

重庆侏罗系杨氏璧山上龙(一淡水蛇颈龙)的再研究¹⁾

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摘要 侏罗纪的蛇颈龙类化石主要发现于欧洲,在世界的其他地区则比较少见。亚洲的蛇颈龙化石,尤其是侏罗纪的属种大多破碎而难以鉴别(Sato, 1998)。到目前为止, *Bishanoptiosaurus youngi* (Dong, 1980)和 *Yuzhouptiosaurus chengjiangensis* (Zhang, 1985)是亚洲地区最为完整的侏罗纪蛇颈龙类化石,并且化石产自对于蛇颈龙而言比较罕见的淡水沉积,因此这些材料对于了解该类群的系统发育、历史动物地理和古生态来说非常重要。

本文重新详细描述了采自中国重庆自流井组东岳庙段的杨氏璧山上龙²⁾(董枝明,1980)。愈合情况不好的椎体和椎弓以及耻骨的边缘形态表明,杨氏璧山上龙的正型标本是一个幼年个体的头后骨架。我们的研究表明杨氏璧山上龙主要依分叉的荐肋为特征,而这一性状在初次发表时作为颈肋特征被描述。璧山上龙的其他特征包括侧扁的神经棘以及狭窄的乌喙骨和肱骨上有一个突。经过重新修理的标本显示,坐骨和耻骨相对的面呈沟槽状,这一现象表明它们之间的接触关系要较原来描述的情况复杂,是一种依靠软骨的连接,而非直接接触。本文对杨氏璧山上龙的腰带部分进行了重新复原。

O'Keefe (2001)的支序分析支持将 Plesiosauria 二分为 Plesiosauroidea 和 Pliosauroidae,后者包含两个科:Pliosauridae 和 Rhomaleosauridae。这两个科主要依据头骨特征相区分。璧山上龙曾被归入 Rhomaleosauridae(董枝明,1980)。尽管是个有效种,但由于头骨缺失,并且只有少部分头后骨骼特征可以用于科的鉴别,因此杨氏璧山上龙与其他蛇颈龙的系统关系仍然不清。就目前的材料而言,杨氏璧山上龙可以归入 Pliosauroidae,但是科级地位还难以确定。

蛇颈龙主要生存于海洋环境。除了中国以外,非海相沉积物中的蛇颈龙化石还见于英国、加拿大和澳大利亚,而璧山上龙也不是在中国发现的惟一淡水蛇颈龙类,其他一些材料如 *Yuzhouptiosaurus chengjiangensis* 仍有待进一步研究。以前对东岳庙段的动物和植物群的研究证明该段为亚热带淡水沉积(蔡绍英,1988;孟繁松、陈大有,1997)。杨氏璧山上龙的发现为研究蛇颈龙入侵淡水环境增添了更多信息。虽然迄今知道的淡水蛇颈龙类标本都很破碎,但它们在地理和时代上的广布性表明在蛇颈龙类的大部分历史时期中淡水种类是普遍存在的。

关键词 重庆璧山,侏罗系,自流井组,蛇颈龙,解剖学

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2) 在以往的有关文献中,化石产地璧山和杨氏璧山上龙分别被写成“璧”山和杨氏“璧”山上龙。值此机会,我们在此将其纠正。

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RESTDY OF BISHANOPLIOSAURUS YOUNGI DONG 1980, A FRESH WATER PLESIOSAURIAN FROM THE JURASSIC OF CHONGQING

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Abstract *Bishanopliosaurus youngi* Dong , 1980 from the Jurassic Dongyuemiao Member of the Ziliujing Formation in Chongqing Municipality , China is redescribed in detail. The holotype of *B. youngi* is the postcranial skeleton of a young individual , but so far the most complete plesiosaurian fossil known from the Asian Jurassic. Our restudy indicates that *B. youngi* can be diagnosed by the bifurcated sacral ribs combined with the compressed neural spine , narrow coracoid , and the humerus with a peculiar projection. *B. youngi* is a valid taxon , but its phylogenetic relationships with other plesiosaurians remain uncertain mainly because of the lack of cranial features. Previous studies on the Dongyuemiao fauna and flora indicate that the sediments are of subtropical freshwater origin. The discovery of *B. youngi* added further information on the freshwater invasion of plesiosaurians. Freshwater plesiosaurians so far known are very fragmentary , but their wide geographic and temporal distributions suggest that the presence of plesiosaurians in freshwater environment was not uncommon in most of their history.

Key words Bishan , Chongqing , Jurassic , Ziliujing Formation , Plesiosauria , Anatomy

1 Introduction

Jurassic plesiosaurians are well represented by a large number of beautifully preserved specimens from Europe , but are poorly known from the equivalent strata of other countries. There are a number of occurrences of plesiosaurians from Asian countries , but many of them , especially those from the Jurassic , are very fragmentary and non diagnostic (Sato , 1998). *Bishanopliosaurus youngi* (Dong , 1980) and *Yuzhoupliosaurus chengjiangensis* (Zhang , 1985) are so far the only Jurassic plesiosaurians known from Asia and retain significant parts of the skeleton. In addition to the rarity of the occurrence of nearly complete postcranial skeleton from the Asian Jurassic , depositional environments of those Chinese specimens are suggested to be an inland lake. Plesiosaurian remains from freshwater deposits are very rare. Considering their importance in plesiosaurian biogeography and biostratigraphy , it is necessary to restudy those taxa in detail in the light of increasing information available for other plesiosaurian taxa. The purpose of this contribution is to give a detailed redescription of the holotype of *B. youngi* for our further understanding of the anatomy and biogeography of the freshwater plesiosaurians. We also discuss the taxonomic status and phylogenetic relationships of the taxon in the present paper.

2 Geological Background

According to Dong (1980) , the holotype of *B. youngi* was excavated from a sandy mudstone stratum of the Dongyuemiao Member of the Ziliujing Formation in Bishan County , Chongqing Municipality (on March 14 , 1997 , Chongqing was designated as a municipality and separated from the

Sichuan Province), China. Many publications designate the Ziliujing Formation and its equivalents as Lower Jurassic (e. g. Deng, 1985; Dong, 1980; Luo and Wang, 2000; Wu and Tong, 1994). A few studies on local molluscan fauna (Cai, 1988) and flora (Meng and Chen, 1997) of nearby sites, however, correlate the Dongyuemiao Member with Middle Jurassic. The occurrence of *B. youngi* itself does not offer a strong support to either claim, because plesiosaurians are known from both Lower and Middle Jurassic, although they are far greater in both diversity and number in the Lower Jurassic.

Abundance of molluscs and plants characterizes the biota of the Dongyuemiao Member, indicating that the sediments are of freshwater origin and deposited in subtropical climate (Cai, 1988; Meng and Chen, 1997). There are, however, few published accounts on vertebrate fossils from this particular member of the Ziliujing Formation. In contrast to the rich dinosaur fauna of the upper part of the Jurassic series of the region and neighboring areas (Dong et al., 1985), vertebrates from the lower part is relatively poorly known. Recently, Luo and Wang (2000) reported the occurrence of a number of prosauropod and theropod dinosaurs from the member in Gongxian County, Sichuan Province (about 200 km southwest of Bishan) and emphasized the importance of the Ziliujing fauna in relation to other dinosaur faunas.

