Swiss Journal of Geosciences (2019) 112:307–324
https://doi.org/10.1007/s00015-018-0329-0

Postcranial skeleton of *Birgeria liui* (Osteichthyes, Actinopterygii) from the Longobardian (Ladinian, Middle Triassic) of Xingyi, Guizhou, South China

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Received: 6 February 2018 / Accepted: 7 November 2018 / Published online: 22 November 2018

Abstract

The large carnivorous ray-finned fish *Birgeria liui* Jin, 2001 from the Middle Triassic marine Zhuganpo Member, was previously briefly described based on an incomplete specimen, which lacked the skull and the anterior part of the body, hence with many of its morphological characteristics missing or misidentified. Herein, we report a new well preserved specimen of *B. liui* from the early Late Ladinian of South China, which shows the most complete and articulated postcranial skeleton for an adult specimen of *Birgeria*. The new informations relate to the number of neural arches and their changes along the vertebral column, the articulation between the neighboring haemal spines in the caudal region, the presence of ribs, the endoskeleton and the pattern of lepidotrichia of all fins and the covering of scales. We also update some characters of the postcranial skeleton of a few of other Birgeria species, based on direct observations.

Keywords Actinopterygii · *Birgeria* · Vertebral column · Fins · Middle Triassic · China

Abbreviations

IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China
MCSNB	Museo Civico di Scienze Naturali 'E. Caffi', Bergamo, Italy
MPUM	Paleontological Museum of Milano University, Milano, Italy
PIMUZ	Paläontologisches Institut und Museum, Universität Zürich, Zürich, Switzerland
XNGM	Xingyi National Geopark Museum, Wusha, Guizhou Province, China
Ax	Axonost
Axpl	Axonost plate
Bfu	Basal fulcra
Bo	Baseost
Ha	Haemal arch
Hs	Haemal spine
Lp	Lepidotrichia
Na	Neural arch
Ns	Neural spine
Pv	Pelvic plate
R	Ribs
Ro	Radial ossification
S	Scale
Sn	Supraneural

Editorial handling: M. J. Benton.

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1 Introduction

Birgeria was one of the largest predatory fishes from the Triassic, spanning almost the entire period with a cosmopolitan distribution. This genus was erected by Stensiö (1919) on material from the Middle Triassic Muschelkalk of Bayreuth (Germany), previously known as *Saurichthys*

mougeoti Agassiz, 1843. In 1921, Stensiö gave a detailed description of birgeriids from the Lower Triassic of Spitsbergen and referred them to the type species *Birgeria mougeoti*. Later, one of the Spitsbergen specimens was identified as a new species, *B. aldingeri*, by Schwarz (1970) and the others were referred to as *B.* cf. *aldingeri* by Romano et al. (2017). Besides, Stensiö (1921) referred to this genus also two little known species of *Saurichthys*, both from Europe and previously described as *S. acuminatus* Agassiz, 1844 and *S. annulatus* Winkler, 1880. Only *Birgeria acuminata* has been redescribed by Boni (1937) based on fragmentary skull material from the Norian of Lombardy (N. Italy), and Gozzi (2006) added some informations on the base of new specimens recovered from the Zorzino Limestone at the end of the last century in Lombardy. Aldinger (1931) described a new species, *B. stensiöi*, from the Middle Triassic of Monte San Giorgio and Schwarz (1970) and Romano and Brinkmann (2009) added more information about the same species. Stensiö (1932) himself erected a further species, *B. groenlandica*, from the Lower Triassic of East Greenland (which was later described in detail by Nielsen (1949)) and placed *Xenestes velox* Jordan, 1907 in *Birgeria*. Lehman (1948) erected *B. nielseni* from the Lower Triassic of Madagascar and later provided a detailed description (Lehman 1952). Jin (2001) named *B. liui* from the late Middle Triassic, based on a posterior part of the fish, and Liu et al. (2006) erected *B. guizhouensis* from the early Upper Triassic, both species from South China. Unfortunately, the type specimen of the latter species appears to be lost as we were not able to locate it. Recently, Romano et al. (2017) added a new species, *B. americana*, from the Lower Triassic of Nevada, based on a fragmentary skull (see Table 1). A few other species remain very poorly known owing to the scanty material on which they are based (Romano and Brinkmann 2009).

Fragmentary remnants of *Birgeria* sp. were also reported from Lower Triassic of Nevada (Romano et al. 2017), Madagascar (Beltan 1977, 1980, 1996; Guffroy 1956), Siberia (Berg et al. 1967), British Columbia (Schaeffer and Mangus 1976); Middle Triassic of Poland (Chrzastek 2008), South China (Jiang et al. 2016); Late Triassic of South China (Liu et al. 2006), Bolivia (Beltan et al. 1987), Italy (Gozzi 2006), Slovenia (Jurkovsek and Kolar-Jurkovsek. 1986; Kolar-Jurkovsek 1991).

Birgeria liui was originally described based on the holotype from the Middle Triassic marine Falang Formation of Changdi, Yunnan province, South China: unfortunately, the specimen lacks the skull and anterior part of the body. Herein, we report a new well preserved specimen of *B. liui* from the early Late Ladinian of South China. This new specimens is ascribed to the species *B. liui* on the basis of a complete correspondence to the holotype and only known specimen (Jin 2001). Although the preservation of the skull of the new specimen is too scarce to provide valuable information, the same shows the most complete and best preserved postcranial skeleton for *Birgeria*. We must keep in mind that the holotype lacks the skull (Jin 2001), so that the comparison has been made only on the postcranial skeleton morphology. The detailed description of the new postcranial elements yielded previously unknown or misidentified anatomical information, which substantially enhances our understanding of the species *B. liui* as well as of the genus *Birgeria* itself.

2 Materials and methods

The new material of *B. liui* has been collected in the middle part of the Zhuganpo Member of the Falang Formation at Nimaigu section (Wusha, near Xingyi City, Guizhou Province, South China) (Fig. 1). Detailed excavation at Nimaigu section has been carried by a joint team formed by Peking University, University of California, Davis and Universitá degli Studi di Milano. The 5.1 m thick fossiliferous level yielding the Xingyi Fauna was exposed bed-

Table 1 Species and distribution of *Birgeria* Stensiö, 1919

Species	Distribution
B. groenlandica Stensiö, 1932	Lower Triassic, East Greenland
B. americana Romano et al., 2017	Lower Triassic, Nevada
B. nielseni Lehman, 1948	Lower Triassic, Madagascar
B. aldingeri Schwarz, 1970	Lower Triassic, Spitzbergen
B. velox (Jordan, 1907)	Middle Triassic, California
B. mougeoti (Agassiz, 1834)	Middle Triassic, Germany
B. stensiöi Aldinger, 1931	Late Anisian, Middle Triassic, Switzerland
B. liui Jin, 2001	Late Ladinian, Middle Triassic, South China
B. guizhouensis Liu et al. 2006	Early Carnian, Late Triassic, South China
B. acuminata (Agassiz, 1844)	Norian, Europe
B. annulata (Winkler, 1880)	Triassic, Europe

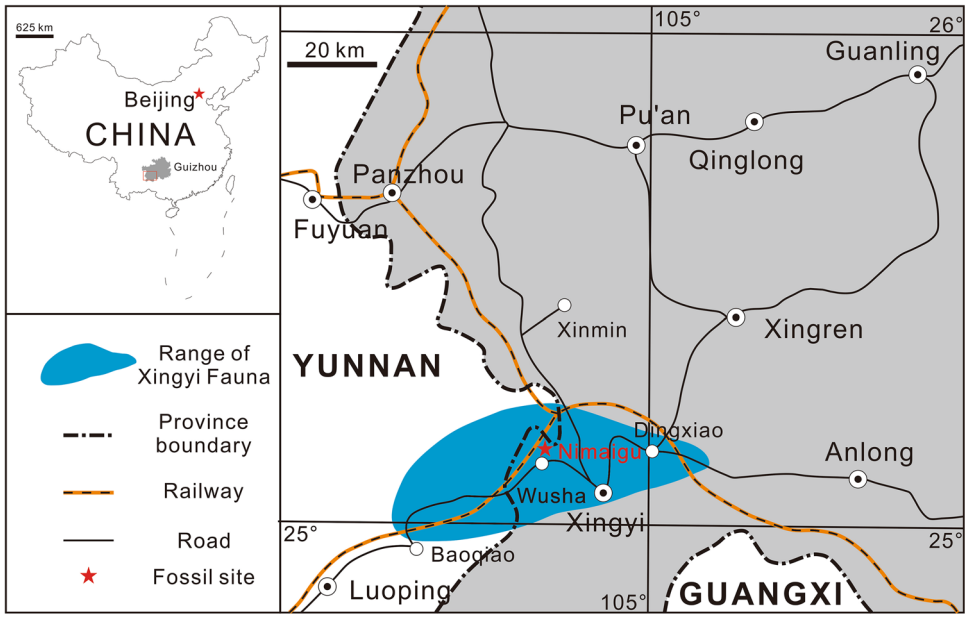


Fig. 1 Geographical position of the fossil site

by-bed and exact information of each individual fossil was recorded. The specimen of *B. liui* comes from layer 45 (Fig. 2). The age of the Xingyi Fauna was confirmed to be early Longobardian (Late Ladinian, Middle Triassic) on the basis of ammonoid biostratigraphic correlation (Zou et al. 2015) and isotopic dating (Li et al. 2016).

The specimen is stored in the Xingyi National Geopark Museum (Wusha, Xingyi City, Guizhou Province, China). It was prepared mechanically by thin steel needles under the binocular microscopes Nikon SMZ645. The photos of the specimen were taken by Canon EOS 6D and Nikon D3100, with a micro NIKKOR 60 mm lens. The drawings were made directly on photographs with Adobe Photoshop CC and Corel DRAW X6.

