Subholostean fish group, which probably appeared in the East as well, a few million years before. The more advanced Neopterygian fish group, though commonly found in the European Middle-Triassic deposits, is much more successful in the East as early as in the Pelsonian. Nonetheless, the further important evolutionary step of the Neopterygians is so far represented by the Norian Italian faunas of the Calcare di Zorzino.

REPRODUCTIVE PATTERNS OF THE MESOZOIC AQUATIC REPTILES

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The first group of reptiles to return to the water is the Mesosuria, an anapsid group, which are freshwater animals, lived in the Permian (the later Palaeozoic). Most aquatic groups of reptiles were more resent and lived in the sea of the Mesozoic, including the Ichthyosauria, Sauropterygia, Hupehsuchia, Thalattosauria, and some lineages of the Crocodyliformes and Squamata. Choristodera, a crocodile-like reptilian group, has long been considered to be semi aquatic and lived in a river-lake system. Recent discovery indicates that the early members of the group may have been fully aquatic. All of the aforementioned groups are diapsid reptiles. There is a few of those groups, such as crocodyliforms and some lineages of squamates to continue their semi aquatic or aquatic ways of life to the present day. Most recently, the earliest turtle, *Odontochelys*, which bears teeth but did not have a complete carapace, is considered as an aquatic animal.

During the transition from a terrestrial to an aquatic environment in all groups of aquatic reptiles, many changes happened to the skeleton anatomy. Of those changes, the most significant ones can unquestionably be attributed to radically different requirement of support and locomotion. It is universal that the pelvis is tightly fixed with the vertebral column through a rigid and immovable sacro-pelvic joint in terrestrial or most semi-aquatic reptiles, which is important for supporting the body weight and conducting the terrestrial locomotion of the animals whether they are oviparous or viviparous (Fig. 1A). It is obvious that aquatic reptiles no longer need to support the body weight and do complicated ways of walking in the water and, thus, a lightly built sacrum and movable sacro-iliac joint could be expected for these reptiles (Fig 1. B, C), which, by extension, would certainly influence the way of the reproduction of these reptiles, enhancing the process of giving birth of live young for the viviparous reptiles in a vulnerable aquatic environment. So, viviparity could have been indirectly reflected by the pattern of the sacro-pelvic joints in aquatic forms.

Reptiles normally lay eggs. Viviparity (giving birth of live young) has been indipendently evolved many times in squamates. In extant squamates, there are intermediate stages between oviparity and viviparity, which are traditionally referred to the category of 'ovoviviparity'. Recently, the viviparity is often defined as giving birth to autonomous, free-living offspring, whatever their state of maturity. Viviparous modes of reproduction in modern squamates can be further distinguished based on the nutritional patterns; for instance, 'lecithotrophy' (the provision of nutrients via yolk) and 'matrotrophy' (the maternal provision of nutrients) represent extremes of a continuum. Taxa can thus be described according to the relative contributions of nutrient sources. However, it is difficult to determine the nutritional pattern in fossil viviparous species.

In fossil reptiles, viviparity has been documented for some ichthyosaurs, mosasauroid squamates, and some lineages of the Sauropterygia. For the later, the direct evidence has been known until Cheng et al. reported the two gravid specimens of *Keichousaurus* (a eosauropterygian) discovered from the Chinese Triassic in 2004. Most recently, one of the early members of the Christodera, *Hyphalosaurus*

baitaigouensis was proved to be viviparous on the basis of a gravid specimen from the Early Cretaceous lake deposits of China in 2010. Up to now, all of the viviparous groups mentioned earlier, except for the mosasauroid squamates, show a lightly built pelvic girdle and a chain-like, movable sacro-pelvic joint, i.e., the sacral ribs are structurally simple and rod-like, which form loose articulations with both the vertebral column medially and the ilium laterally. Such a sacro-pelvic joint is also true in the earliest turtle (Fig. 2). There has been no evidence to demonstrate that any species with a chain-like sacro-pelvic joint is oviparous or not aquatic in either fossil or extant reptiles. With such a chain-like sacro-pelvic joint, viviparity could be expected for the earliest turtle, *Odontochelys*, the Hupehsuchia, Thalattosauria, and the metriorhynchid crocodiliforms of the Jurassic.