3 Systematic Paleontology

Diapsida Osborn, 1903

Sauropterygia Owen, 1869

Plesiosauria de Blainville, 1833

Pliosauroida (Seeley) Welles, 1943 sensu O'Keefe, 2001

Bishanopliosaurus Dong, 1980

Type and only known species *Bishanopliosaurus youngi* Dong, 1980.

Revised diagnosis As for the type and only known species.

Bishanopliosaurus youngi Dong, 1980

Holotype IVPP V 5869, an incomplete postcranial skeleton of a young individual composed of 63 vertebrae, ribs, most of pectoral and pelvic girdles, humeri and femora, and disarticulated paddle elements.

Revised diagnosis Short-necked plesiosaurian (pliosauroid) with at least 17 cervicals, 19 dorsals, 3 sacrals, and 26 caudal vertebrae. In addition to features common among pliosauroids such as short cervicals with well-developed zygapophyses, this taxon has bifurcate sacral ribs as a unique character. Narrow coracoid, projection in humerus, and compressed neural spine are potentially diagnostic (see the Discussion).

Locality and horizon Bishan County, Chongqing Municipality, China; Lower or Middle Jurassic Dongyuemiao Member, Ziliujing Formation.

4 Redescription and Comparison

Our further examination reveals that the preserved vertebral column is composed of fifteen cervicals, nineteen dorsals, three sacrals and twenty-six caudals instead of five cervicals, twenty-one dorsals, two sacrals and thirty-one caudals as suggested by the original description. The fifteen cervicals does not include the atlas and axis but the two pectorals that bear the rib facet on both parapophysis of the centrum and the diapophysis of the neural arch. In comparison with other contemporary plesiosaurians, the number of the cervicals is very low, even after adding two for the missing atlas and axis (Table 1). The rest of the preserved column appears to be almost complete,

judging from the lack of significant morphological gaps throughout the series and from comparable numbers in other known plesiosaurs. The centrum is short and amphicoelous, with no notochordal pit, in all vertebrae. There is a suture between the neural arch and centrum, and in a few vertebrae the neural arch is naturally detached, indicating that this is a very young individual ("juvenile" *sensu* Brown, 1981). In the following description, the combination of "# " and Arabic number indicate the position of the vertebra within the preserved vertebral column. For example, "# 1 " does not represent the atlas but the antermost vertebra of the preserved column.

表 1 杨氏璧山上龙(古脊椎动物与古人类研究所 V 5869)和里阿斯的蛇颈龙类脊椎数比较
Table 1 Number of vertebrae in *Bishanoptiosaurus youngi* (IVPP V 5859) and Liassic plesiosaurs

	Cervicals (颈椎)	Dorsals (背椎)	Sacrals (荐椎)	Caudals (尾椎)	Data Source (数据来源)
<i>Bishanoptiosaurus youngi</i>	17 + *	19	3	26	Pers. Obs.
<i>Archaeonectrus rostratus</i>	24	24	2	34	Owen (1865)
<i>Macropata longirostris</i>	34 or 25 **	22 or 24	3 or 4	22	White (1940)
<i>Rhomaleosaurus cramptoni</i>	27	30 ***	?	34	Carte & Baily (1863)
<i>Microcleidus homalespondylus</i>	38	22	2	10 +	Owen (1865)
<i>Microcleidus homalespondylus</i>	45 *	17	3	20 +	Watson (1909, 1911)
<i>Plesiosaurus dolichodeirus</i>	46 or 47 **	21	3 +	28	Storrs (1997)
<i>Peloneustes philarchus</i>	23 or 24 **	About 20	?	?	Andrews (1913)
<i>Attenborosaurus conybeari</i>	38	21	2	5 +	Sollas (1881)
<i>Thalassiodracon hawkinsi</i>	31	23	5 ?	29 +	Owen (1840)
<i>Plesiosaurus macrocephalus</i>	29	20	2	?	Owen (1840)
<i>Occitanosaurus toumemirensis</i>	46 **	16	4	?	Bardet et al. (1999)

* 包括缺失的环椎和枢椎 including missing atlas and axis; ** 在参考资料中“胸椎”归于颈椎 the “pectorals” counted as cervicals in references; *** 该数可能包括胸椎和荐椎 the number may include pectorals and/or sacrals.

Anterior cervicals of the preserved series have broad zygapophyses that are as wide as the centrum is. On the ventral surface of these cervicals there are a pair of depressions and foramina lateral to the ventral ridge along the midline. One cervical (vertebra # 3) has an additional ridge lateral to the ventral ridge, and a ventral foramen is located between the two ridges. The intervertebral faces of these vertebrae are slightly compressed ovoid in outline. The neural spine is laterally compressed, and the dorsal end is elongated, teardrop-shaped and slightly concave.

The cervical rib facet is entirely located in the parapophysis of the centrum. It is a concave and uneven surface, with a weakly-developed longitudinal ridge and pits in the anterior cervicals (Fig. 1A). Such a ridge is missing in more posterior cervicals. Cervical ribs are poorly preserved. The right rib of the vertebra # 6 has a constriction in the middle of the shaft, giving an outline of hourglass. An isolated rib was found with one of the postermost cervicals, and it has a single spherical head and a short anterior process (see the Discussion for details). In the two postermost cervicals the rib facet is compressed, with its upper half on the short diapophysis (Fig. 1B). The ventral ridge is only weakly developed in those postermost cervicals (Fig. 1C) and entirely absent in the dorsals behind. The two postermost cervicals are very similar to the sacrals in overall morphology, but they are distinguishable from the latter based on the presence of a weakly developed ventral ridge along the midline and the less pronounced dorsal half (diapophyseal portion) of the rib facet.

In the dorsal series, the centrum is spool-shaped, the intervertebral face is almost round in outline, and the rib facet becomes spherical and moves onto the laterally directed transverse process formed by the combination of the parapophysis and diapophysis. There are two or more ventral foramina but no ventral ridge. The neural spines are anteroposteriorly longer than those in the

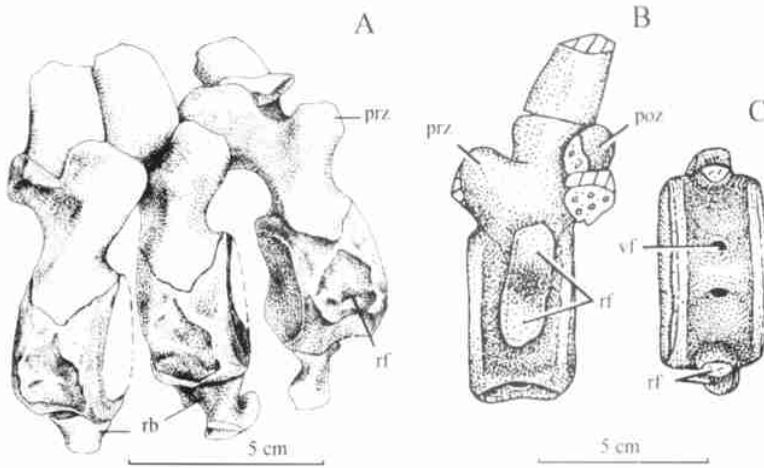


图 1 杨氏璧山上龙所保存脊柱中的第二到第四颈椎右侧视(A)、第十五脊椎左侧视(B)和腹视(C)

Fig. 1 Some anterior vertebrae of *Bishanoptosaurus youngi* Dong, 1980, cervical vertebrae # 2-4 in right lateral view (A) and vertebra # 15 (the second pectoral) in left lateral (B) and ventral (C) views

Abbreviations 简字说明:poz, postzygapophysis 后关节突;prz, prezygapophysis 前关节突;rb, proximal end of a rib 肋骨近端;rf, rib facet 肋骨关节面;vf, ventral foramen 腹孔

cervicals, but zygapophyses are smaller. The dorsal end of the neural spine is elongate and ovoid in dorsal view.

