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产自中国云南禄丰组(下侏罗统)的 爬行动物不完美硕鳄的再研究¹⁾

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摘要:一般认为植龙类在三叠纪末期灭绝,但有研究显示它们可能在欧洲和亚洲延续到了侏罗纪最早期。来自亚洲的证据是产自中国云南禄丰组(? 赫唐阶-锡内穆阶)的不完美硕鳄(*Pachysuchus imperfectus*)。重新研究显示不完美硕鳄正型标本和植龙类存在许多不同点,它可能属于一个保存较差的、分类位置无法确定的蜥脚型类恐龙头骨。这一属种的归入标本也无法明确归入某一类群,因此亚洲没有可靠的晚于三叠纪的植龙类化石记录。欧洲的侏罗纪植龙类化石也存在着同样的问题。因而认为,植龙类的化石记录仅限于三叠纪晚期。

关键词:云南,下侏罗统,蜥脚型类,植龙类

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THE ENIGMATIC REPTILE *PACHYSUCHUS IMPERFECTUS* YOUNG, 1951 FROM THE LOWER LUFENG FORMATION (LOWER JURASSIC) OF YUNNAN, CHINA

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Abstract Phytosaurs are generally considered to have become extinct at the end of the Triassic Period, but several records have suggested that they survived into the basal Jurassic in Europe and Asia. The Asian record consists of *Pachysuchus imperfectus* from the Lower Lufeng Formation (? Hettangian-Sinemurian) of Yunnan, China. However, this specimen differs from phytosaurs in numerous respects and is more likely a poorly preserved, indeterminate sauropodomorph dinosaur skull. The referred specimens of this species are also regarded as indeterminate, thereby removing the post-Triassic record of phytosaurs from Asia. The European records of Jurassic phytosaurs are also shown to be doubtful, suggesting that this clade was restricted to the Late Triassic.

Key words Yunnan, Lower Jurassic, Sauropodomorpha, Phytosauria

The Lower Lufeng Formation of Yunnan has produced a globally important fauna of Early Jurassic reptiles and synapsids, including numerous sauropodomorph dinosaurs, tritylodontids and protosuchian crocodylomorphs (e. g. Young, 1951; Sun et al., 1985; Sun and Cui, 1986;

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Luo and Wu, 1994). One of the more obscure taxa from this assemblage is the supposed phytosaur *Pachysuchus imperfectus*, which was described by C C Young (1951) on the basis of a single badly damaged partial snout. Although fragmentary, this specimen is potentially of wider significance as, if correctly identified as a phytosaur, this would represent the youngest-known occurrence of this clade, which is otherwise known primarily from the Late Triassic (Buffetaut, 1993). Indeed, the identification of *P. imperfectus* as a phytosaur was initially used to bolster support for a Late Triassic age for the Lower Lufeng Formation (Young, 1951), although other biostratigraphical correlations now place this unit within the Early Jurassic (Luo and Wu, 1994).

The specimen (Institute of Vertebrate Paleontology and Paleoanthropology [IVPP] V 40), collected from the Dark Red Beds northeast of Lufeng, was initially referred to the sauropodomorph dinosaur '*Lufengosaurus magnus*' (Young, 1947:37), but was later redescribed and identified as a phytosaur (Young, 1951:25). Although *Pachysuchus imperfectus* has been mentioned in the literature on numerous occasions, often in the context of either palaeobiogeographical distributions or Triassic/Jurassic (Tr/J) faunal turnover (e. g. Simmons, 1965; Westphal, 1976; Dong, 1980; Buffetaut and Ingavat, 1982; Sun et al., 1985, 1992; Sun and Cui, 1986; Padian, 1989; Buffetaut, 1993; Luo and Wu, 1994; Lucas, 2001; Wu and Sun, 2008), it has never been redescribed. Indeed, it was noted that the holotype specimen had been lost (Sun and Cui, 1986; Buffetaut, 1993). Several authors followed Young's identification of the specimen as a phytosaur, at least tentatively (e. g. Simmons, 1965; Buffetaut and Ingavat, 1982; Sun et al., 1985; Buffetaut, 1993), while others regarded it as an indeterminate archosaur of uncertain affinities (e. g. Padian, 1989; Sun et al., 1992; Luo and Wu, 1994; Lucas, 2001; Wu and Sun, 2008), although none of these opinions was based on a first-hand examination of the specimen. A recent search of the IVPP collections relocated the holotype, allowing it to be re-described and compared with other Lower Lufeng taxa and phytosaurs. Here, we show that the holotype of *P. imperfectus* is not a phytosaur, but an indeterminate sauropodomorph dinosaur, and that the referred specimens are also indeterminate, thereby removing the only post-Triassic records of phytosaurs from Asia.