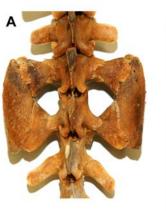
The early members of mosasauroid squamates have been demonstrated to be viviparous; their sacro-pelvic joint is not chain-like although partly movable. In other words, the sacral ribs of those squamates were fused to the vertebral column medially but loosely contact to the ilium laterally although the articular facet is dorso-ventrally somewhat expanded. Such a morphotype is present in the extant semi aquatic lizard, *Amblyrhynchus*, but the latter is an oviparous lizard (Fig. 3). This implies that the viviparous mosasauroids were most probably semi aquatic and the partly movable sacro-pelvic joint indicates that any reptile with such a sacro-pelvic joint dose not show a firm relationship to certain reproductive pattern. In this case, mesosaurs with a partly movable sacro-pelvic joint could be semi aquatic and either viviparity or oviparity could be expected for the reptiles. Same to the later choristoderans in which the sacro-pelvic girdle is not fully chain-like.

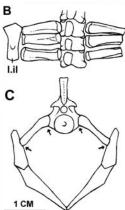
FIGURE CAPTION

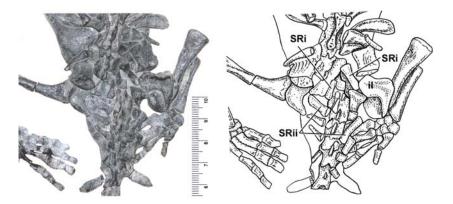
Figure 1. **A**, the pelvic girdle of an alligator in dorsal view, showing rigid vertebral column-sacral ribs-ilium contacts. **B**, the pelvic girdle of a pachypleurosaur in dorsal view, showing movable vertebral column-sacral ribs-ilium joints. **C**, the posterior view of the pelvic girdle of B, showing a chain-like sacro-pelvic joints pointed by arrows. Abbreviations: **1.il**, left ilium.

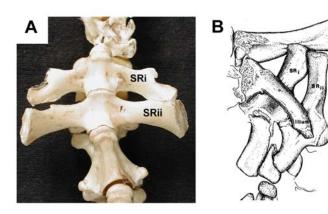
Figure 2. The posterior part of the skeleton of *Odontochelys* (holotype, IVPP V15639), showing the rod-like sacral ribs which indicate a chain-like sacro-pelvic joint. Abbreviations: **il**, ilium; **SRi** and **SRii**, sacral ribs 1 and 2.

Figure 3. The sacral vertebrae of a semi aquatic lizard (**A**), the extant *Amblyrhynchus* (oviparous) and a mosasauroid (**B**), the Cretaceous *Aigialosaurus* (its close relative, *Carsosaurus*, has been documented to be viviparous) in ventral view, showing fused joints between the sacral ribs and vertebral column. Abbreviations: **SRi** and **SRii**, sacral vertebrae 1 and 2; **F**, femur.









THE DIVERSITY OF SAURICHTHYIDS FROM MIDDLE TRIASSIC (ANISIAN) OF SOUTHWESTERN China

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A detailed systematic work is fulfilled of rencently discovered saurichthyids, from Middle Triassic (Anisian) of southwestern China, and eight species are recognized based on more than 150 well preserved specimens. Besides two referred to Saurichthys, the remaining taxa pertain to three generic-level morphotypes (Type A (in review), Type B and Type C) of remarkable diversity both in anatomy and ecological adaptation: Type A mainly characterized by boot-like cleithrum, dorsally situated pectoral fins and some other correlated features, this group probably represents a new lineage adapted to surface water with similar lifestyle and locomotion pattern as extant needle fishes; Type B posseses wide and flat skull roof with peculiar arrangement of dermal bones and proportions of endorcranium, its comparatively blunt teeth suggesting different food-intake strategy and ecologic niches from Saurichthys; Type C, as a typical benthic form, is distinguished evidently from other saurichthyids by possession of extremely narrow part of skull roof between orbitals, dorsaloventrally compressed skull with sensory canal openings in skull roof conspicuously large while the ones in mandible rather degenerated, transverse processes extending laterally in abdominal neural arches, all fins distally rounded in contour. With such considerable richness and diversity, therefore, the flourishing of saurichthyids in Anisian also reflects the rapid recovery of Triassic marine ecosystem following early Triassic stagnant stage after the end-Permian extinction.