The last of the six vertebrae in Fig. 2 ("sv1") is the first sacral vertebra, as indicated by its compressed rib facet on the neural arch and centrum. We identify the vertebra illustrated in Figure 3 of Dong (1980) as another sacral vertebra. This vertebra superficially resembles the aforementioned two posteriormost cervicals (pectoral vertebrae) in which its rib facet is dorso-ventrally elongate and extends onto the neural arch. However, it differs from the pectorals in lacking a ventral ridge along the ventral midline and bearing the robust dorsal half of its rib facet as in other plesiosaurs (see Seeley, 1877; Welles, 1943, 1962). As noted by the original description, this vertebra and the preceding one have peculiar bifurcated ribs (Figs. 3A to C). These ribs possess an additional short branch that projects dorsolaterally from the middle of the main body that extends ventrolaterally and posteriorly. In these two sacrals, the short transverse process is massive, and its dorsal surface is flattened with a ridge on its posterior side.

Caudals are all similar in the first half of the preserved series then rapidly decreases in size towards the posterior end. The centrum is hexagon-shaped and almost platycoelous in the first half (Figs. 3D and E), then becomes square-shaped and deeply amphicoelous in posteriormost caudals. The rib facet in the caudal series is located on the centrum just ventral to the suture with the neural arch. Chevron facets are located on both anteroventral and posteroventral edges, and in general, facets on the posterior edge are larger than anterior ones.

Pectoral girdle elements are disarticulated and attached to blocks of posterior dorsal vertebrae. They are partly overlapping each other, making it difficult to reconstruct their original spatial relationships. Our identification of dermal elements is not completely unambiguous.

The exposed portion of the clavicular arch, presumably interclavicle (Fig. 2), appears to be the ventral side because of its convexity. Its left side is complete except for the very lateral end, while its right side is not entirely observable because much of it is covered by a part of the scapula. The anterior end of the element forms a blunt apex. The posterior edge is concave on the left sides, and a very small portion of the counter part of the right is visible under the overlapping scapula.

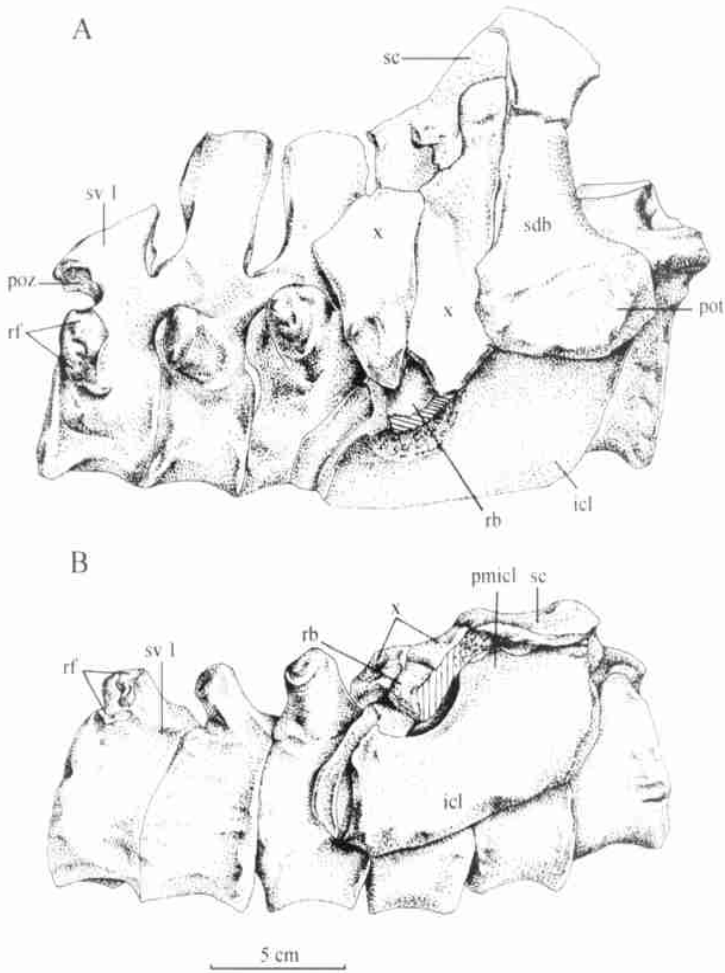


图 2 杨氏璧山上龙的最后部背椎、第一个荐椎以及一些肩带骨侧视 (A) 和腹侧视 (B)

Fig. 2 Posteromost dorsal and the first sacral vertebrae and some of the pectoral girdle elements of *Bishanopliosaurus youngi* Dong, 1980 in lateral (A) and ventrolateral (B) views

Abbreviations as in Fig. 1 plus 简字说明如图 1 加上 icl, interclavicle 间锁骨; pmicl, posteromedian process of interclavicle 间锁骨的 后中突; pot, posterior tip of dorsal blade of scapula 肩胛骨背突后端; sc, scapular 肩胛骨; sdb, dorsal blade of scapula 肩胛骨背突; sv 1, the first sacral 第一荐椎; X, uncertain 不肯定 (see the Description 见文中记述)

Much of its posteromedial process is overlapped by the displacement of other girdle elements. As a whole, the interclavical is most similar to that of *Eurycleidus megacephalus* (Andrews, 1922a).