Further specimens of *B. acuminata* from the Norian Zorzino Limestone of Lombardy (N. Italy) (MPUM9334, MCSNB-V-4850, 5172) and of *B. stensiöi* from the Middle Triassic Besano Formation of Monte San Giorgio (PIMUZ T1761, T2768, T2775, T4780) were studied and used for comparison.

The anatomical terminology used herein follows that used in the previous major papers describing *Birgeria* (Nielsen 1949; Romano and Brinkmann 2009).

3 Systematic palaeontology

Class Actinopterygii Cope, 1887 (sensu Rosen et al. 1981)

Superorder Chondrostei Müller, 1844 (sensu Patterson 1982)

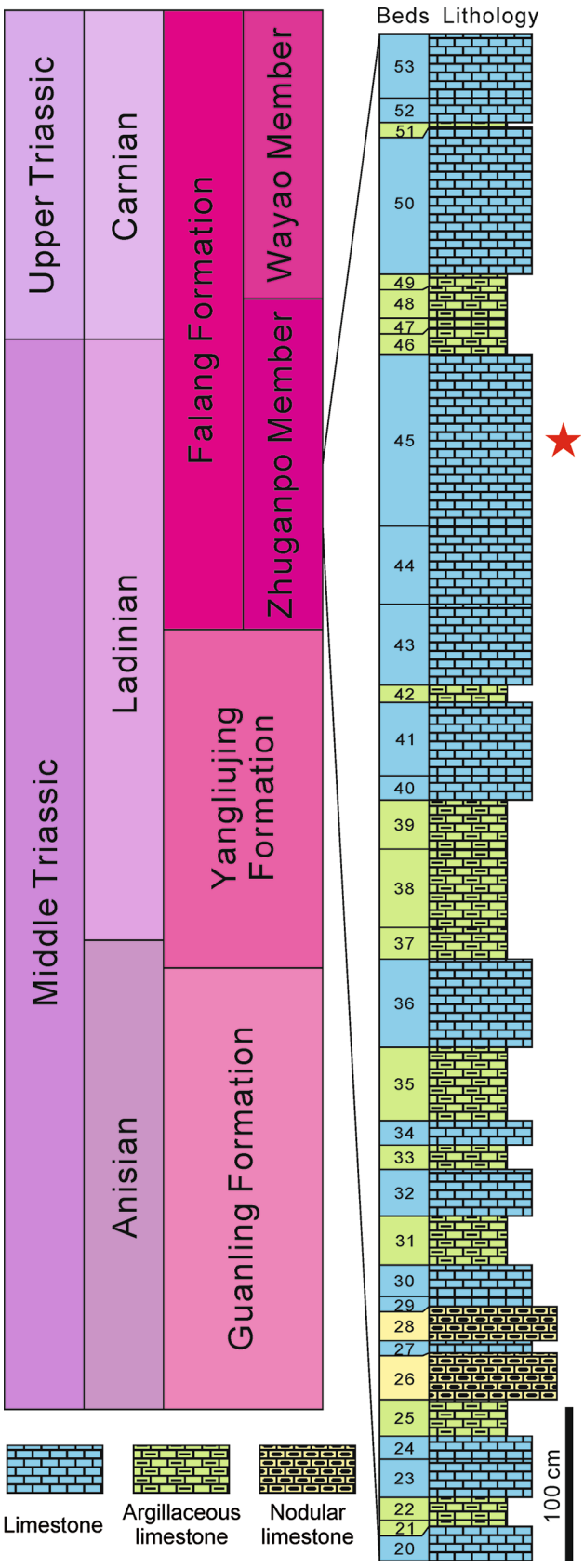
Order Birgeriiformes Heyler, 1969

Family Birgeriidae Aldinger, 1937

Genus *Birgeria* Stensiö, 1919

Diagnosis. Following Stensiö (1921) concerning the skull, but amended for the postcranial skeleton. Large fishes usually up to 1.5–2 m, possibly up to four m (based on very fragmentary material, A.T. pers. obs.) in Late Ladinian (Middle Triassic) species. Body almost totally naked, with lateral line bearing small scales (at least in a few species) and a large scale field covering the tail body lobe and part of the caudal peduncle; scales narrow and thick, without ganoine, very closely packed without peg-and-socket articulation. Head low and broad. Ossifications in the primordial neurocranium and visceral skeleton strongly developed. Myodome in a primitive stage of development. Mouth large; suspensorium oblique. Maxilla of usual palaeoniscid-type with a sculpture of tooth-like tubercles. Dentition well developed; teeth pointed and conical with a vertically striated, two-edged enamel cap; basally of this sometimes only a vertical very fine striation; sometimes in addition rather coarse vertical ridges, which then in their turn have the fine striae; no plici-dentine is developed. Along the lateral margin of the maxillary and the dental there is a row of rather small teeth; medially of them another row of much higher and strong teeth occurs. The pterygoid and the mixicoronoid have small teeth.

Axial skeleton well ossified along the persistent notochord, both dorsally and ventrally; diplospondyly in the caudal region. Neural arches paired up to the posterior part of the dorsal fin but with median neural spine in the caudal region; supraneurals up to the middle part of the dorsal fin. Parapophyses bearing ribs in the posterior abdominal region; haemal arches with spines abutting each other in the posterior caudal region. Radials well developed in the pectoral fin. Mallet-like (sledgehammer-like) pelvic plates. Dorsal fin somewhat anterior to the anal fin, both of them



◀**Fig. 2** Stratigraphic column of the local series with detail of the fossiliferous layers at Nimaigu site, with indication of layer where the presented material was found (red star)

showing almost the same shape and size. In the dorsal fin endoskeleton, ossified axonosts only in the anterior part, with a far posterior axonost plate, but a complete series of baseosts; anterior pterygiophores could fuse in some species. In the anal fin, single elements in the anterior half, possibly elongated axonosts, followed by an incomplete series of shorter axonosts, a posteriormost axonost plate and a complete series of baseosts. Caudal fin large, completely heterocercal, deeply forked and nearly equilobate in outline. Lepidotrichia of all fins numerous and close-set; fringing fulcra absent from every fin, basal fulcra present in median fins, especially developed along the dorsal margin of the tail. Lepidotrichia in the ventral lobe of caudal fin with very long proximal segment, becoming gradually shorter and shorter dorsally; proximal segment of lepidotrichia in the dorsal lobe very elongate to reach the body lobe.

Birgeria liui Jin, 2001

Emended diagnosis (*possible autopomorphic characters). Species reaching, possibly exceeding, 1 m in total length. *At least 84 neural elements, of which about 62 are paired, the remaining yielding a median spine. Anterior supraneurals as long as the corresponding paired neural elements. Haemal elements well ossified along the whole body; *ribs articulate with well-developed process on parapophyses; *proximal part of haemal spines tightly articulate with each other along the whole caudal region. Pelvic plates with length of the proximal shaft almost equal to the distal plate width. *Axonosts and baseosts of dorsal fin respectively about 13 and 38, last four axonosts without direct articulation with the corresponding baseosts. *Anterior part of anal fin endoskeleton made of 16 single elements, possibly elongate axonosts, followed by a double series of 8 axonosts, plus a posteriormost plate, and 20 baseosts, only the foremost two baseosts having a direct articulation with the corresponding axonosts. *Distal segments of the foremost lepidotrichia considerably long in all fins except the pectorals; lepidotrichia of dorsal and anal fins more than 100, about 40 in the ventral lobe of the caudal fin and more than 100 for the dorsal lobe. Posterior scale-field from about half-way between the end of dorsal fin and base of the body lobe. Intersecting angle of the dorsal and ventral margins of the caudal fin between 70° and 80°.

Holotype. IVPP V 12569 (Jin 2001, fig. 1, Pl. 1–2), Fig. 3.

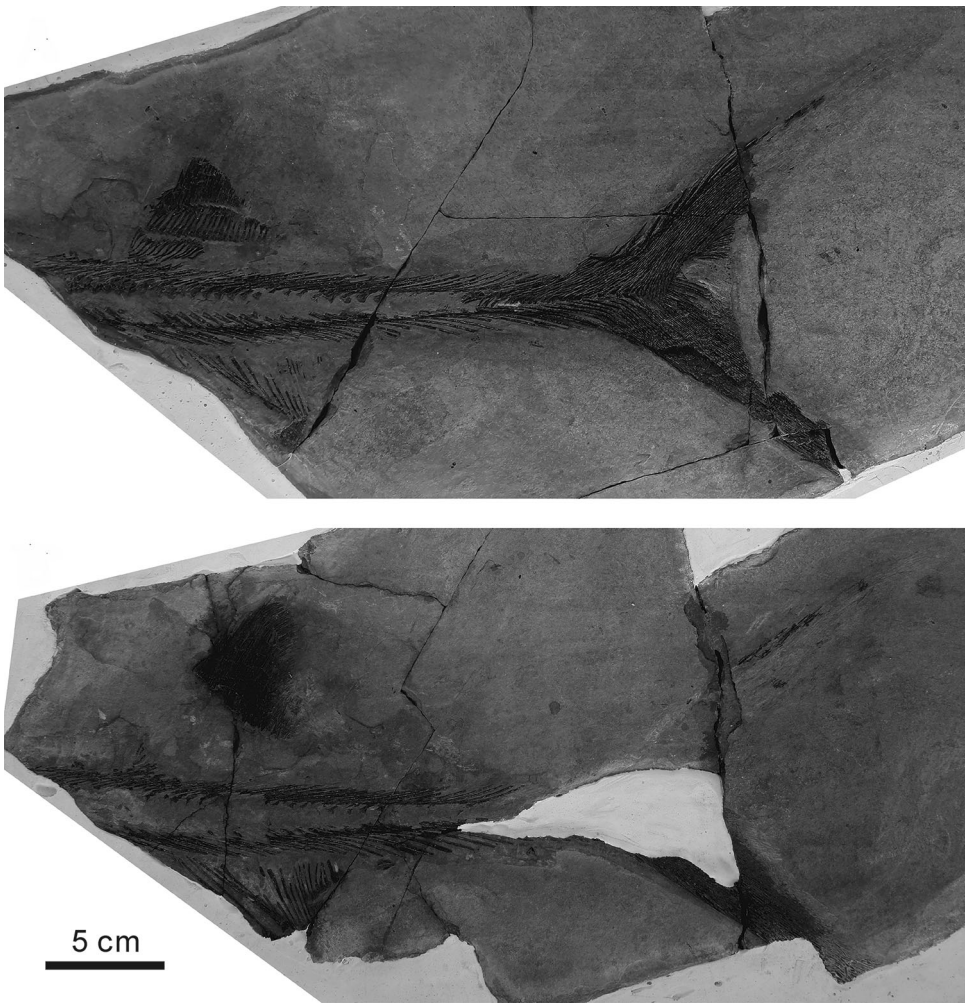


Fig. 3 The holotype of *Birgeria liui* (IVPP V 12569), part and counterpart

Supporting material. XNGM WS-45-F21 (Figs. 4, 5, 6, 7, 8, 9, 10, 11, 12, 13) from Nimaigu village, Wusha District, Xingyi City, Guizhou Province, South China.