A NEW TRIASSIC ACTINOPTERYGIAN FISHES FROM LUOPING, YUNNAN PROVINCE

WEN WEN

Chengdu Center of China Geological Survey

Chengdu Center of China Geological Survey has found a middle Triassic lagerstätte in 2007 during geological mapping. This lagerstätte yielded thousands of fully articulated and exquisitely preserved vertebrate marine fossils. The founder called it Luoping biota according to its locality (Zhang, 2008). The majority of vertebrate fossils are fish fossils. As we all know, halecomorphs are very prosperous from the lower Triassic to early upper Triassic. These years, many halecomorphs were found in Triassic layers in Guizhou and Yunnan, south China. This article is to describe a new kind of halecomorphs.

MORPHOLOGICAL STUDY ON THE MIXOSAURUS PANXIANENSIS FROM THE MIDDLE TRIASSIC OF GUIZHOU, CHINA

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INTRODUCTION

The Panxian fauna from the Middle Triassic of Guizhou preserved a large number of fancy and complete marine reptiles with large biodiversity, for which *Mixosaurus* acount the biggest part (Hao et al., 2006). As are all ichthyosaurs, *Mixosaurus* is a mosaic of primitive and derived characters (Callaway, 1997), so studying the *Mixosaurus* is quite significant for understanding the evolution of ichthyosaurs. Thanks to the enrichment and excellent preservation condition of the collection in Geological Museum of Peking University (GMPKU), four specimens from the Middle Triassic of Guizhou, China provide us with much complete and detailed morphological information of *M. panxianensis*. Analysis based on skull length, body length, length of external nares, distance between posterior margin of external nares and anterior margin of orbit, longitudinal diameter of orbit, vertebrae centrum height & length, neural spine height & length, the angles between neural spine and body shows that there exist some laws in the process of individual growth, and the changes of three ratios-centrum height/length, neural spine height/length and neural spine height/centrum height, and that of angles between neural spine and body presents a resembling pattern, which indicates that neural spines and vertebrae centrum's have some morphological link.

MATERIAL AND METHOD

The specimens studied in this article are deposited in Geology Museum of Peking University, bearing the numbers GMPKU-P-1033 (holotype of *M. panxianensis* Jiang, 2006), GMPKU-P-1038, GMPKU-P-1039 (paratype of *M. panxianensis*) and GMPKU-P-1065 (broken into three parts, numbered respectively as GMPKU-P-1039 (1), (2) and (3)), and will be called 1033, 1038, 1039 and 1039 for short. 1038 and 1065 are preserved better than 1033 and 1039 in that both 1033 and 1039's tails are incomplete. It is worth mentioning that 1038 and 1065's caudal vertebra are preserved pretty well. Measurements are taken using dial calipers and tapeline, and recorded to the nearest 0.1 mm by dial calipers and 0.1 cm by tapeline. Taken measurements include: a) length of whole body, b) length of skull, c) length of external nares, d) distance between the posterior margin of external nares and the anterior margin of orbit, e) longitudinal diameter of orbit, f) anteroposterial length, dorsal-ventral height of vertebrae centrums; g) anteroposterial length, dorsal-ventral height of neural spine; h) angles between neural spines and body.

SYSTEMATIC PALAEONTOLOGY

ICHTHYOSAURIA de Blainville, 1835

MIXOSAURIDAE Baur, 1887

Diagnosis. (**Revised in Jiang et al., 2006**)—Premaxilla posteriorly pointed, lacking supranarial process; dorsal margin of orbit formed by supraorbital crest; skull roof distinguished by long sagittal crest on nasal, frontal, and parietal; enlarged anterior terraces of upper temporal opening reaching nasal; mid-caudal vertebral centra with significant height increase.

MIXOSAURUS Baur, 1887

Diagnosis. (**Revised in Jiang et al., 2006**)—Humerus relatively short and wide, being about as long as broad; maxilla with dental groove (plesiomorphic character absent in *Phalarodon*).

Mixosaurus panxianensis Jiang, 2006.

Holotype.—GMPKU-P-1033.