It is difficult to identify the paired elements ("x" in Fig. 2) on the other side of the block. It may represent the posteromedial portion of the interclavicle that has a median suture as in *Eurycleidus megacephalus*. An alternative interpretation is that the element in question is a part of clavicles that are similar to the paired clavicles of polycotyloid plesiosaurs (Williston, 1903) or *Rhomaleosaurus thomtoni* (Andrews, 1922b). The element "x" is very thin and it is unlikely to represent a constituent of the stout pectoral midline bar formed by the scapula or coracoid as in many Upper Jurassic plesiosaurs (Andrews, 1910). Such a possibility, however, cannot be ruled out, because the base of the pectoral bar is present in the coracoid and this area of the coracoid is

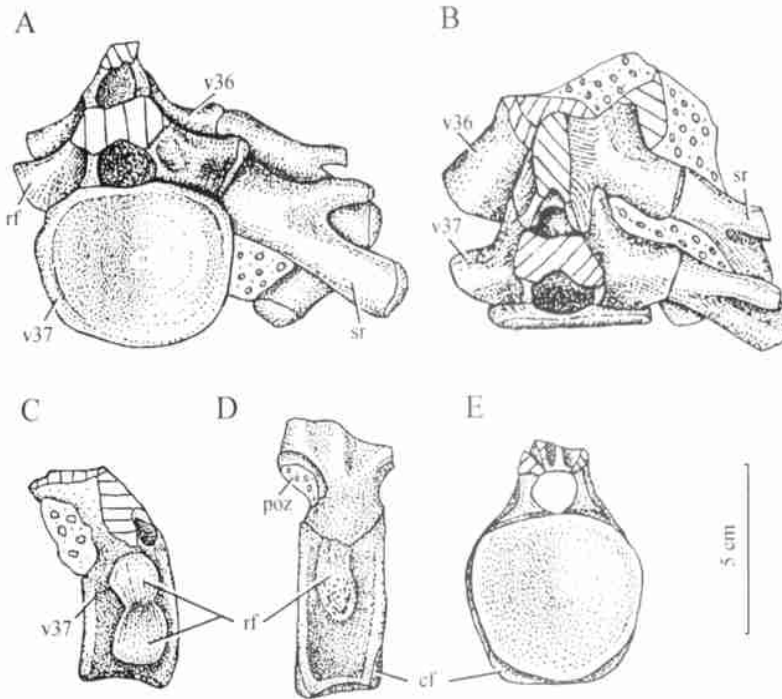


图 3 杨氏璧山上龙的两荐椎(所保存脊柱中的第 # 36 和第 # 37 脊椎)后视(A)和背视(B)、第 # 37 脊椎左侧视(C)以及一前尾椎(所保存脊柱中的第 # 44 脊椎)右侧视(D)和前视(E)

Fig. 3 Sacral and caudal vertebrae of *Bishanopliosaurus youngi* Dong, 1980, sacral vertebrae (vertebrae # 36 and # 37) in posterior (A) and dorsal (B) views; vertebra # 37 (? sacral 3) in left lateral view (C); an anterior caudal (# 44 of preserved column) in right lateral (D) and anterior (E) views

Abbreviations: as in previous figures plus 简字说明如前面诸图加上 cf, facet for chevron 与脉弧的关节面; sr, sacral rib 荐肋; v36, v37, vertebrae # 36 and # 37 of preserved column 所保存脊柱中的第 # 36 和第 # 37 脊椎

actually thin (see below). There is a fragment between the elements, which may be a rib head.

The right scapula is missing most of the dorsal and ventral plates (Fig. 4), while the dorsal blade appears to be the only part preserved for the left scapula, although identification of the latter is somewhat speculative (Fig. 2; also see the Discussion). The remains indicate that the scapula was of typically plesiosaurian triradiate form, but the expansion of the posterior tip of the dorsal blade is uncommon for a plesiosaurian and rather similar to that of Triassic sauropterygians such as *Pistosaurus* (Sues, 1987) and *Corosaurus* (Storrs, 1991). The glenoid is about twice as large as the articular facet for the coracoid, and they are located at the posterior end of the stout body of the scapula. A peculiar feature is a sharp, shelf-like projection along the ventrolateral edge as in *Leptocleidus superstes* (Andrews, 1922a). Only a small portion of the edge of the pectoral fenestra is preserved.

The following additions to the original description are needed for the coracoid. The glenoid is much larger than the scapular facet, and there is a small notch anteromedial to the scapular facet in the right coracoid, probably representing a part of the pectoral fenestra (Fig. 5A). The maximum width from the glenoid to the symphysis is 146.8 mm, which is less than the half of the length of the bone. The coracoid is very thin and mostly damaged in the area anteromedial to this small notch, but the base of the anterior projection along the medial line is preserved. Our reconstruction of the coracoids differs from Dong's (1980: Fig. 5) in that the gap between the left and right coracoids in the anterior portion is narrower but the size of the anterior extension is speculated. The lateral edge

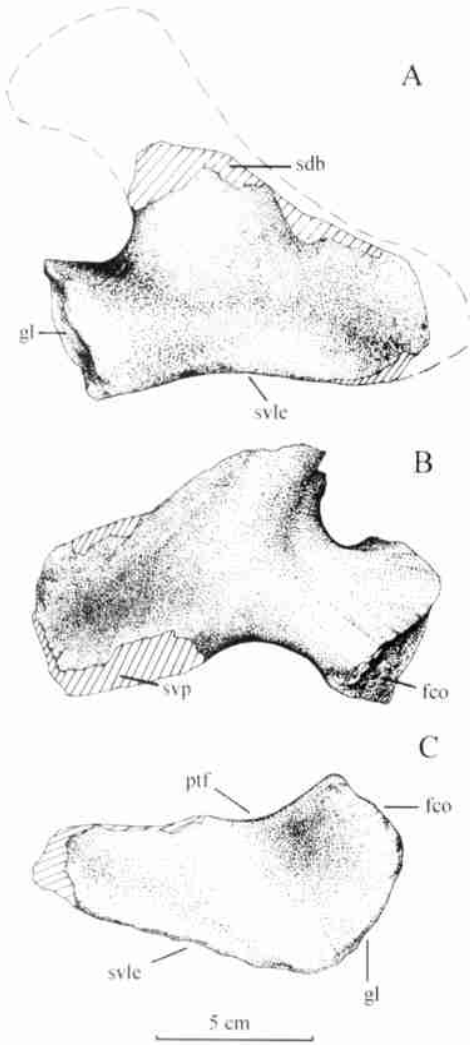


图 4 杨氏璧山上龙的右肩胛骨外侧视(A)、内视(B)和腹视(C)

Fig. 4 Right scapular of *Bishanoptiosaurus youngi* Dong, 1980 in external (A), internal (B), and ventral (C) views

Abbreviations as in previous figures plus 简字说明如前面诸图加上 fco, facet for coracoid 与乌喙骨的关节面; gl, glenoid 肩臼; ptf, pectoral fenestra 肩带孔; svle, ventrolateral edge of scapular 肩胛骨外侧缘; svp, ventral plate of scapular 肩胛骨腹板

posterior to the glenoid is straight and perichondrally ossified, but the posterior edge is unfinished. The two coracoids are united along the midline except for the posterior one-fifth. There is no posterolateral expansion of the coracoids. According to Zhang (1985), the coracoid of *Yuzhoupliosaurus chengjiangensis* (from the Middle Jurassic Xintiangou Formation of Beipei, about 50 km northeast of the locality of *B. youngi*) is also plate-like and lacks the posterolateral expansion but it appears relatively longer (with a length about 2.7 times the width of the bone) and is posteriorly well separated from its mate.