Age. Early Longobardian, late Ladinian, Middle Triassic (Zou et al. 2015).

4 Description

Specimen XNGM WS-45-F21 is a well-preserved fish of 76 cm in standard length (SL) and 94 cm in total length (TL), fairly complete except for the most posterodorsal part of the skull and a small part of haemal elements in the abdominal region that got lost during the collection. Unfortunately, the preservation of the skull is to scarce to provide valuable information, so we neglect the skull itself in the following description.

4.1 Axial skeleton

The ossifications of the axial skeleton are almost completely preserved, except for a small part of the middle-ventral region. The vertebral centra were not ossified through the whole length of the body, leaving the notochord uncostricted.

In the dorsal region, the axial skeleton consisted of neural arches and median supraneurals, although they are differentiated in the different body regions.

About 84 ossified neural elements are visible. The first 51 neural arches are paired, strongly ossified and have a well-developed spine region. They have also a posterior-lateral process at the base of the spine, which articulates in a notch on the anterior margin of the following arch (Fig. 5a, b). Thus, the paired neural arches of each side were tightly articulated to each other, while the corresponding spines were not in contact. After the 51st neural element, the articulation gradually became weaker and weaker until the neural arches lose their joints. Beginning with the 75th neural arch, the space between neural arches suddenly becomes broader, most likely because there were cartilaginous interdorsal elements indicating a possible diplospondyly in the caudal region (Fig. 6).

Beginning from the 63rd neural arch, the neural spine is median. It was noteworthy that the anteriormost median

Fig. 4 Specimen XNGM WS-45-F21 (without skull)

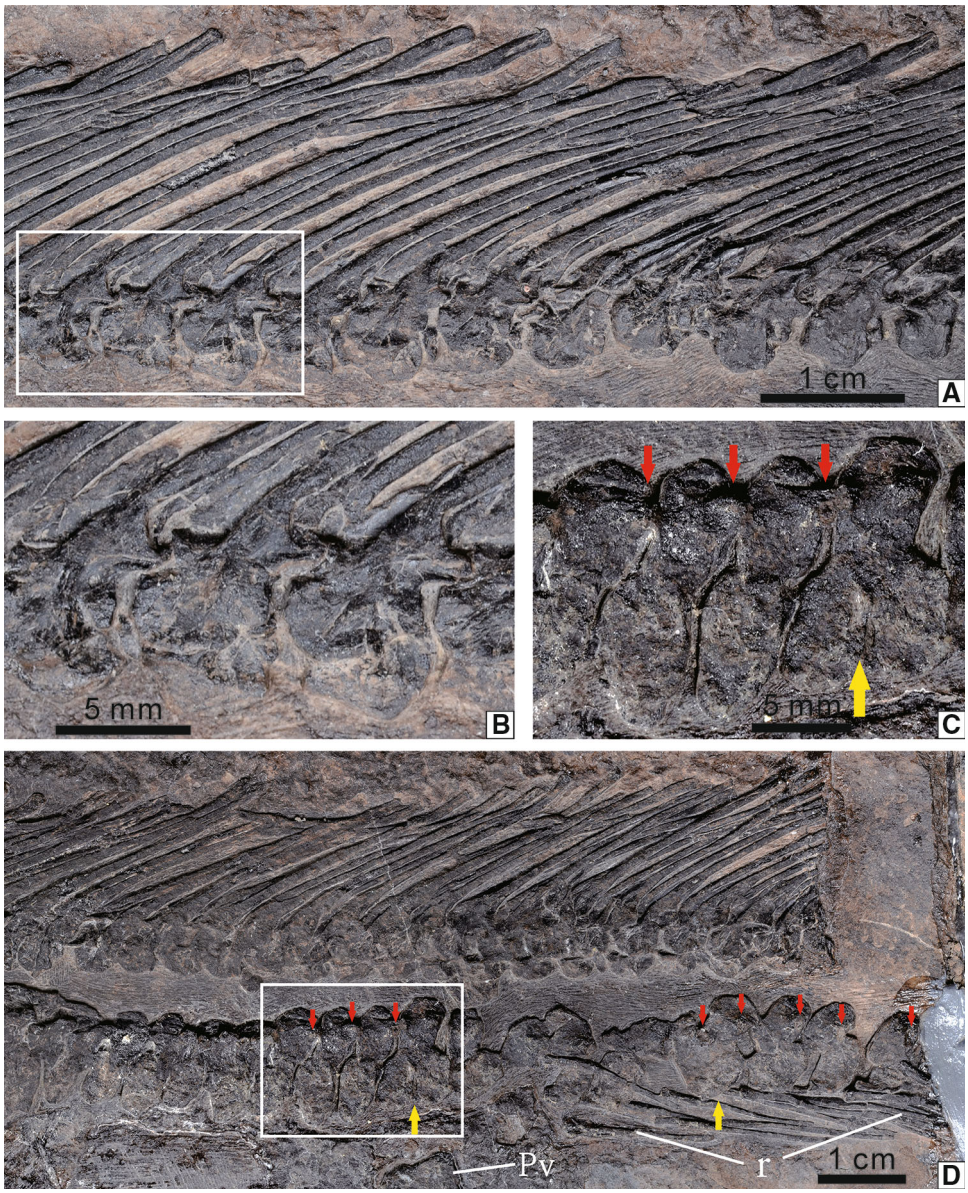


Fig. 5 XNGM WS-45-F21. **a** Posterior neural arches in the abdominal region; **b** close-up of articulation between neural arches (white rectangle in **a**); **c** close-up of parapophyses, red arrows indicating the process on the parapophyses, yellow arrow indicating fusion of parapophyses (white rectangle in **d**)); **d** parapophyses in middle abdominal region, red arrows indicating the process on the parapophyses, yellow arrows indicating the fusion of parapophyses

neural spines are longer than the most posterior paired ones and that there are five paired elements between the end of the supraneurals series and the first median neural spine.

For the first 66 neural elements, the neural spines tilt posteriorly almost in the same angle (about 20° respect to the notochord axis). From the 67th neural spine onward,

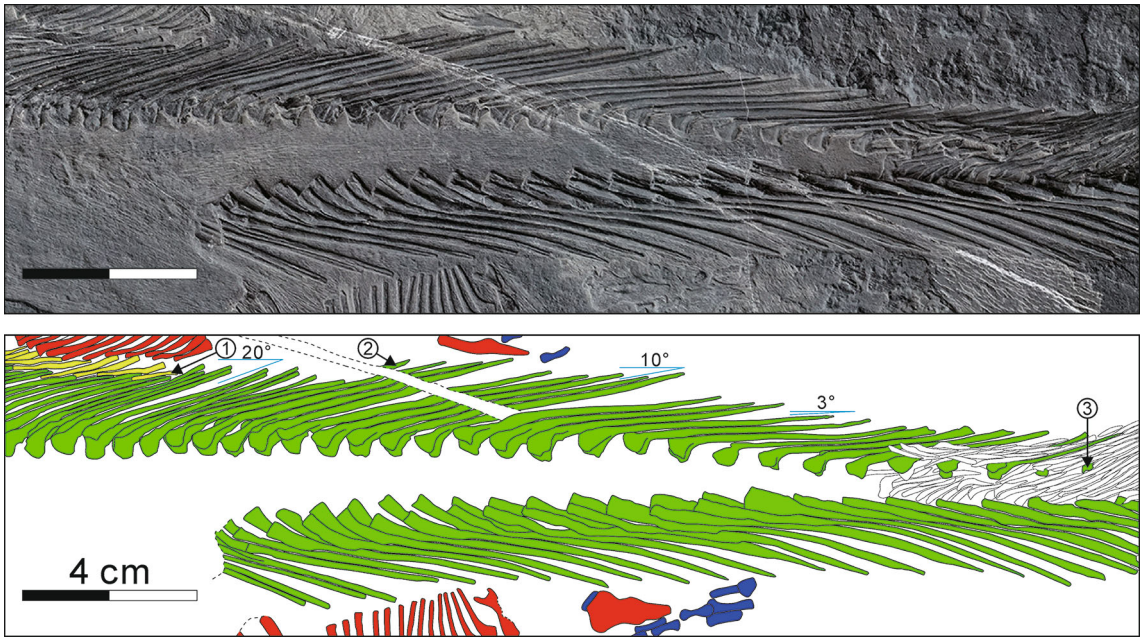


Fig. 6 Axial skeleton of XNGM WS-45-F21 in the caudal region, arrow ① indicating the last supraneural, arrow ② indicating the first median spine, arrow ③ indicating the last visible neural element; blue angle indicating the inclination degree of neural spines. In red the axonosts of both dorsal and anal fins; in blue, the baseosts; in green the neural and haemal elements; in pale yellow, the supraneurals; in white, the scales of the caudal region

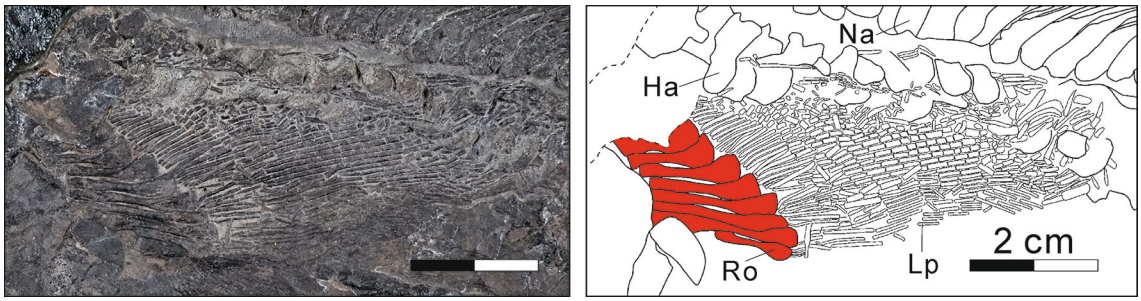


Fig. 7 XNGM WS-45-F21, photograph and line drawing of the pectoral fin. In red, the radials

the inclination decreases to about 10°, and five elements beyond the spines are lying almost horizontally only about 3°–4° with respect to the notochord axis (Fig. 6).