1 Systematic palaeontology

Saurischia Seeley, 1887

Sauropodomorpha von Huene, 1932

Sauropodomorpha gen. et sp. indeterminate

1947 *Lufengosaurus magnus* Young, p. 37

1951 *Pachysuchus imperfectus* Young, p. 25, fig. 5

Material IVPP V 40 (holotype of *Pachysuchus imperfectus* Young, 1951), a partial snout consisting of a very fragmentary left premaxilla, left maxilla, ? both nasals and other indeterminate bone fragments (Figs. 1-2).

Locality and horizon Dark Red Beds, Lower Lufeng Formation (? Hettangian-Sinemurian, Lower Jurassic; Luo and Wu, 1994). Collected from a quarry southwest of Huangchiatien (Dahuangtian in more recent publications; Luo and Wu, 1994), to the northwest of Lufeng, Yunnan Province (Young, 1947, 1951).

Description A block of matrix adhered to the rostral end of the left maxilla contains some small fragments of bone that probably represent the left premaxilla (Figs. 1-2). A short, rounded process visible in medial view might represent the maxillary process of the premaxilla (Fig. 2B). The rest of the bone is too poorly preserved to yield any useful information.

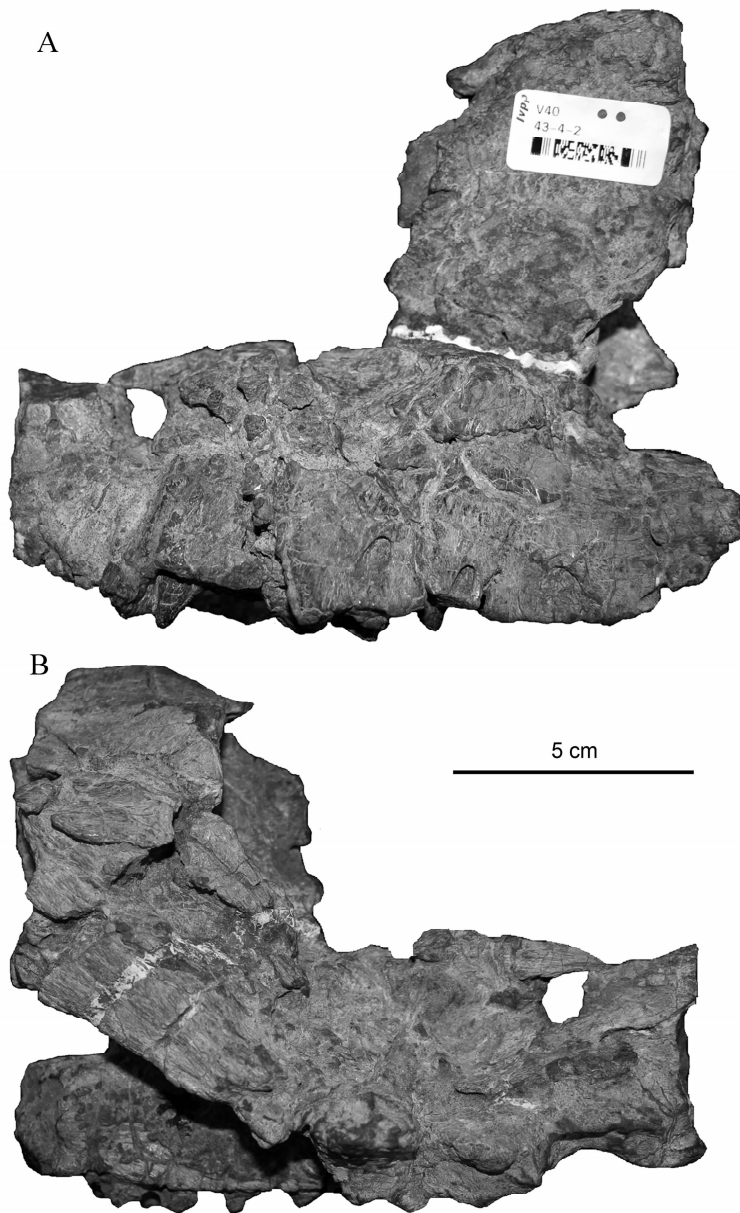


Fig. 1 Holotype specimen of '*Pachysuchus imperfectus*' (IVPP V 40)
A. left lateral view; B. right lateral view