The nearly complete left humerus (Fig. 5B-D) has an almost straight shaft, in contrast to the curved humerus of primitive sauropterygians and *Plesiosaurus dolichodeirus* (Storrs, 1997: Fig. 10). Its tuberosity is inclined slightly posterior to the capitulum. There is a pronounced bump or projection ("bph" in Figs. 5B and D) near the proximal end of the posterior edge of the shaft. In ventral view, there is an elongate shallow fossa near the anteromedial edge of the proximal half of the humerus, indicating muscle attachment. The shaft gradually expands towards its distal end, but the exact width at the distal end is not available due to the covering matrix. Epipodial facets are not differentiated.

Both ilia are completely preserved, but our determination of the right and left remains speculative owing to the lack of definitive features. In our interpretation, the internal surface near the sacral end is slightly raised along the anterior edge (Fig. 6A). The dorsal end is flattened and slightly curved, while the ventral end is stout, with an outline of a rounded triangle in cross section. Loss of the contact between the ilium and pubis is a synapomorphy of the Plesiosauria (O'Keefe, 2001; Storrs, 1991), and *B. youngi* appears to have such a condition, but articular facets are not clearly differentiated. There is a minor

notch at the anterolateral corner of the acetabular end (Fig. 6B). As noted by Dong (1980), the ilium is twisted in its shaft so that the long axis of the ventral end projects anterolaterally.

The nearly complete pubis and ischium are from the right side, judging from their concavity, and well described by Dong (1980). Our reconstruction, however, differs from Dong's (1980: Fig. 6) in the manner of articulation of the two bones. As illustrated by us (Figs. 6D and E), if

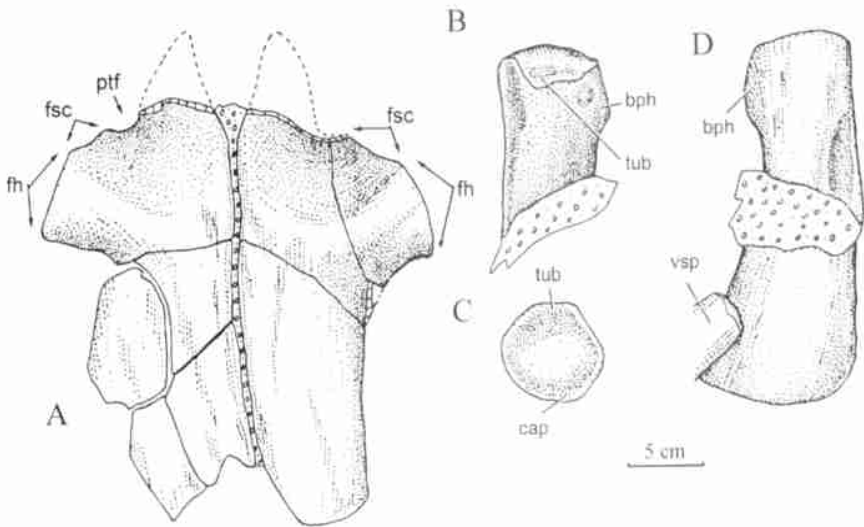


图5 杨氏璧山上龙的乌喙骨和左肱骨腹视(A、D)、背视(B)和近端视(C)

Fig. 5 Coracoids and left humerus of *Bishanopliosaurus youngi* Dong, 1980 in ventral (A, D), dorsal (B), and proximal (C) views

Abbreviations as in Fig. 4 plus 简字说明如图4加上 bph, projection along the proximoposterior edge of the humerus 位于肱骨后上缘的隆状突; cap, capitulum 肱骨大结节; fh, facet for humerus 与肱骨的关节面; fsc, facet for scapular 与肩胛骨的关节面; tub, tuberosity 肱骨小结节; vsp, vertebral spine 脊椎神经棘

they are adequately placed in articulation at the acetabulum, the two bones may not have met distally such that the puboischiatic fenestra (= the orbicular foramen of Dong, 1980: Fig. 6 [fo]) was medially open. This is also indicated by the fact that the opposite edges of the two bones are grooved, suggesting that a cartilage was attached in life. The medial edges of the two bones are almost straight, instead of making a diamond-shaped vacuity in center as in the original reconstruction. The fenestration may have been closed medially by cartilage. The anterolateral margin of the pubis is not square-shaped but round, which is comparable to the situation seen in juveniles of some plesiosauroids in which an ontogenetic variation has been studied (Welles, 1962).

Both femora are complete, and slightly longer than the humerus (Figs. 7A to C; Table 2). The femur is slightly larger at the proximal end than the humerus, but the expansion at the distal end is less significant. The trochanter is a pronounced projection distodorsal to the capitulum. Facets for the tibia and fibula are poorly differentiated at the distal end. The bone expands nearly symmetrically, to a slightly greater degree posterolaterally than anteromedially. The distal expansion of the femur is proximodistally shorter when compared with that of *Y. chengjiangensis*.

There are three epipodial elements preserved, of which two were identified as a pair of tibiae and one fibula by Dong (1980). The tibia still remains the shape of a long bone with a constriction of the shaft (Figs. 7D and G). The fibular edge of the tibia is much shorter and more concave than the anteromedial edge. In contrast to Dong's (1980: Fig. 7) reconstruction, we believe that the broader end represents the proximal end of the tibia as in majority of Jurassic plesiosauroids with similar epipodial morphologies (e. g., Dames, 1895; Owen, 1865; Storrs, 1997). In some later plesiosauroids whose tibia lost the shape of a long bone (e. g., Late Jurassic plesiosauroids in Andrews, 1913), however, there is no significant difference in width between proximal and distal ends. There is a subtle difference in the convexity of dorsal and ventral surfaces of the tibia, and we identified the side shown in Fig. 7D as a dorsal view of the tibia to match the difference in the convexity at the distal end of the femur.

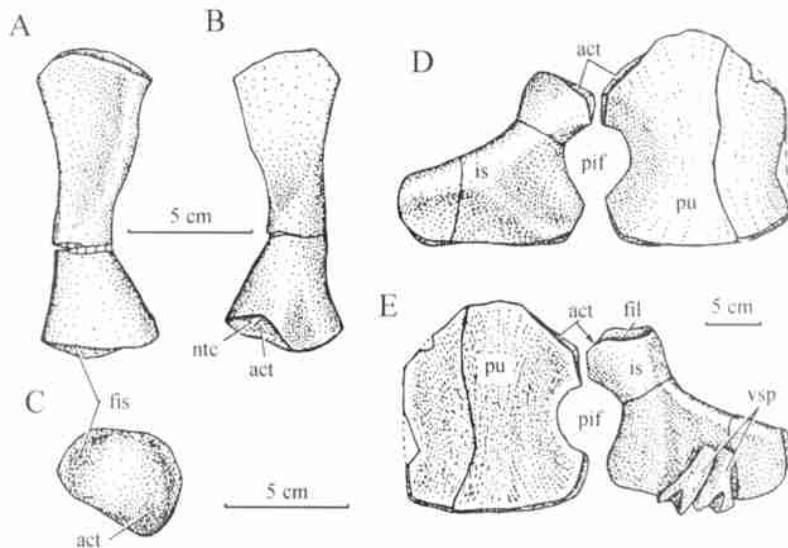


图 6 杨氏璧山上龙的腰带, ? 左肠骨内视 (A)、外视 (B) 和关节视 (C) 以及右坐骨和耻骨外视 (D) 和内视 (E)