There is a series of unpaired supraneurals related to the first 57 paired neural elements. Like the corresponding neural spines, the supraneurals are inclined the same way and slightly curved backwardly. The supraneurals were somewhat shorter than their corresponding neural spines and remain the same length but the very last ones. The most posterior supraneural is almost in correspondence to the last axonost of the dorsal fin endoskeleton and about five neural elements in front of the first median neural spine (Fig. 6).

Ventral to the notochord, the axial skeleton lacks 16–17 vertebral segments, corresponding to about 11.7 cm in length, just in front of the anal fin. The missing part was clearly originally present, as the whole skeleton is perfectly articulated, and got lost during the collection.

There are about 50 paired haemal elements (parapophyses) in the abdominal region, but only 40 of them are visible: they are closely arranged, each lying just opposite to the corresponding neural arch, with the ratio 1:1. The shape of the parapophyses is different in the anterior and posterior abdominal regions. The first 27 elements are made of a short oval proximal region which appears quite thick, followed distally by a somewhat larger and thinner plate, antero-ventrally directed (Fig. 5c, d). Although the proximal region shows a developed process, no ossified ribs are preserved (Fig. 5c). Beginning from the 28th couple of haemal elements, located just behind the pelvic fin plate, the shape of the parapophyses changes, their two regions becoming more similar to each other in shape and

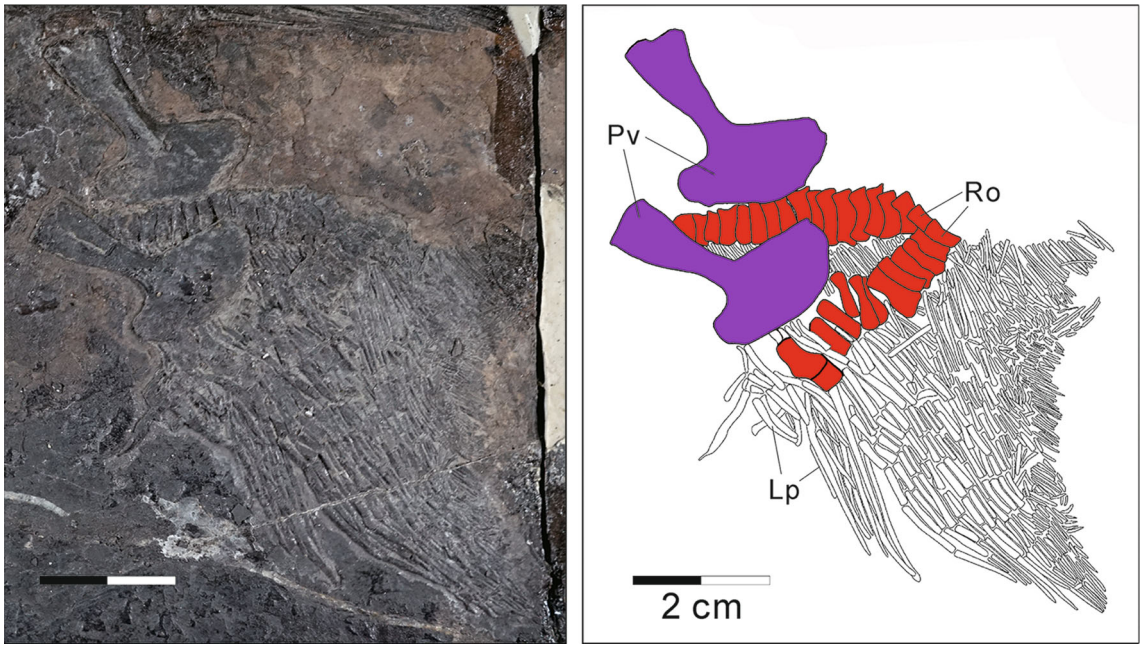


Fig. 8 XNGM WS-45-F21, photograph and line drawing of the pelvic fin. In violet, the pelvic plates, in red, the radials

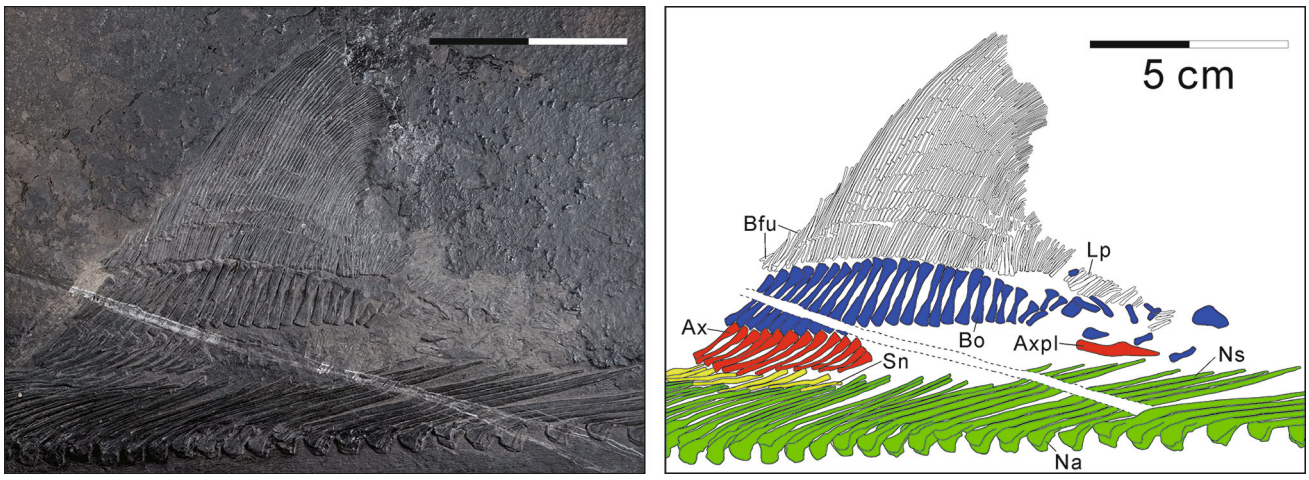


Fig. 9 XNGM WS-45-F21, photograph and line drawing of the dorsal fin. In red the axonost series; in blue, the baseost series; in green the neural elements; in pale yellow, the posteriormost supraneurals

size and having a stronger constriction between them (Fig. 5d). Also their longer axis is more antero-ventrally directed. A sharp notch is well present, especially in the posterior margin. Well ossified ribs are present in this region. The proximal ends of the ribs were enlarged and articulated with the process on the posterior edge of the proximal part of the paraphophysis, and all of them are preserved detached from these processes. The first rib is about 17 mm in length, about double the length of the complete parapophysis. The following ribs gradually increase in length posteriorly.

It is worth mentioning that sometimes adjacent distal regions of the parapophyses are fused, as in the case of the 31st–32nd parapophyses. However, the fusion is not so common.

Unfortunately, the transition from parapophyses to haemal arches provided with a haemal spine, is not visible in the specimen. In the caudal region, about 21 haemal arches were preserved up to the beginning of the caudal fin, and provided by a haemal spine, lying opposite to the interspace between corresponding neural arches. Compared with the neural arches, the haemal arches are less expanded and appear quite narrow and elongate. The proximal region of the spines is antero-laterally expanded on both right and left sides, so that the concave proximal region of one spine houses the posterior margin of the previous one. Only the

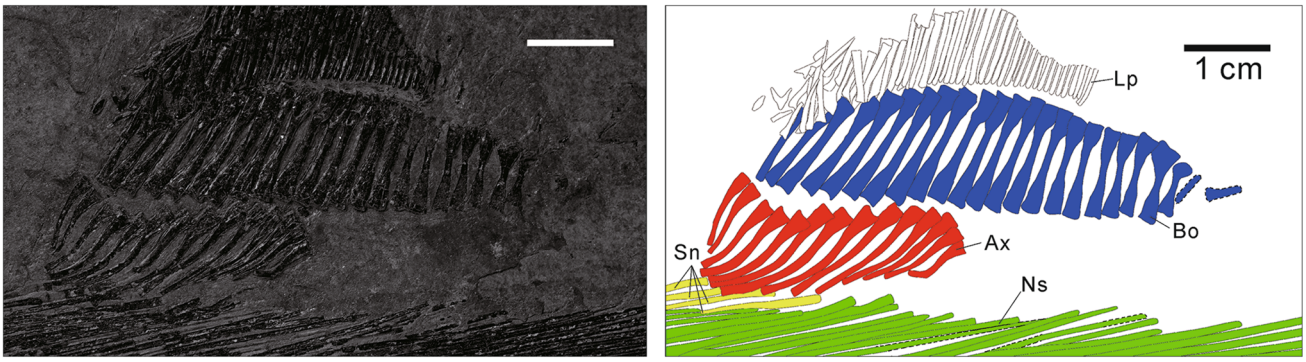


Fig. 10 The holotype of *B. lui* (IVPP V 12569), photograph and line drawing of the dorsal fin. In red the axonost series; in blue, the baseost series; in green the neural elements; in pale yellow, the posteriormost supraneurals