The left maxilla (identified as the premaxilla by Young [1951, fig. 5]) is represented by the rostral part of the main tooth-bearing ramus and the ascending process (Figs. 1A and 2A). The latter is broken at its base and displaced medially relative to the rest of the maxilla. Ventrally, the margins of the maxillary tooth row are broken and it cannot be determined if a lateral plate was present or absent. The maxilla is broken caudally; nine alveoli are preserved, the first of which contains an unerupted tooth crown. In lateral view, the rostral part of the maxilla is approximately twice as tall dorsoventrally as the caudalmost part of the tooth-bearing ramus.

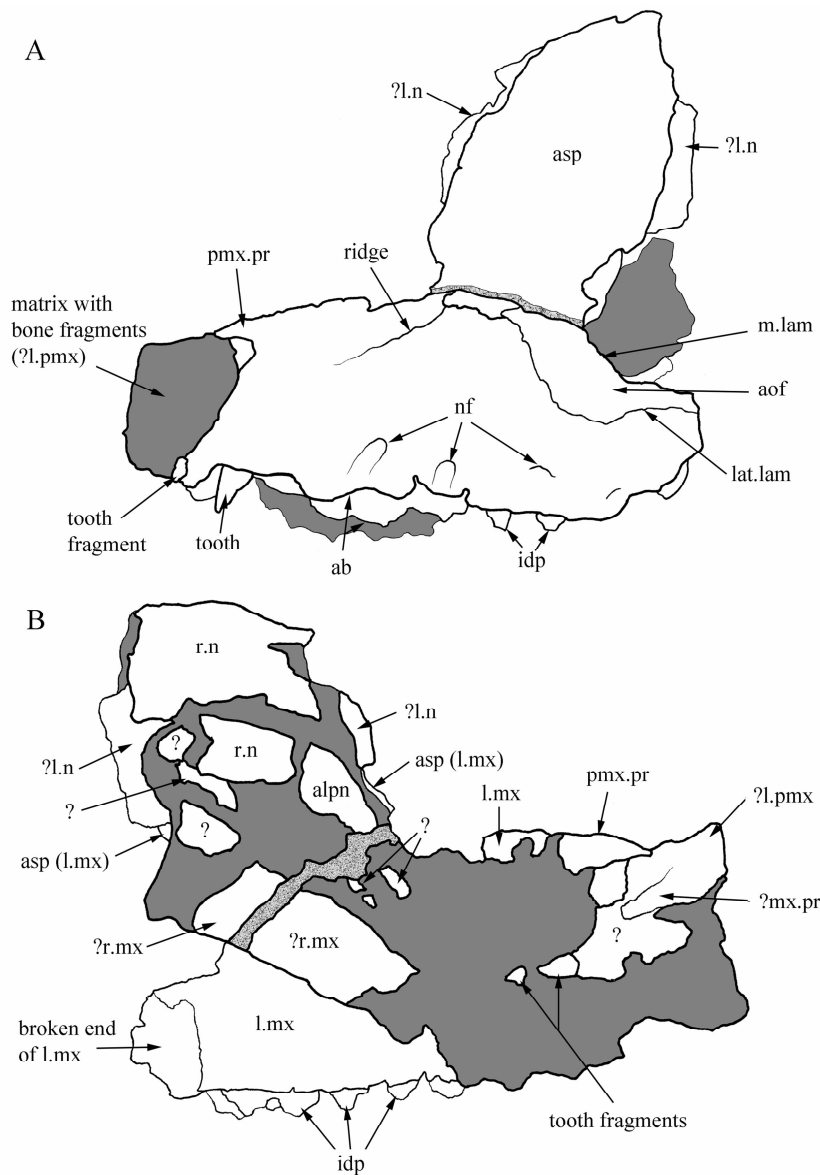


Fig. 2 Interpretative drawings of the holotype specimen of '*Pachysuchus imperfectus*' (IVPP V 40)

A. left lateral view; B. right lateral view

Abbreviations; ab. alveolar borders 齿缘; alp.n. anterolateral process of nasal 鼻骨外前支; aof. antorbital fossa 眶前窝; asp. ascending process 上升支; idp. interdental plates 齿间板; l. left 左侧; lam. lamina 板状结构; lat. lateral 外侧; m. medial 内侧; mx. maxilla 上颌骨; n. nasal 鼻骨; nf. nutrient foramen 滋养孔; pmx. premaxilla 前上颌骨; pr. process 分支; r. right 右侧; '?' signifies an indeterminate bone fragment; even grey fill indicates matrix; stippled grey fill indicates plaster