Fig. 6 Pelvic girdle of *Bishanopliosaurus youngi* Dong, 1980, ? left ilium in internal (A), external (B), and articular (C) views; right ischium and pubis in external (D) and internal (E) views

Abbreviations as in Fig. 5 plus 简字说明如图 5 加上 act, acetabulum 髋臼; fil, facet for ilium 与肠骨的关节面; fis, facet for ischium 与坐骨的关节面; is, ischium 坐骨; ntc, notch 缺口; pif, puboischiatic fenestra 耻坐孔 (= obturator foramen 闭孔 of Dong, 1980: Fig. 6 [fo]); pu, pubis 耻骨

表 2 杨氏璧山上龙(古脊椎动物与古人类研究所 V 5869)骨骼测量

Table 2 Measurements of skeletal elements of <i>Bishanopliosaurus youngi</i> Dong, 1980 (IVPP V 5859) (mm)				
	Centrum L (椎体长)	Centrum H (椎体高)	Centrum W (椎体宽)	Neural Spine H (神经棘高)
Antermost cervical (# 1)(最前面颈椎)	25.3	39.4	40.6	N/A
Posterior cervical (# 10)(后面颈椎)	32.1	45.2	51.4	62.5
Postermost cervical (# 14)(最后一个颈椎)	31.9	54.7	65	76
Dorsal (# 34)(背椎)	34.8	N/A	62.1	est 68.1
Sacral (# 37)(荐椎)	30.4	51.6	62.7	N/A
Anterior caudal (# 44)(前尾椎)	27.4	51.2	57.6	N/A
Postermost caudal (# 61)(最后一个尾椎)	est 15	30.4	29.2	N/A
	Maximum L(最大长) W at sacral end(荐椎端宽)		Longer D at acetabular end(髋臼端较大直径)	
Ilium(肠骨)	128.7	45.9	52.4	
	L along median symphysis(沿联合长)		Maximum W(最大宽)	
Pubis(耻骨)	167.8		185.7	
Ischium(坐骨)	158.5		138.9	
	L(长)	W at proximal end(近端宽)	W at distal end(远端宽)	H at distal end(远端高)
Humerus (left)(左肱骨)	246.8	67	N/A	N/A
Femur(right)(右股骨)	257.8	70.5	114.5	46
Epipodial/tibia(小腿骨/胫骨)	83.7	69	63	36.5

Abbreviations 简字说明: D, diameter 直径; est, estimated 估计数; H, height 高度; L, length 长度; N/A, not available 缺数据; W, width 宽度; # 1, indicating the position of the vertebra within the preserved column 表明该脊椎在所保存脊柱中的位置。

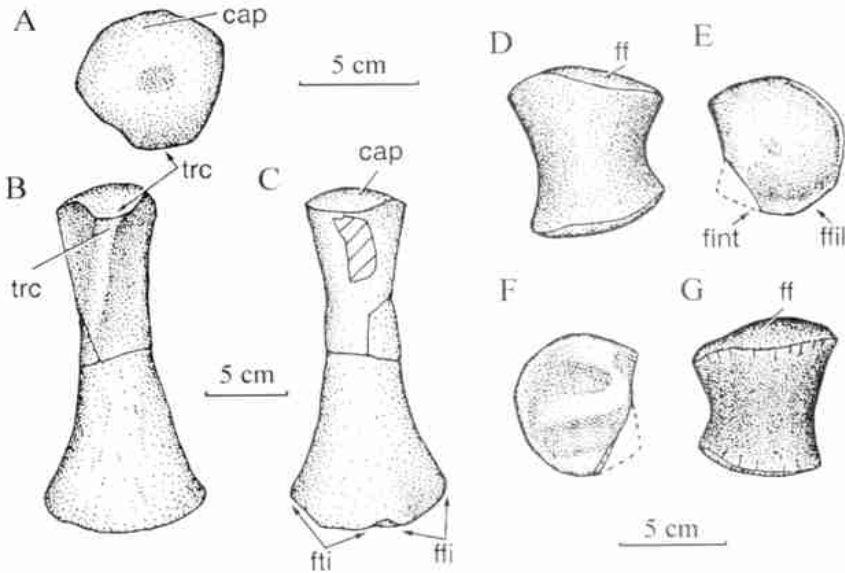


图 7 杨氏璧山上龙的右股骨近端视(A)、背视(B)和腹视(C),左胫骨背视(D)和腹视(G)以及左腓骨背视(E)和腹视(F)

Fig. 7 Some elements of the hind-limbs of *Bishanopliosaurus youngi* Dong, 1980, right femur in proximal (A), dorsal (B), and ventral (C) views; left tibia in dorsal (D) and ventral (G) views; left fibula in dorsal (E) and ventral (F) views

Abbreviations as in Fig. 5 plus 简字说明如图 5 加上 ff, facet for femur 与股骨的关节面; fii, facet for fibula 与腓骨的关节面; ffil, facet for fibulare 与腓侧附骨的关节面; fint, facet for intermedium 与中央附骨的关节面; fti, facet for tibia 与胫骨的关节面; trc, trochanter 转子

The fibula is very thin and flat, and although it is identified as the left according to Dong (1980), it is impossible to determine based on its morphology only. One side of the flat bone is evenly concave, while the other side is irregular. The unusual curvature of the edge of the spatium interosseum (Dong, 1980: Fig. 7) was resulted from the damage of the distomedial corner of the fibula, and we restored the outline (Figs. 7E and F) that is semilunate shape typical of Early Jurassic plesiosaurs such as *Plesiosaurus dolichodeirus* (Storrs, 1997). Unlike *P. dolichodeirus* and many other Liassic forms (Owen, 1865), however, the length is only slightly larger than its width in the fibula of the IVPP V 5869. The edge of the spatium interosseum is the only part of the edge that has perichondral ossification. Orientation of the bone cannot be determined morphologically due to poor ossification. The presumed distal end has an angle near the broken median edge, and it seems to represent the divide of the facets for the fibulare and intermedium (Fig. 7E).

5 Discussion

5.1 Validity of the Taxon

Most of the features listed by Dong (1980) as diagnosis of *B. youngi* are either common for pliosauroids or attributable to ontogenetic change. Jurassic pliosauroids affinities include the relatively tall centrum with a longitudinal ridge on the ventral midline, the femur longer than humerus, and epipodials longer than wide. The small size of the ilium and the rounded outline of the pubis are most likely related to the ontogeny. A few characteristics of the vertebra, rib, and coracoid, however, need a further discussion to verify their validity as taxonomic characters.

Although the short cervical centrum is common for the Pliosauroidea *sensu* O'Keefe (2001),

members of plesiosauroid Polycotyliidae and *Morturneria seymourensis* (Chatterjee and Small, 1989) also have characteristically short centra. The relative length of the centrum changes ontogenetically. As Brown (1981) demonstrated that the length of the centrum relative to the height and width in juvenile *Cryptoclidus* is always shorter than those in more mature individuals throughout the column. The short centrum of *B. youngi* is predictable because of its immaturity.