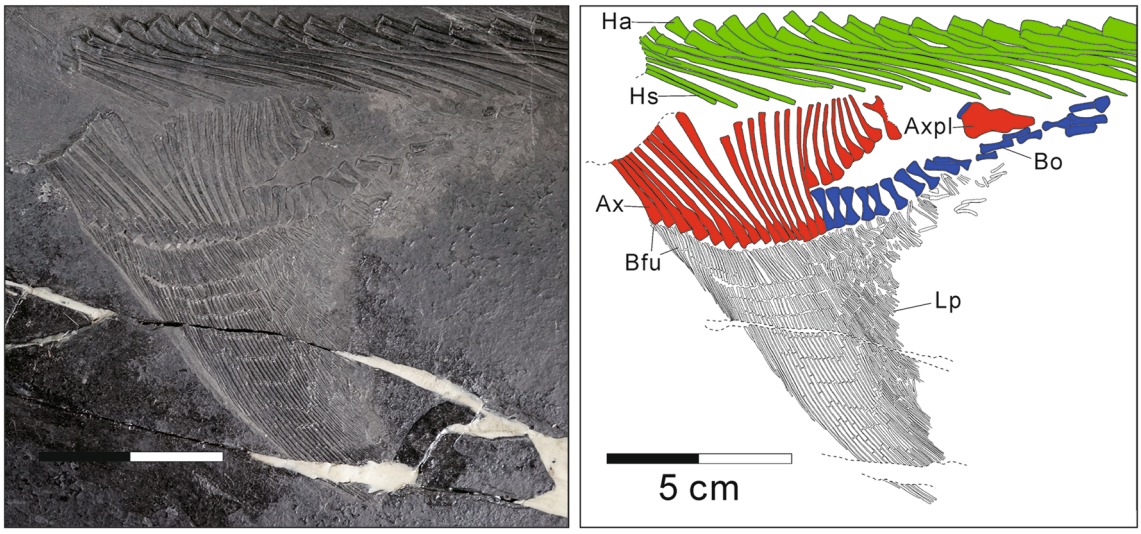


Fig. 11 XNGM WS-45-F21, photograph and line drawing of the anal fin. In red the axonost series; in blue, the baseost series; in green the haemal elements

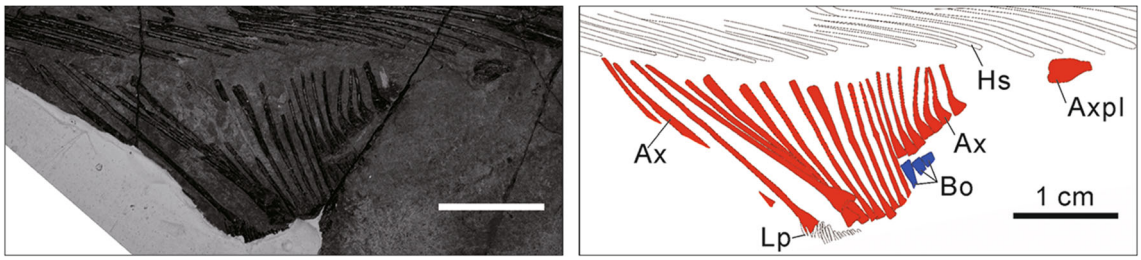


Fig. 12 The holotype of *B. liui* (IVPP V 12569), photograph and line drawing of the anal fin. In red the axonost series; in blue, the baseost series

distal region is laterally compressed and in a few cases they appear to bifurcate (Fig. 6). Direction of the haemal spines is more backward inclined than that of the corresponding arches and they make a very stiff proximal area just below the arches themselves. Acting as support for the more ventral fin rays in the tail, there are other four haemal elements that show the same articulate pattern, and that we consider as 'normal' haemal spines, although somewhat modified. They are followed by the hypurals, only a few being at least partly visible.

4.2 Pectoral girdle and fins

Most of the elements of the dermal pectoral girdle have been lost during the excavation, with only the cleithrum and two to three endoskeletal shoulder-girdle ossifications

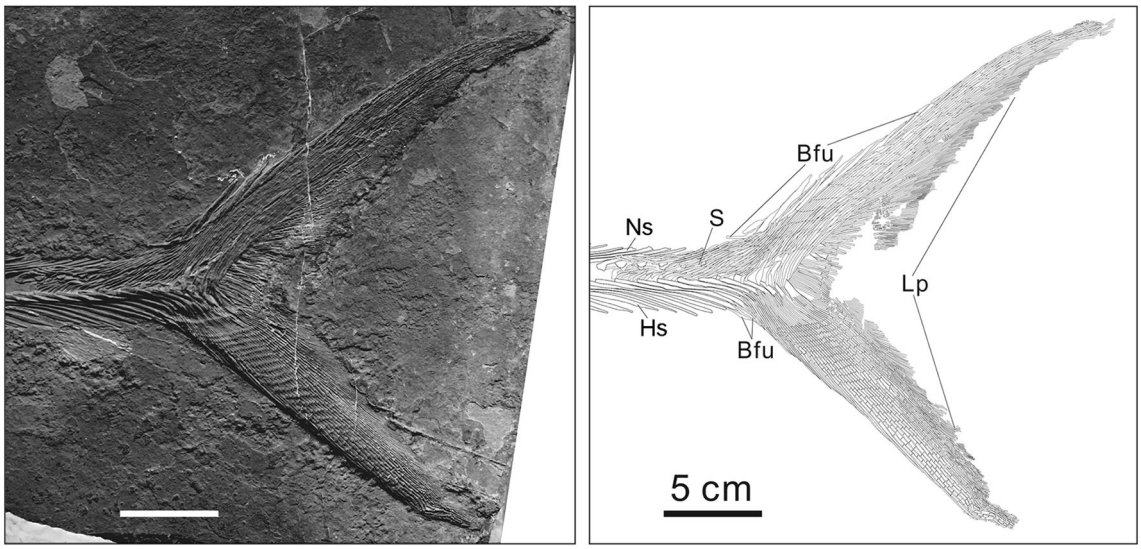


Fig. 13 XNGM WS-45-F21, photograph and line drawing of the caudal fin

recognizable. The incompletely preserved cleithrum is slender and somewhat curved, with a large notch occupying the whole posterior margin. The endoskeletal shoulder-girdle ossifications almost provide no useful information.

The pectoral fins (Fig. 7) are partially preserved so that it is not possible to estimate their shape. The left pectoral fin preserves about 40 closely-set lepidotrichia. The lepidotrichia are densely segmented, with the proximal segments relatively longer than the distal ones. In the longer rays, the lepidotrichia are made of more than 10 elements. Seemingly, the lepidotrichia are not branched throughout their length.

For the supports of the pectoral fins, only eight rod-like pterygiophores are visible. They are distinctly expanded distally and each supports at least five lepidotrichia.

4.3 Pelvic girdle and fins

The paired pelvic fins (Fig. 8) partly overlap each other so that their shape cannot be evaluated with certainty. They are slightly closer to the pectoral fins than to the anal one. They are fairly large, with lepidotrichia closely-set. The lepidotrichia increase rapidly in length from the anteriormost and then decrease posteriorly, but it is not possible to state which one is the longest, nor the total number of the pelvic fin rays (possibly around 40). The anterior four or five leading lepidotrichia are segmented but unbranched and their last segments are considerably long. On the contrary, the more posterior lepidotrichia are segmented and dichotomically branched distally. Also the proximal segments of the pelvic fin rays are relatively longer than the more distal ones, except for the last segment of the anterior leading lepidotrichium. The rays of the pelvic fin are made of 10 elements, less than those of the pectoral fin. No basal fulcra and fringing fulcra are visible.

The pelvic fin supports consist of a large pelvic plate and a series of radials. The pelvic plate consists of an oblong distal element, with a proximal shaft in the anteromedial direction. The proximal shaft is rod-like and gradually broadens proximally. The length of the proximal shaft is more or less equal to the width of the distal plate. There are about 17 endoskeletal radial ossifications, with only the anterior half most probably having a direct articulation with the pelvic plate. They are massive, rod-like elements, with depth being about twice than the length.

4.4 Dorsal fin

The dorsal fin (Fig. 9) is considerably large and it is situated in the posterior half of the body, its insertion being at 66% of the standard length (SL). The base of the fin is 122 mm long, thus about 16% of the SL. The dorsal fin faces the anal one for about 47 mm (6.2% of the SL). Its outline is strongly falcate, the anterior margin being almost straight while the posterior one shows a strong concavity due to the very short rays in the posterior half. Thus, the fin is made of two very distinct regions, a strong, anterior one provided by long strong rays and a much lighter posterior one.

There are about 115 lepidotrichia preserved, preceded by 4–5 thin basal fulcra. The lepidotrichia are stiff and close-set. The anterior 27 lepidotrichia increase quickly in length as well as in number of segments. The rays are segmented throughout their length but possibly unbranched (the very distal part is missing): the proximal segments of the anterior 12 lepidotrichia are somewhat shorter than

those of the following ones. The last distal segment of the anteriormost 18 rays are considerably long. After the 27th lepidotrichium there is a marked decrease in length. The rays are evenly segmented throughout their length and dichotomically branched in their distal part. In the posterior half of the fin, the lepidotrichia are supposed to be very short, made of a stout proximal segment followed by just a branched one as preservation is not nice enough to give a sound restoration of the distal part of the rays.