Its anterodorsomedial corner possesses a short, rostrally tapering premaxillary process, which curves slightly ventrally as it extends rostrally and which has a dorsoventrally convex lateral surface. The area immediately caudal to the process is badly preserved and cracked, due to pre-burial taphonomic processes. Rostrally, the surface caudal to the ascending process appears to

have been gently concave and probably received the maxillary process of the premaxilla. This concave area is bounded posteriorly by a low ridge, which arises on the lateral surface of the maxilla and rises obliquely to merge with the rostral margin of the ascending process. The remainder of the lateral surface of the maxilla is flat to very gently concave rostrocaudally. A shallow antorbital fossa is present and is backed by a medial lamina. This lamina is broken dorsally, so its full extent cannot be determined. The fossa excavates the caudal margin of the ascending process and is bordered laterally by a short lateral lamina, which is continuous with the caudal margin of the ascending process dorsally, and extends caudally along the tooth-bearing ramus to form the ventral rim of the antorbital fossa; it cannot be determined if the lateral lamina continued as a sheet in this area due to breakage. Four neurovascular foramina pierce the lateral surface of the tooth-bearing ramus; each of these is situated at the apex of a shallow, rostrally extending groove. In dorsal view, the broken base of the ascending process has a sub-triangular cross-section. The ascending process is covered with a thin veneer of matrix, which obscures its true margins, but it appears to have been a tall, almost vertically oriented (though this may have been affected by deformation) and mediolaterally compressed sheet of bone. In medial view, the alveoli are separated by sub-rhomboidal interdental plates, which define a corresponding row of special foramina, whose ventral margins are missing due to breakage. It appears that the rostral part of the maxilla was expanded medially to meet its counterpart on the midline, though this is difficult to confirm due to the poor preservation of the specimen.

The right nasal (interpreted as part of a premaxilla by Young [1951, fig. 5]) has been extensively cracked and is missing its caudal part, but most of the rostral section, including the anterolateral process and at least part of the anteromedial process, is present (Figs. 1B and 2B). In anterior or posterior view, the nasal is strongly arched mediolaterally, a feature accentuated by crushing. The lateral surface is strongly concave dorsoventrally and weakly concave anteroposteriorly. A short rostromedially extending spur close to the midline might represent the base of the anteromedial process, while a long, tapering triangular structure probably represents the anterolateral process, which would have contacted the maxilla. A thin plate of bone that is closely appressed to, and largely obscured by, the left maxillary ascending process might represent the left nasal.

Several bone fragments visible on the right hand side of the specimen might represent parts of the right maxilla or premaxilla, but they cannot be identified with confidence due to poor preservation (Figs. 1B and 2B). Contrary to Young's description (1951, fig. 5) there is no evidence for a septomaxilla; this area is the anteromedial part of the right nasal.

Only the tip of the unerupted tooth in left maxillary tooth position one can be seen. The lingual surface appears to be flat, lacking a concavity and ridge, while grooves cannot be seen labially. No denticles are present and the crown tip is very slightly recurved. The enamel has a roughened, granular, almost wrinkled texture (this same texture can also be seen on three other tooth fragments adhered to the specimen). The crown base and root are not visible.

2 Comparisons

Although the specimen does bear a superficial similarity to a broken phytosaur rostrum, many details of the anatomy indicate that *Pachysuchus imperfectus* is not referable to this clade. IVPP V 40 possesses many features that are not present in phytosaurs (e. g. Westphal, 1976; Hungerbühler, 2002; Stocker, 2010), including: a distinct anterodorsomedially positioned premaxillary process on the anterior ramus of the maxilla; interdental plates; a series of large nutrient foramina set within deep sulci on the lateral surface of the maxilla; medial and lateral laminae forming the walls of the antorbital fossa; and labiolingually compressed tooth crowns with a granular enamel coating. Although nutrient foramina are also present on the lateral sur-

faces of the premaxillae and maxillae in phytosaurs, in these taxa these foramina are numerous, narrow, anteroposteriorly elongate slits that are not recessed within deep sulci (e. g. Westphal, 1976; Hungerbühler, 2002; Stocker, 2010), whereas in *P. imperfectus* the foramina are large, limited in number and set at the apices of distinct excavations within the bone surface. Similarly, some phytosaur teeth also exhibit labiolingual compression of posteriorly positioned tooth crowns, but this is not developed to the same extent as in V 40; in addition, the enamel of phytosaur teeth is smooth, not granular (PMB, pers obs). Finally, some phytosaur skulls possess extensive ornamentation on the lateral surfaces of the tooth-bearing bones (e. g. Westphal, 1976), but this is absent in V 40.