The original diagnosis of *B. youngi* (Dong, 1980:p. 192) states that the cervical rib is double-headed in anterior cervicals, while the rib is single-headed and has a branch in posterior cervicals. The number of cervical rib head(s) has been an important taxonomic character in plesiosaurian classification since 19th century (Seeley, 1892; also see Brown, 1981). In general, early plesiosaurians have double-headed ribs, and later forms have single-headed ribs. Tarlo (1960), however, noted that one side of a centrum of the holotype of *Pliosaurus andrewsi* has a double facets while the other has a single, and that anterior cervicals have double rib facets but postermost cervicals single rib facet in *Pliosaurus brachyspondylus*. Therefore, it is subject to variation within the single individual. The longitudinal ridge of the rib facet in anterior cervicals is very weak, which suggests that the double heads of these ribs in *B. youngi* are not distinct in comparison with those of *Pliosaurus brachydeirus* and *Liopleurodon pachydeirus* (Tarlo, 1960). Incomplete ossification of the IVPP V 5869 is apparently responsible for such an ambiguity. In addition, none of the poorly preserved anterior cervical ribs clearly show the two heads. Thus, presence of double-headed anterior cervical ribs is suggested but not proven. Presence of single-headed ribs in the posterior cervicals in *B. youngi* is supported by the lack of the longitudinal ridge in rib facets, as well as by the single-headed rib found with the postermost cervical.

The vertebrae that bear branched ribs are identified as sacrals in our study, not as posterior cervicals as in original description. Therefore, the "bifurcated sacral rib", instead of the cervical rib, characterizes *B. youngi*. Sacral ribs are rarely described in detail, but to our knowledge, such a bifurcated rib is unique among the plesiosaurians. Andrews (1913) regarded "a number of peculiarly shaped bones" (p. 74) as the sacral or anterior caudal ribs of a *Peloneustes evansi* skeleton. Their triangular shape with two "facet for contact with next rib" (Andrews, 1913: Text-Fig. 29) may somewhat resemble to but not same as the branched rib of *B. youngi*.

We agree with Dong (1980) in regarding the elongate coracoid with the straight lateral edge posterior to the glenoid as a potential diagnostic feature of *B. youngi*, although it certainly requires the discovery of adult specimens for the confirmation of ontogenetic variation. Plesiosaurian coracoid is subject to a substantial ontogenetic change as documented for *Cryptoclidus* (Andrews, 1895). However, there are a number of specimens such as young individuals of *Cryptoclidus* in Andrews (1895), holotypes of *Leurospondylus ultimus* (AMNH 5261; Brown, 1913) and *Fresnosaurus drescheri* (CIT 2758; Welles, 1943) in which the coracoid already shows the outward curvature of its lateral edge in spite of immaturity. Pliosauroids in general have relatively narrow coracoid in comparison with other plesiosaurians, although they still have the outward curvature of the lateral edge of the coracoids. It is necessary to document a growth series of the coracoid in pliosauroids to verify the nature of the narrow, straight-edged coracoid of *B. youngi*.

The expansion of the dorsal end of the dorsal blade of the scapula perhaps serves as an additional diagnostic feature. However, we think that it is wise to wait for a discovery of better specimens to confirm its position and extent, because the fragmentary nature of the left scapula leaves ambiguity.

The pronounced projection at the posterior edge near the capitulum of the humerus is another potentially diagnostic feature of *B. youngi*. It probably represents the attachment site for *M. latissimus dorsi* and/or other muscles that pull the humerus backward and upward. The humerus of *Simolestes vorax* (Andrews, 1913) also bears a pronounced projection, but at the midway of the posterior edge of the shaft. Tarlo (1960), who rejected its value, noted that this feature does not exist in the immature individual of the same species. Presence of a pronounced projection in the

young individual of *B. youngi* implies a further development in adults, but its significance in comparison with the growth series of other plesiosaurian taxa remains speculative.

The neural spine of the holotype of *B. youngi* is laterally compressed. According to O'Keefe (2001), the presence of the laterally compressed neural spine is a diagnostic feature of the Plesiosauroidea with reversals in a few taxa such as polycotyliids, but not known among the pliosauroids studied by him. Morphology of the neural spine has a variation along the cervical column in plesiosaurians, however, as documented by Andrews (1913) for *Peloneustes* and Williston (1903) for *Dolichorhynchops*. While regarding this character as potentially diagnostic, we think the comparison of a complete cervical series is necessary to determine the significance of the compressed neural spine of *B. youngi*.

B. youngi remains as a valid taxon characterized primarily by the bifurcated sacral ribs. The narrow coracoid without a lateral expansion, the development of a projection on the posterior edge of the humerus near the capitulum, and the compressed neural spine may also be added as diagnostic characters. However, it requires an examination of adult individuals to determine the possibility of ontogenetic and/or intraspecific variation.

5.2 Phylogenetic Affinity

O'Keefe (2001) is the first to conduct a large-scale cladistic analysis of the Plesiosauria that gave a definition of each family and diagnostic characters in phylogenetic framework. His phylogeny supported the major dichotomy of the Plesiosauria, i. e., Plesiosauroidea and Pliosauroidae, but the latter does not include the Polycotyliidae that is a group of the Cretaceous short-necked plesiosaurians that used to be placed within the Pliosauroidae (Brown, 1981; Welles, 1943). Within the Pliosauroidae, O'Keefe (2001) recognized two monophyletic groups, Families Pliosauridae and Rhomaleosauridae, to the latter *B. youngi* was assigned by Dong (1980). Bremer indices and bootstrap supports for the monophyly of each group were relatively low in comparison with other families but nevertheless supported (O'Keefe, 2001: Fig. 20). Relationships among analyzed rhomaleosaurids are poorly supported partly due to the conservatism of the group, while pliosaurids have a better resolution (O'Keefe, 2001). Diagnostic features of each family are mostly from the skull, and there are only a few postcranial characters available to examine the familial affinity of *B. youngi*. Even for those characters, none of them is exclusive to a particular clade and subject to homoplasy.

B. youngi has rhomaleosaurid affinities because it fulfills the diagnostic postcranial features of the group. At the same time, it does have pliosaurid affinity for the very same reason because they do not conflict with rhomaleosaurid characters, although one of the two such characters is not confirmed because of missing data. The presence of compressed neural spine of *B. youngi* even questions its pliosauroid affinity, because it is a diagnostic feature of the Plesiosauroidea *sensu* O'Keefe (2001). Considering the homoplasy of postcranial characters, the lack of overwhelming number of the cranial characters that characterize plesiosaurian families, and immaturity, we do not think it is wise to assign this taxon to a particular family defined by O'Keefe (2001) although anatomic features currently available parsimoniously suggest that *B. youngi* is most probably a pliosauroid.