The dorsal fin endoskeleton includes two rows of pterygiophores, i.e. axonosts and baseosts (sensu Nielsen 1949), as well as one axonost plate. However, only the baseost series appears to be fully ossified. The axonost series consists of 13 slender rod-like ossifications, situated at the anterior one-third of the fin. They are backwardly inclined and slightly curved, increasing in length up to the middle of the series and then decreasing posteriad. The anteriormost four or five axonosts are dumbbell-shaped, expanded both proximally and distally, whereas the rest of axonosts are rod-like, only expanded distally. The last four axonosts seem to have lost a close articulation to their corresponding baseosts. As the same pattern is visible in the holotype (Fig. 10), we suppose that this was the original anatomical position of these bony elements while the 'empty' space was actually filled by cartilaginous elements. The axonost plate is situated at nearly the posteriormost part of the dorsal fin. It is transversely elongated, slender, rod-like in shape and somewhat convex in its dorsal margin.

The baseost series contains at least 38 ossifications. The anterior 23 baseosts, which are preserved in situ, are dumbbell-shaped, expanded both proximally and distally: they first increase slowly in length and then decrease gradually posteriad. The remaining baseosts are most probably not preserved in situ, showing some scattering: they appear to be more or less rod-like except for the last one. The last baseost is a little far from the others, possibly due to taphonomic processes, and it is a quite large plate, subtriangular in shape. The anterior 14 baseosts have a one-to-one relationship with the axonosts (when compared with the holotype, we suppose that the first axonost has been lost during the collection), whereas there are no ossified axonosts corresponding to the remaining baseosts. The number of baseosts is about twice the number of corresponding metameres and one-third the number of the corresponding lepidotrichia.

4.5 Anal fin

The anal fin (Fig. 11) is about the same size as the dorsal fin and it is located between 73.6 and 88.9% of the S.L., thus somewhat posterior to the dorsal fin. Its outline is roughly triangular and very falcate, the anterior margin being almost straight whereas the posterior one being strongly concave because of the rapidly shortened rays in the posterior part of the anal fin.

Five slender basal fulcra are anterior to the lepidotrichia. There are at least 110 lepidotrichia, which appear stiff, as the segments are quite elongate, and closely set. The 38 anterior rays increase rapidly in length. They are segmented and unbranched but the most posterior ones: the basal segment of the first 22 lepidotrichia is a little shorter than that of the following 16 ones (the same as for the foremost lepidotrichia of the dorsal fin); the last segment of the 31 anterior lepidotrichia is considerably longer than the proximal bases. Also, in the second group the lepidotrichia show a much regular segmentation, giving rise to almost straight articulation lines, aligned to those in the first group, and convex in the distal part of the fin. Although the very distal part of this region is missing, it seems that the longest lepidotrichia do not branch, the branching being present only as the more posterior lepidotrichia shortened.

In the posterior half of the fin, lepidotrichia quickly decrease in length. They are segmented throughout the whole length and branch at least twice. The distal segments are thinner than those in the anterior region, while the length of each single segment is quite constant along most of the fin. The most posterior part of the fin appears very low, but the preservation in this delicate area is not nice enough to allow a very detailed restoration.

The anal fin endoskeleton consists of two series of pterygiophores, i.e. axonosts and baseosts, as well as one axonost plate. The axonosts consists of 24 elongate and slender ossifications, the first 16 being the only ray supporting elements. The first nine axonosts are nearly straight and postero-ventrally inclined, being by far the longest ones. The following seven are somewhat shorter: they are slightly curved and more vertical than the first ones. Eight much shorter elements follow, separated from the fin-base by the baseost series. They show an enlarged distal end, although they do not articulate directly to the corresponding baseost. They also decrease in length posteriorly. The last ossified element shows a quite different shape with a bifurcate proximal end. Between this element and the axonost plate there is an empty space, corresponding to about five preceding elements. The axonost plate is situated in the posterior part of the fin, but possibly not at the very end. It is an elongate symmetric triangular bone, thinning backwards, with wavy dorsal and ventral margins.

The baseosts consists of about 20 hourglass-shaped ossifications, situated in the posterior two-thirds of the fin. They are fairly short and stout and they slightly decrease in length backwards. Their distal articular ends are somewhat larger than those of the anterior axonosts, each giving support to three-four lepidotrichia. The foremost eight baseosts have a one-to-one relationship with the hindmost

eight ossified axonosts: however, apart from the first two that are closely articulate, there is a large triangular space between axonosts and baseosts with no ossification, even if the distal end of axonosts and the proximal one of the baseosts are enlarged as for articulation. We consider this large unossified gap to be an original anatomical feature as we observe exactly the same in the holotype of *B. liui* (Fig. 12).

4.6 Caudal fin

The large caudal fin (Fig. 13) was strongly heterocercal, deeply forked and almost symmetrical in the outline of ventral and dorsal lobe. The dorsal and ventral edges of the fin make an angle of about 76° between them. The lepidotrichia are situated close to each other and the precise number of the lepidotrichia is unknown as the preservation of the tip of the dorsal lobe does not allow a definitive count. About 40 rays are in the ventral lobe and more than 100 in the dorsal one. The proximal ends of the lepidotrichia articulate to the last haemal spines and the series of hypurals, which are mostly covered by the scales of the body lobe. All lepidotrichia show a long to very long proximal segments, followed by short and regularly segmented elements, at least in the ventral lobe. In the latter, the proximal segments shorten toward the boundary with the dorsal lobe, leaving a small narrow area uncovered by both basal segments of the rays and scales of the body lobe. The lepidotrichia of this latter are distally well segmented and most of them branch once at the far end, but probably more in the dorsalmost rays of the lobe. The short segments just following the first ones are very expanded laterally, so that the base of the ventral lobe is very thick and probably also very stiff, also because the segments were very strictly packed. In the distal region, the lepidotrichia are made of more regular segments, almost circular when considered the two halves. The fin rays decrease quickly in length and the ventral lobe is then quite narrow in dorso-ventral width. No fringing fulcra have been detected.

Starting from the anterior end of the dorsal lobe, the rays inserted below the scales of the body lobe and the exposed part of the proximal segments are again very long, even if it is almost impossible to check the actual segmentation, and branching, of these rays.

4.7 Squamation

The squamation was entirely reduced to the posterior portion of the central region of caudal peduncle and on the body lobe of the tail (Fig. 13). Anteriorly, the scales can reach about the 68.5% of the length of the caudal peduncle, three to four haemal arches behind the axonost plate of the anal fin. The scales are entirely devoid of ganoine, long and narrow, about 9 mm in average length at the beginning of the scale field. They are also very thick and densely packed without any apparent articulation, making probably a very stiff area. There are more than 10 strong basal fulcra on the dorsal margin of the body lobe and about three on the ventral margin of the caudal fin (Fig. 13).

4.8 Probable gut content

A probable gut content is preserved between the pectoral and the pelvic fins (Fig. 4). It is a wavy tube and with a short detached part near the anal opening. The gut content is three-dimensionally preserved but no remains are identifiable on the surface. Furthermore, there are no evidences for the presence of a spiral valve.

5 Comparison and discussion

Most of the previous works on *Birgeria* mostly focused on the skull anatomy (Stensiö 1921, 1932; Nielsen 1949; Lehman 1948, 1952; Romano and Brinkmann 2009; Romano et al. 2017) especially for Early Triassic species that show a 3D preservation in carbonatic or siliceous nodules. With this kind of preservation, coupled with a random surface collection, large specimens are usually found in fragments; skulls are the most resistant parts to survive weathering when exposed. On the other hand, most of the Middle and Late Triassic fish remains are preserved as flattened specimens on slabs, which usually make unavailable most of endocranial anatomy but helps in showing well preserved dermal and postcranial elements. Also, material from Monte San Giorgio, Lombardian Prealps and southern China is mainly from extensive excavations, so that complete specimens can be recovered more easily.

Among the species of *Birgeria*, it is possible to compare the postcranial skeleton mostly with *B. groenlandica* from the Early Triassic, *B. stensiöi* from the Middle Triassic and *B. acuminata* from the Late Triassic, of which either complete specimens or large amount of material is available. However, as for *B. groenlandica* only very small specimens are available and no data about ontognetic changes in *Birgeria* are known, we mostly focus on comparing *B. liui* with *B. stensiöi* and *B. acuminata*. Unfortunately, we could not make a comparison with *B. guizhouensis* as the holotype and only known specimen could not be located and the original description is quite poor (Liu et al. 2006). This comparison should be very interesting as this species and *B. liui* come from the same area (South-Western Guizhou Province) and their age is quite close, being probably separated by no more than 2–3 My (Late Ladinian to Early Carnian). The same is for

Table 2 Meristic comparison among *B. groenlandica B*, *stensiöi*, *Birgeria liui* and *Birgeria acuminata*

	New Specimen of *Birgeria liui*	Holotype of *B. liui*	*B. groenlandica*	*B. stensiöi*	*Birgeria acuminata*
Neural arches	≈ 84	?	≈ 80	≈ 80	≈ 80
Pectoral fin					
Radial ossification	8	?	10	11	9–10
Lepidotrichia	> 40	?	≈ 40	44	43
Pelvic fin					
Radial ossification	≈ 17	?	13	13	?
Lepidotrichia	≈ 40	?	50	50–60	> 60
Dorsal fin					
Axonost	13	14	13-15	3 (?)	17
Baseost	≈ 38	> 24	30	24 (?)	21
Axonost plate	Present	?	Present	Present	?
Distal radial ossification	Absent	Absent	3–4	Absent	Absent
Lepidotrichia	≈ 115	> 50	53–57	55–60	> 40
Fulcra	5	?	Absent	Absent	?
Anal fin					
Axonost	16 + 8	14 + 7	17 + 5	17 + 7	17 + 4
Baseost	≈ 20	> 3	10	6–8	4
Axonost plate	Present	Present	Present	Present	Present
Lepidotrichia	≈ 110	>50	60-62	53	≈ 80
Fulcra	6	?	absent	≥ 2	?
Caudal fin					
Lepidotrichia	> 140	> 60	65	37	> 95
Fulcra	> 10; 3	> 12; 2–3	14; 0	14; 2–3	15
Intersecting angle of the dorsal and ventral margins of the caudal fin	76°	70°	40°	65°	73°

Birgeria sp. in Liu et al. (2006) apparently from the same horizon as *B. guizhouensis*.