All of the above-mentioned features are, however, present in sauropodomorph dinosaurs (e. g. Galton and Upchurch, 2004; Upchurch et al., 2004). Sauropodomorphs are the most abundant tetrapods in the Lower Lufeng fauna (Young, 1951) and it seems likely that *Pachysuchus imperfectus* is simply a poorly preserved example of this group (Fig. 3). Among early sauropodomorphs, IVPP V 40 does not bear any unique features or a unique character combination. However, as far as can be determined on the basis of the fragmentary material available, it cannot be referred to the Lower Lufeng sauropodomorph taxa *Jingshanosaurus xinwaensis* Zhang & Yang, 1994, *Lufengosaurus huenei* Young, 1941a, *Xixiposaurus suni* Sekiya, 2010, *Yunnanosaurus huangi* Young, 1942 or *Y. robustus* Young, 1951. *L. huenei* and *Y. robustus* each have diagnostic maxillary characters that are absent in V 40 (Barrett et al., 2005, 2007) and all of these taxa possess combinations of maxillary and dental characters that do not allow referral of V 40 to any of these species (Zhang and Yang, 1994; Barrett et al., 2005, 2007; Sekiya, 2010). Nevertheless, given the poor preservation of V 40, it is possible that some or all of these features have been altered taphonomically. The presence of granular tooth enamel suggests that *P. imperfectus* may represent a taxon close to the origin of sauropods (Yates, 2004; Upchurch et al., 2007). An isolated maxilla from the Lower Lufeng Formation representing a primitive sauropod (Barrett, 1999), bears many similarities to V 40 and it is possible

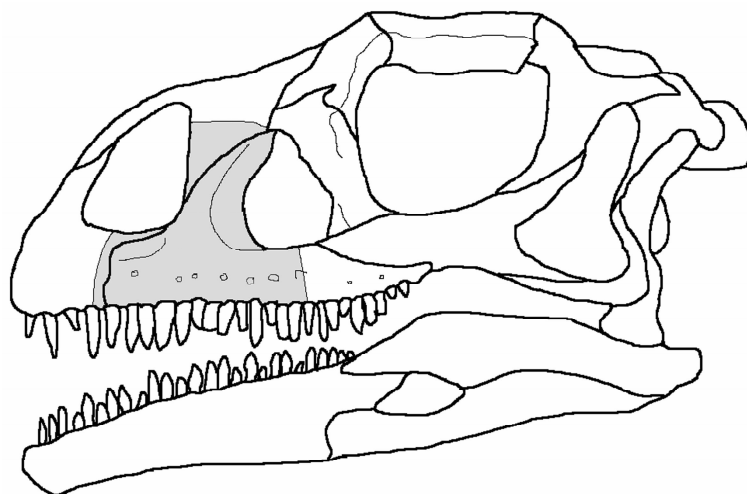


Fig. 3 Outline drawing of the skull of the basal sauropodomorph dinosaur *Massospondylus carinatus* from the Lower Jurassic of southern Africa

Based on Bernard Price Institute for Palaeontological Research (BPI) specimen BPI/1/4934, right side of skull, reversed; shaded area represents the anatomical region represented by the skull fragment of *Pachysuchus imperfectus*

that both of these specimens pertain to the same unnamed taxon. Nevertheless, several other sauropodomorph taxa from the Lower Lufeng Formation require revision and additional description ('*Gyposaurus sinensis*' Young, 1941b, '*Lufengosaurus magnus*' Young, 1947 and '*Yunnanosaurus robustus*' Young, 1951) and it is possible that future study might ally *P. imperfectus* with one of these taxa. However, for the time being we regard the holotype specimen of '*P. imperfectus*' as taxonomically indeterminate, representing the remains of a fragmentary sauropodomorph dinosaur.