Paratype.—GMPKU-P-1039.

Diagnosis.—Jugal with short posteroventral process; external contact between jugal and quadratojugal absent (plesiomorphic character that is absent in other mixosaurid species). Straitigraphy.---

Description.—Most of the osteological characters observed hitherto indicate clearly that 1038 and 1065 can be classified as *Mixosaurus panxianensis*, such as, premaxilla posterirly pointed, nasal frontal and parietal comprise a sagittal crest, which extends as long as 12 cm and 2.3 cm high in 1065, and Jugal with short posteroventral process, etc. However, there are also some characteristics quite bizarre or valuable as follows: a) postorbital extends dorsally to the margin of anterior terrace of upper temporal fenestra, separating the postfrontal and the supratemporal, which is not decided when denominated by Jiang et al., 2006; b) a notch that is definitely neither a damage nor artificiality presents at the posterior edge of ulna in 1065, and this phenomenon is found for the first time in this species, which may be interpreted as sexual dimorphism.

MORPHOLOGICAL STUDY

Body size

In the process of discerning growth pattern of Mixosaurus, absolute size is not as valuable as relative size. Due to bad preservation condition, the whole length of 1033 and 1039 is not accessible. However, the skull length of all specimens is easy to obtain, thus we can get the age sequence of them on basis of skull length: 1038 (13.7 cm) < 1039 (19.5 cm) < 1065 (22.5 cm) < 1033 (25.4 cm). Skull length/body length of 1038 and 1065 is 0.261 and 0.228, which has a diffidence of 14.5%, bigger than measurement error, suggesting that this ratio decreases with age.

Considering that most of the diagnoses of either Mixosauridae or *Mixosaurus* are distributed among skull, relative size of parts comprising skull seems quite significant. Figure 2 shows length of external nares, distance between posterior margin of external nares and anterior margin of orbit and longitudinal diameter of orbit of *M. panxianensis*. It's evident that these three values increase with age except the length of external nares of 1033 may be smaller than real value due to deformation. The ratios of the three values are 1:2.14:4.23 (1038), 1:1.74:3.65 (1039), 1:1.42:2.87 (1065) and 1:2.68:4.22 (1033). So the external nares becomes relatively larger with age.

Vertebrae

As mentioned above, vertebrae are preserved well only in 1038 and 1065, though some dorsal

vertebrae are overlapped by ribs and in this situation, the number of vertebrae are estimated using even length of centrum. 1065 is the best preserved adult individual among the four specimens, so we use it as a frame to discuss the other specimens. 1065 has about 44 dorsal vertebrae (numbered from 1 to 44 with a prefix 'D', D1 is epistropheus) and 63 caudal vertebrae (numbered in the same style of dorsal vertebrae but with a prefix 'C').

Three ratios are calculated: centrum height/length, neural spine height/length, neural spine height/centrum height and then plotted in Figure 3. In dorsal regions, the ratio of dorsal vertebrae centrum height/length (Fig. a) keeps nearly horizontal in the range of 0.8 and 1.4, with an average of 1.2. But this ratio is as high as 1.6 in 1039, which might be attributed to stress difference and anisotropism. The caudal can be divided into three segments based on this ratio: C1 to C16, C17 to C37, C38 to C63. In the first segment, this ratio ranges between 1.49 and 2.00, and is quite stable in the anterior part but in the posterior part it shows a dramatic linear increase. In the second segment, it mostly exceeds 2.0, and the maximum value 2.33 locates at C27 (1065) and 2.41 locates at C26(1038). The third segment firstly descends linearly and then stays stable around 1.49 to the end. The whole pattern of this ratio is a curve with its middle part convex upside, showing that mid-caudal vertebral centra have significant height increase, which verify that this specimen belongs to Mixosauridae (Jiang et el., 2006).