Axial skeleton. There are only small differences in number of neural elements, about 85 in *B. liui* and about 80 in *B. stensiöi* and *B. acuminata*. The neural arches in the abdominal region are paired and they articulate tightly with each other along the same side; in the caudal region neural arches lose this articulation, leaving space between them for a possibly cartilaginous element in the caudal region, thus showing diplospondyly. This is almost the same we observed also in *B. stensiöi* and *B. acuminata*. In Early Triassic species, such as *B*.cf. *B. aldingeri* from Spitsbergen (Stensiö 1921, pl. 21 Fig. 4) small interdorsals are present between well developed neural arches (basidorsals) bearing a median spine. Although Nielsen (1949) described a similar condition in *B. groenlandica*, interdorsal are not visible in Nielsen 1949, pl. 18, fig. 2). In *B. acuminata*, anterior supraneurals are slender and longer than the corresponding neural spines. In *B. stensiöi* and *B. liui* anterior supraneurals are somewhat shorter than the posterior ones and as long as the length of the corresponding neural spines. In *B. stensiöi* and *B. liui*, haemal arches are well ossified along the whole body, while in *B. acuminata*, the haemal arches seem not to be ossified in the abdominal region. In *B. liui*, ribs articulate with well-developed process on haemal arch but in *B. stensiöi* ribs appear to be fused to the haemal arch. In the caudal region, haemal spines of *B. liui* have a stronger articulation between each other than those of *B. stensiöi* and *B. acuminata*, but in *B.* cf. *B. aldingeri* the haemal spine appears to be detached from the corresponding haemal arches and not supporting each other, as in the other species.

Endoskeleton of paired fins. Difference in number of radial ossifications of paired fins are listed on Table 2. However, differences are mostly due to preservation. Pelvic plate of these four species is generally mallet-like (sledgehammer-like) in shape, consisting of a proximal shaft and a distal plate. In *B. groenlandica*, *B. stensiöi* and *B. liui*, proximal shaft is quite enlarged and length of the proximal shaft almost equals the distal plate width, but in

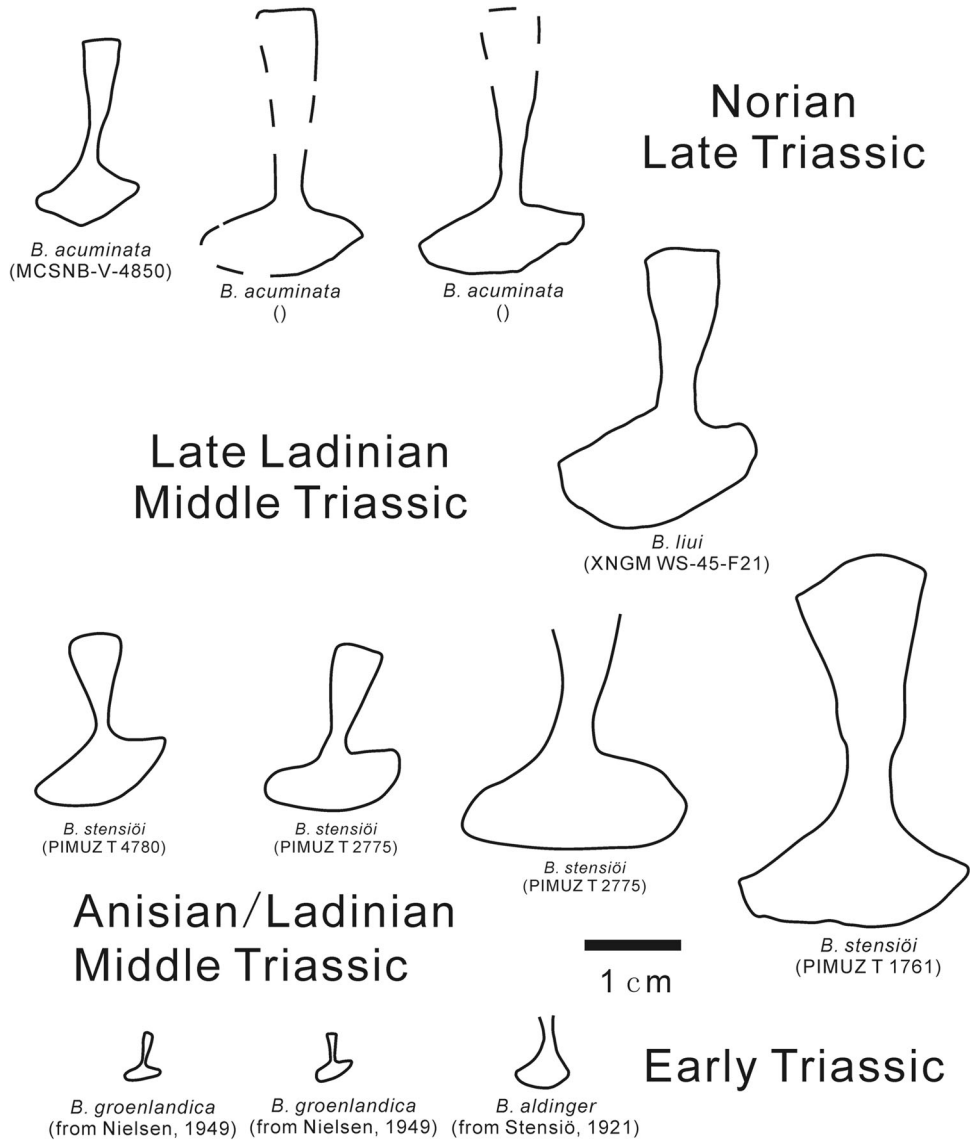


Fig. 14 Pelvic plates of *Birgeria*

B. acuminata, the proximal shaft is more slender and not so enlarged. The distal plate can show a different outline in specimens of same species, although the number of available specimens is too low to define an intraspecific variability (Figs. 14, 15)

Endoskeleton of dorsal fin. Except for the difference in number (Table 2), the ossified elements in the species *B. liui, B. groenlandica* and *B. acuminata* have a similar pattern. These species have ossified axonosts only in the anterior part, but a complete series of baseosts; last few axonosts lost direct articulation with the corresponding baseosts. In *B. groenlandica* there are also a few small distal ossifications just at the anteriormost part of the fin (Nielsen 1949). In *B. stensiöi* there is only a series of elongate elements in the anterior region, the number being highly variable (Romano and Brinkmann 2009, pers. obs.) in the different specimens where this region is well preserved (from 3 to 15). These elements are possibly due to the fusion between axonosts and baseosts. Axonost plate is known in all species but in *B. acuminata*, probably because of the poor preservation of the region.

Endoskeleton of anal fin. All four species show the same pattern: single elements in the anterior half, possibly elongated axonosts, followed by an incomplete series of axonosts and a complete series of baseosts. There are small differences between *B. groenlandica* and the other species, again possibly due to the small size of the specimens of the former species. In *B. groenlandica*, anteriormost baseosts are very short, they increase in length and then decrease again; there is no empty space between the last axonosts and the axonost plate and each axonost has a direct articulation with the corresponding baseosts (Nielsen 1949). In the other three species, the baseosts gradually decrease in length posteriorly, with the first one being the longest. The

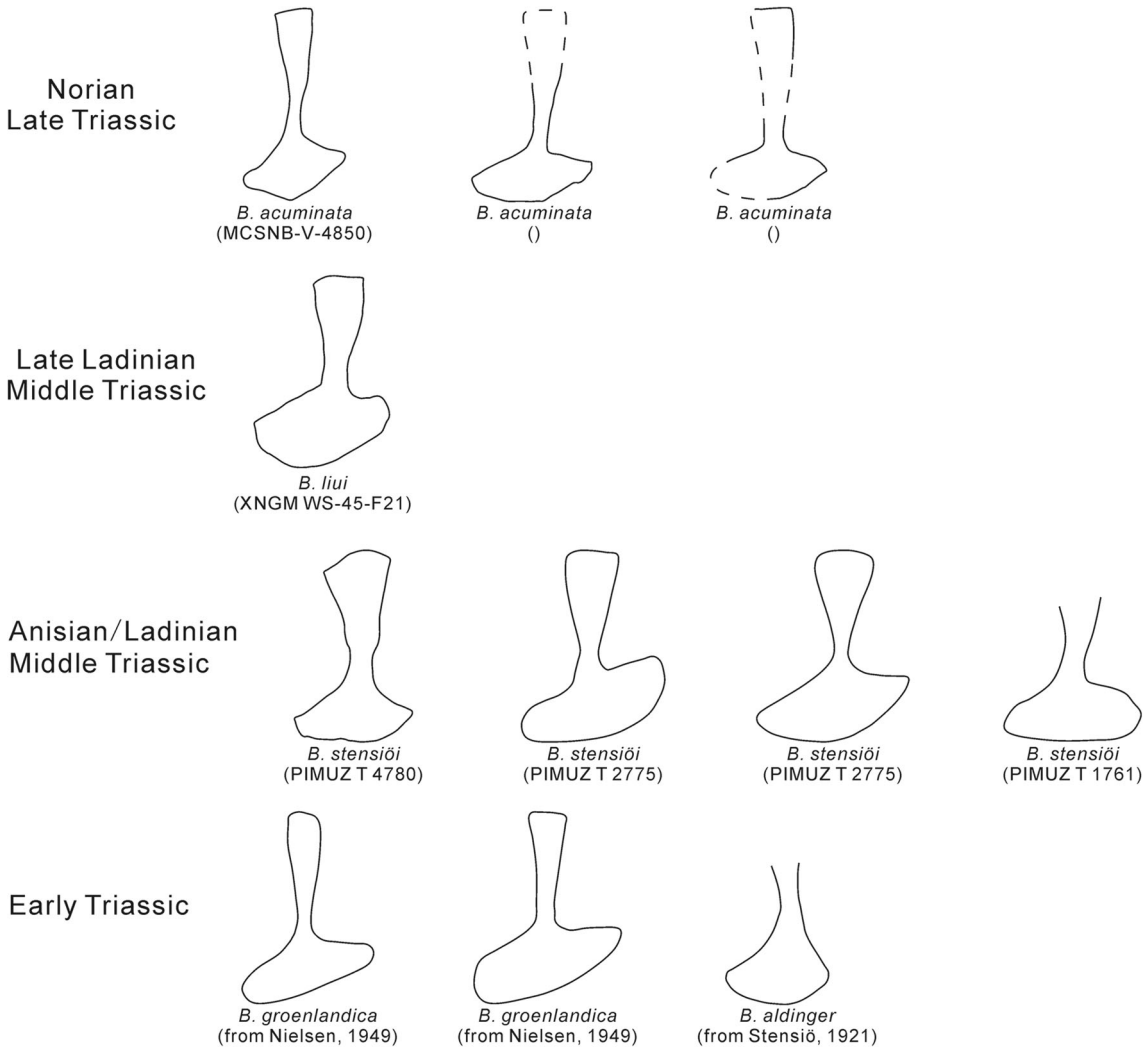


Fig. 15 Pelvic plates of *Birgeria*, adjusting to the same size

axonosts series does not reach the axonost plate and only anteriormost baseosts articulate directly with the corresponding axonosts, leaving a large space devoid of ossified elements.