Three other specimens were referred to '*P. imperfectus*' by Young (1951, fig. 5. 2-2A and 5.3): a partial basicranium (IVPP V 87a) and two teeth (V 56a and V 87b). Unfortunately, none of these specimens could be located in a search of the IVPP collections and they are presumed to be lost. The following discussion is based solely on the information and figures provided in Young (1951). None of these specimens was associated with the holotype specimen. The basicranium was found in association with a specimen of '*Microchampsia scutata*' (a small ? protosuchian archosaur of uncertain validity and relationships; Wu and Sun, 2008) and five indeterminate vertebrae; it was referred to '*P. imperfectus*' largely by default, as Young (1951) ruled out referral to a saurischian. The figures and description of the specimen suggest that the basicranium could be referred to a large number of archosaur clades, including sauropodomorphs (contra Young, 1951) and this specimen is regarded as indeterminate herein, belonging to an archosaur of uncertain affinities. One of the teeth (V 56a) was previously referred to '*Lufengosaurus magnus*' (Young, 1947:43 and fig. 12; listed as part of V 56) and moved from '*L. magnus*' to '*P. imperfectus*' on the basis of its size, which was deemed too large to allow referral to the former taxon. IVPP V 87b was also referred to '*P. imperfectus*' on the basis of size and its circular cross-section. However, size alone is clearly an inadequate criterion to support this referral, and Lufeng sauropodomorphs occupied a wide range of body sizes that could certainly have encompassed that of the animal represented by these teeth. Moreover, both referred teeth are fragments preserving no features of systematic value. Their sub-circular cross-sections could simply reflect the fact that they may represent the basal part of the tooth crown or root, rather than supporting referral to any particular clade. There are no compelling reasons to refer either of the teeth to Phytosauria. As a result, there is currently no evidence for the presence of a phytosaur in the Lower Lufeng Formation fauna.

3 Discussion

Reports of Early Jurassic phytosaurs are rare and controversial, and re-evaluation of '*Pachysuchus imperfectus*' removes the only post-Triassic record of this clade from Asia. All remaining claims of Jurassic phytosaurs are based on fragmentary material (teeth and partial mandibles) from Europe (Huene and Mauberge, 1954; Buffetaut et al., 1991; Buffetaut, 1993; Maisch and Kapitzke, 2010). Establishing the presence or absence of this clade in the Jurassic is of some significance as it is generally believed that all phytosaurs became extinct at, or just prior to, the Tr/J boundary (e. g. Padian, 1989). Therefore, the confirmed presence of phytosaurs in post-Triassic deposits would potentially alter the known pattern of extinction dynamics across this important interval.

Huene and Mauberge (1954) described several teeth from the Hettangian of Hettange-Grande, France as a possible phytosaur. This identification was given tentative support by Buffetaut (1993), who ruled out theropod dinosaurs as the source of the teeth. However, the teeth are similar to those of the marine crocodylian *Dakosaurus* (P Havlik, pers comm, 2011). Similar comments apply to other teeth from the same locality and horizon, originally described as '*Megalosaurus terquemi*', which were considered as a possible phytosaur by Buffetaut et al. (1991). Another possibility, mentioned by Buffetaut (1993), is that if these teeth do pertain

to phytosaurs, they may have been reworked, rather than representing genuine post-Triassic survivors. Nevertheless, given the general similarities between the teeth of many crurotarsan archosaurs from disparate clades, caution should be exercised when using isolated teeth as evidence for major lineage extensions.

The only other proposed post-Triassic phytosaur is a mandibular fragment from Watchet, England (Maisch and Kapitzke, 2010). The specimen was collected from the ‘pre-*Planorbis* beds’ of the Lias Group and plausibly represents a phytosaur symphysis. However, although Maisch and Kapitzke (2010) interpreted this horizon as earliest Hettangian in age, they stated that the specimen was collected in situ from a shale layer below the base of the *Psiloceras planorbis* Zone. As the first occurrence of the ammonite *Psiloceras* marks the base of the Jurassic system in the UK (e. g. Cope, 2006), this specimen must, by definition, pertain to the latest Triassic section of the Lias Group. Consequently, it provides no evidence for the post-Triassic survivorship of phytosaurs.

4 Conclusions

The holotype of ‘*Pachysuchus imperfectus*’ is reinterpreted as the poorly-preserved snout of a sauropodomorph (? basal sauropod) dinosaur and specimens referred to this taxon are shown to be taxonomically indeterminate. This removes the only post-Triassic record of phytosaurs from Asia. Phytosaur records from the earliest Jurassic of Europe are either ambiguous or erroneous and there is no convincing evidence to support the survival of the clade beyond the Triassic, suggesting that phytosaur remains might have biostratigraphical utility for dating Late Triassic deposits.

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