B. youngi has a unique combination of the characters analyzed by O'Keefe (2001), such as the presence of the lateral compression of the neural spines (character 130), the presence of the concave anterior margin of the pubis (character 144), and the absence of the angled humerus (character 150), as well as rhomaleosaurid and pliosaurid characters. Such a combination contradicts any taxa analyzed by O'Keefe (2001). Therefore, it has no taxonomic equivalence, and the deletion of this taxon from the phylogenetic analysis is not justified in terms of taxonomic equivalence ("safe taxonomic reduction" of Wilkinson, 1995). Poor preservation and immaturity of the only specimen of *B. youngi*, however, are serious problem for the phylogenetic analysis at this stage. Because of the poor preservation, only 38 out of the 166 characters of O'Keefe's data matrix are available for coding *B. youngi*. That is, as much as 77% of the data are missing. Furthermore, it is expected that the

ontogenetic variation would affect several characters that are related to the proportion or the prominence of element(s), such as long/broad epipodials (O'Keefe's character 161), and it further increases uncertainty in coding. Discovery of mature and better-preserved specimens is important to establish phylogenetic relationships of *B. youngi* with other plesiosaurians.

5.3 Freshwater Plesiosaurians

Because of the occurrence of a vast majority of their fossils from marine sediments, most plesiosaurians were definitely inhabitants of marine realm. Their capability in surviving other environments has been discussed in a very limited extent. Plesiosaurian remains are reported from at least potentially non-marine environment of the following countries: England, Canada, and Australia, in addition to China.

The Upper Wealden Clay of Berwick, Sussex, yielded the holotype of a plesiosaurian *Leptocleidus superstes* (Andrews, 1922a), and is also famous for its varied dinosaur fauna including *Iguanodon* and *Baryonyx*. Sedimentary sequence of the Upper Wealden Clay indicates a change from a lacustrine/lagoonal to a fluvial/mudplain environment (Ross and Cook, 1995).

The holotype of *Leurospondylus* from the "Edmonton Formation" (Brown, 1913) is a juvenile individual, and Russell (1931) reported the occurrence of additional isolated plesiosaurian vertebrae provisionally referred to *Leurospondylus*. The taxon itself is invalid as non-diagnostic (Welles, 1962), but the material referred to *Leurospondylus* are definitely plesiosaurian. Although the type specimen could be from a marine stratum ("Drumheller Marine Tongue") of the Horseshoe Canyon Formation (Brinkman and Eberth, 1987), referred specimens are associated with terrestrial biota, freshwater bivalves, plants, but not with marine fossils. Also, the stratum that yielded the referred specimens has channel-like structure, suggesting a fluvial environment (Russell, 1931).

There are growing number of records of Australian plesiosaurians from non-marine environments (Cruickshank, 1997), although published materials are very fragmentary. Bartholomai (1966) first reported the occurrence of *Leptocleidus*-like plesiosaurian remains from the freshwater sediments at Mt. Morgan in Queensland. Molnar (1991:p. 633) dated the age of this material as the Early Jurassic and also noted its similarity to *B. youngi*. Rich et al. (1989: Fig. 3) recorded plesiosaurian rib and teeth from the fluvial sediments of the Lower Cretaceous Otway and Strzelecki Groups of southern Victoria. Schroeder (in preparation) is describing a new specimen of *Leptocleidus* with skull from the Lower Cretaceous of Coober Peddy of Western Australia.

B. youngi is not the only Chinese plesiosaur from the freshwater sediments. *Y. chengjiangensis* was described based on an incomplete skeleton that was discovered in sandy shale of the upper part of the Xintiangou Formation of the Middle Jurassic. Taxonomic status of this specimen needs a re-examination, but nevertheless the plesiosaurian fossil is from continental deposits. Other plesiosaurian fossils (*Sinopliosaurus weiyuanensis* Young 1944, *S. fusuiensis* Hou et al. 1975) are very fragmentary and apparently non-diagnostic, but they also suggest the presence of plesiosaurian remains in non-marine Mesozoic sediments of China.

The significance of the occurrence of *B. youngi* is that it is from a definitely nonmarine environment. In addition to the paleogeographic position, the freshwater bivalves and abundance of plant fossils confirm its terrestrial origin (see the Geological Background above). Early or Middle Jurassic age of the specimen indicates that plesiosaurians inhabited freshwater environment early in their history. Wide geographical and chronological distributions of plesiosaurian fossils from non-marine sediments strongly suggest that further discovery of plesiosaurians is expected from nonmarine sediments of the Jurassic and Cretaceous of various parts of the world.

In addition to *Leptocleidus superstes*, two other *Leptocleidus* species, South African *L. capensis* (Cruickshank, 1997) and Australian *L. clemai* (Cruickshank and Long, 1997) are from inshore deposits. Two more *Leptocleidus* specimens are currently under study and expected to give more details of anatomy. One is aforementioned Schroeder's Australian specimen, and the other is a well-

preserved specimen tentatively identified as *Leptocleidus*, from the Lower Cretaceous of Alberta, Canada (Druckenmiller, personal communication). Andrews (1922a) noted the relatively primitive nature of the English *Leptocleidus* and suggested that the freshwater-environment might have served as refugia, and that later short-necked polycotylid plesiosaurs are descendants that re-adapted to marine environment. A close relationship between *Leptocleidus* and the Polycotylidae was refuted in the recent cladistic analysis (O'Keefe, 2001). However, it is an interesting fact that majority of the known freshwater plesiosaurs have affinity of *Leptocleidus* or rhomaleosaurids, and the described specimens of the three *Leptocleidus* species are from near shore environment of the Lower Cretaceous, not the open-marine that is more common for plesiosaurs.

Available evidences are tantalizingly insufficient to determine taxonomic composition of those freshwater plesiosaurs. It is unknown if the plesiosaurian fossils from various depositional environments indicate that plesiosaurs of different taxa or ontogenetic stages lived in different environments, or if plesiosaurs could travel between different environments, for example, as seasonal or reproductive behavior. Needless to say, further research is necessary for plesiosaurs from freshwater and inshore sediments. The Ziliujing Formation and other Mesozoic non-marine deposits in China have a great potential to produce more plesiosaurian materials.

6 Conclusions

Although *Bishanopliosaurus youngi* Dong, 1980 is represented by a young individual, it is considered taxonomically valid because of the presence of the uniquely bifurcated sacral rib and some other skeletal features. The latter, however, may be affected by intraspecific variation.

Phylogenetic relationships of *B. youngi* with other plesiosaurs remain uncertain because of the short of cranial characters. There are only a few postcranial characters that are used to diagnose plesiosaurian families and available to *B. youngi*, but they are not sufficient to determine familial affinity of the taxon. Although the taxon has unique combination of characters unknown to other plesiosaurs, it suffers from the overwhelming number of missing characters. It is apparent that we need a discovery of better specimens.

There are growing number of plesiosaurian fossils from freshwater and inshore sediments around the world although they are often poorly preserved. These freshwater plesiosaurian bearing sediments stratigraphically range from the Lower or Middle Jurassic to the Upper Cretaceous, indicating a wide distribution of plesiosaurs in such a environment. So far most of those plesiosaurs are *Leptocleidus* or have rhomaleosaurid affinity of the Pliosauroidae. It is expected that further explorations to the Ziliujing Formation of China would produce more plesiosaurs that will certainly offer better evidences to answer paleobiological and phylogenetical questions on plesiosaurs from freshwater environment.

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