Lepidotrichia of the dorsal and anal fins. Due to the different quality of specimen preservation, it is possible to have a complete view of all fins only in *B. liui*, so that it appears that there are always more lepidotrichia than in *B. groenlandica*, *B. stensiöi* and *B. acuminata* (see Table 2). In *B. stensiöi* and *B. liui* we can observe that the last segments of foremost lepidotrichia are considerably long in all fins except the pectorals, but in *B. acuminata* we cannot observe these slender last segments. In *B. liui* the dorsal and anal fin show an elongate posterior region made of short rays, but we could not observe this region in the other species, owing to scarce preservation or disarticulation of the specimens before burial (but see Romano and Brinkmann 2009).

Caudal fin. The peculiar outline given by the proximal tip of the caudal lepidotrichia (Fig. 16) is very similar in all species (*B. groenlandica*, *B. stensiöi, B. liui, B. acuminata*) although the area left uncovered by the proximal segments of the lepidotrichia can be somewhat different in the various species. This character has not been recorded by previous authors in their descriptions and the tail restorations followed a more typical paleoniscid pattern (Nielsen 1949; Romano and Brinkmann 2009). Intersecting angle of the dorsal and ventral margins of the caudal fin is quite large in *B. stensiöi*, *B. liui* and *B. acuminata*, normally more than 60°. In *B. groenlandica*, this angle is only about 40°, but, again, we have to consider that we are dealing with juvenile specimens.

Scales. In *B. liui* the caudal scale-field starts from about half-way between the end of anal fin and base of the dorsal body lobe, while in *B. stensiöi*, it begins soon after the end of the anal fin itself Romano and Brinkmann 2009). *B.*

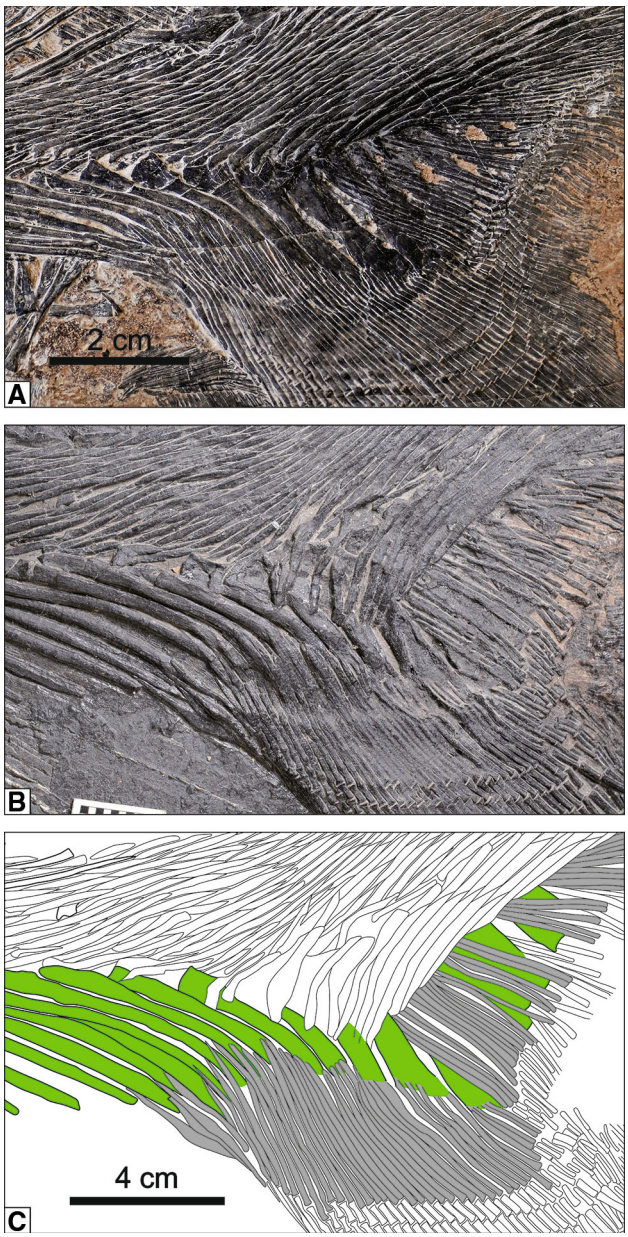


Fig. 16 The ventral region of the body lobe in the caudal fin. **a** *B. acuminata* (MPUM 9334); *B. liui* (XNGM WS-45-F21), **b** photograph and **c** line-drawing. In green, the haemal elements, in gray, the proximal segments of the caudal fin lepidotrichia, in white, the body lobe scales

acuminata specimens show a possible short scale-field (Fig. 16a), but the preservation of the caudal region is not nice enough to state the relationship between the beginning of the field and the anal fin posterior end. In *B. groenlandica*, the field appears small and made of few proportionally larger scales, but this can be due to the small size of the specimens (Nielsen 1949, pl. 10 and pl. 13, fig. 2; Bartsch 1988)). Very small lateral-line scales have been described by Nielsen (1949) for *B. groenlandica* and by Stensiö (1921) for *B.* cf. *B. aldingeri*, but they have never been recorded in stratigraphically younger species.

6 Conclusions

Birgeria proves to be a very homogeneous genus all over the Triassic, especially if compared to the other top predator with a similar stratigraphic distribution, *Saurichthys* (Tintori et al. 2014). So far, about 50 species based on well preserved material are ascribed to the latter genus (see Romano et al. 2012 for an overview of the fossil record, Tintori 2013; Tintori et al. 2014), leaving apart many other species based on very poorly preserved specimens, sometimes just a few teeth or fragmentary bones. Both genera have an almost cosmopolitan distribution, but *Saurichthys* is common to very common in almost all Triassic marine vertebrate sites, often with more than one species, while *Birgeria* is known from fewer sites, probably also because it is usually much rarer than *Saurichthys*. We suppose that *Birgeria* had a more solitary way of life than *Saurichthys*, this latter sometime found on mass mortality surfaces proving they lived in large schools (A.T., field pers. obs. on Luoping Fauna). *Birgeria* individuals could grow much larger than *Saurichthys* ones, this latter usually not being larger than 150 cm, while *Birgeria* could reach at least four m in length in the Late Ladinian (pers. obs.). *Saurichthys* managed to change its scale covering pattern from Late Permian/Early Triassic to Middle/Late Triassic species (Tintori 2013) while *Birgeria* kept the same pattern in the scale field along the body lobe in all the known species (Nielsen 1949; Bartsch 1988, this paper). *Saurichthys* modified the axial skeleton in several ways (Tintori 1990, 2013) while, again *Birgeria* did not change apart a few details. Dorsal and anal fins endoskeleton and ray segmentation are highly variable in *Saurichthys*, but remain very conservative in *Birgeria* (Nielsen 1949; Romano and Brinkmann 2009; this paper). Skull proportions can change a lot in *Saurichthys*, but apparently in Birgeria nothing similar happened (Boni 1937).

As shown above, *Birgeria* had a very low evolutionary rate so that we suspect that *B. guizhouensis* could be a junior synonym of *B. liui*. However, as the type material could not be traced and no other specimens from the early Carnian Guanling Fauna has been so far recorded, we have to consider *B. guizhouensis* Liu et al. 2006 still a valid species although no clear differences to *B. liui* can be detected from the original description and possibly the two species will be considered as a single one (*B. liui* by priority) when new material from sure stratigraphic source will be available.

Finally, the well preserved new specimen reveals previously unknown anatomical details of the postcranial

skeleton of *Birgeria liui* (e.g., the number of neural arches and their changes along the vertebral column, the articulation between the neighbouring haemal spines in the caudal region; the present of ribs; the pattern of endoskeleton and of lepidotrichia of all fins and the coverage of scales) offering at the same time a very nice outlook also for the genus itself. *Birgeria* proves to be a very peculiar and specialized basal actinopterygian genus which ruled the Triassic seas for about 50 my, notwithstanding the big faunal changes the marine environment encountered following the P/Tr crisis (Tintori et al. 2014).

Acknowledgements We thank T. Sato (GMPKU), J. Z. Wang and M. Y. Wang (XNGM) for preparing the specimens, B. Hu and L. Chen for providing the logistic support in the field, C. Romano and J. Kriwet for spending a considerable amount of time and effort reviewing this manuscript and giving many constructive comments. We thank A. Paganoni (MCSNB) and C. Klug and T. Scheyer (PIMUZ) for allowing us to see specimens in their care. This study was financially supported by NSFC (Grants 41572008, 41372016, 40920124002), State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) (nos. 123107, 143108, 173123), China Geological Survey (No. 121201102000150012-09) and Academic Fund of the Peking University Team of Wenbo Scientific Research and Engineering.

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