The anteroposterial length of neural spine can vary in different part of a single neural spine, but here we are only interested in the maximum length. The ratio of neural spine height/length (Fig. 3 c) exhibits linear decrease feature in dorsal part, ranging from 5.3 to 9.1. In the caudal part of 1065, it is a polyline which can also be divided into three segments: C1 to C8 (decrease), C9 to C20 (increase), C21 to C32(decrease) while in 1038, the boundary is different: C1 to C7 (decrease), C8 to C11 (increase), C12 to C24 (decrease). This ratio is smaller in 1038 than in 1065, so we can conclude that neural spine becomes relatively slimmer with age and the whole pattern of this ratio doesn't change much with age. The angles between neural spine and body (Fig. 3 b) stay below 90 degrees in D1 to around D31 in all specimens, which suggests that neural spines in this area are inclined posteriorly. In 1065, it fluctuates around 50 degrees in D1 to D8, and springs suddenly up to 80 degrees from D9 on. Neural spines keep almost perpendicular to the body from D32 to C9. From C10 to C15, this angle ascends steady. It reaches maximum value (142 degrees) at C19 then decreases linearly to the end.

Due to the smallness of absolute size of centra, the ratio of neural spine height/centrum height (Fig. a) in dorsal of 1065 is extremely high (4.0 to 5.5), but in posterior part of dorsal of 1039 it's only 2.5. Quite like the other ratios mentioned above, the ratio of neural spine height/centrum height (Fig. a) also represents a three-segmented feature. In 1065, it remains stably around 1.5 from C6 to C16 and then goes up linearly before reaches maximum value 2.46 at C22, and after that it descends almost at the same speed as it ascends before C22. The resembling thing happens in 1038 except that there is a 5-vertebra lag before 1065 and the maximum value is 1.99 at C16. So the pattern of this ratio may keep unchanged with age, but posteriorly and higher.

CONCLUSION

The morphology change of vertebrae centrum and neural spine have some link. The shape of vertebrae centrum in the anterior part is cylindric and turns gradually to discoidal in the middle, and turns back to cylindric in the posterior part. At the same time, neural spines become slim in the middle part of caudal vertebrae and incline to the anterior. All of this it to form a fan-like and robust tale that

can provide enough propulsion for Mixosaurus to swimming around.

The basic morphological pattern of Mixosaurus tail changes not much with age, while the relative size of skull and external nares is becoming greater. Three ratios-centrum height/length, neural spine height/centrum height, and angles between neural spine and body show a resembling three-segmented feature, so different parts of Mixosaurus are not isolated but organically linked. Study on morphological changes of vertebra of Mixosaurus may cast some light on classification, phylogeny and functional study of Mixoaurus.

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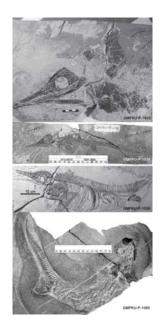
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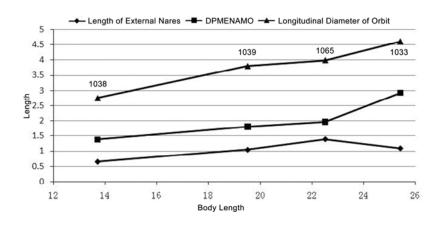
FIGURE CAPTION

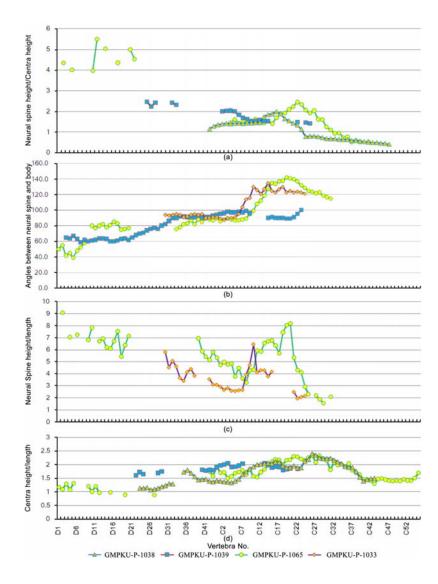
Figure 1. GMPKU-P-1033 (holotype), GMPKU-P-1038, GMPKU-P-1039 (paratype), GMPKU-P-1065 (scale bar equals 1 cm)

Figure 2. Length of external nares, distance between posterior margin of external nares and anterior margin of orbit (DPMENAMO), longitudinal diameter of orbit of *M. panxianensis*

Figure 3. Centra height/length, neural spine height/length, Angles between neural spine and body, and neural spine height/length of Mixosaurus.







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