The first Triassic vertebrate fossils from Myanmar: Pachypleurosaurs in a marine limestone

KHAING KHAING SAN, NICHOLAS C. FRASER, DAVIDE FOFFA, OLIVIER RIEPPEL, and STEPHEN L. BRUSATTE

As ecosystems recovered from the end-Permian extinction, many new animal groups proliferated in the ensuing Triassic. Among these were the sauropthyrgians, reptiles that evolved from terrestrial ancestors and transitioned to a marine environment. The first sauropthyrgians were small, marine-adapted taxa such as pachypleurosaurs, which are known from Middle–Late Triassic deposits, particularly in the Tethyan realm of Europe, and more recently from Lagerstätten in southwestern China. Here we report two pachypleurosaurs from Myanmar, the first Triassic vertebrate fossils from the country. These specimens demonstrate that their entombing rocks in northern Shan State, which have received less study than terrestrial sediments in southern Shan State and whose ages have long been uncertain, are Triassic. The specimens may be among the oldest pachypleurosaurs globally, potentially corroborating biogeographic scenarios that posit an eastern Tethyan origin for pachypleurosaurs, and raise the potential for future discoveries of well-preserved Triassic reptiles in Myanmar.

Institutional abbreviations.—CMLV, Cultural Museum, Lashio, Myanmar; YDBGLV, Geology Museum, Yadanabon University, Myanmar.

Geological and geographical setting

Myanmar is divided into four tectonic provinces. From east to west, these are the (i) Shan-Tanintharyi Block; (ii) Central Cenozoic Belt; (iii) Western Fold Belt; and (iv) Rakhine Coastal Belt (Chhibber 1934; Win Sve 1972; Maung Thein 1973). The pachypleurosaur fossils were collected immediately west of the town of Lashio, in northern Shan State, Myanmar (Fig. 1). They were found in rocks of the Lashio Basin, in the northern part of the Shan Massif, which is part of the Shan-Tanintharyi Block. The Lashio area is composed mainly of sedimentary rocks that date from the Middle Devonian to the Jurassic.

Both specimens were found in a ferruginous, micritic limestone, associated with indeterminate fish bones and scales. The limestone crops out in a mountain range, locally called the Yeawhaung Kyauk-taung (UTM map 2297-9; 22°56′04″ N, 97°42′24″ E). The fossil-bearing limestone is sandwiched between thin- to medium-bedded, light to dark grey, hard and compact limestone and red to purple, uniformly thin-bedded, siltstone and mudstone. Dark grey chert stringers or nodules are intercalated within the fossil-bearing limestone, and minor amounts of ore (lead-zinc) mineralization can be observed in some parts of the bed. This limestone unit apparently grades into the surrounding dolomites.

The fossil-bearing limestone was previously mapped as belonging to the Nwabangyi Dolomite Formation (Garson et al. 1976), considered Late Permian to Middle Triassic in age based on the occurrence of the foraminiferan Glomospirella irregularis in the Kyaukme-Longtawkno area of northern Shan State (Brönnimann et al. 1975). This limestone has been correlated with the Thigaungtaung Limestone (Early–Middle Triassic, Induan–Anisian) of southern Shan State (Brönnimann et al. 1975; Whittaker in Brönnimann et al. 1975; see also the recent review of the “Plateau Limestone” of southern Shan State by Win et al. 2015). Furthermore, Sahni (1936) compiled other records of lower-most Triassic units (Scythian, Induan–Olenekian) at Namhkam (north of Lashio and west of Hsenwi), to which he gave the informal name of the “Na-hkan Beds”. The detailed stratigraphy, correlations, and ages of these various units are in need of revision. Vertebrate fossils may help better constrain their ages (see below).

Description

Pachypleurosaur morphology is best known from complete specimens of Anarosaurus and Dactylosaurus from the lower Muschelkalk (lower Anisian) of the Germanic basin (Sues and Carroll 1985; Rieppel and Lin 1995; Klein 2009, 2012), the late Anisian Serpianosaurus mirigiolensis from the southern Alps (Rieppel 1989), the early and middle Ladinian Neusticosaurus (three species) again from the southern Alps (Carroll and Gaskill 1985; Sander 1989), and the Ladinian (possibly early Carnian) Keichousaurus from southwestern China (Lin and Rieppel 1998; Cheng et al. 2009; Cheng et al. 2004; Holmes et al. 2008). Dianopachysaurus dingi is another well-preserved pachypleurosaur from the Anisian of southwestern China, which has played an important role in pachypleurosaur phylogeny reconstruction (Liu et al. 2011). In this section, we compare the Myanmar specimens to these taxa, especially Keichousaurus and Dianopachysaurus given the geographical proximity of their occurrences (see also Rieppel 2000).
pleurosaurs. Also characteristic of pachypleurosaurs is the homodont dentition comprising numerous small, peg-like teeth. The snout is not constricted and the orbits are large compared to the postorbital region of the skull, as in other pachypleurosaurs. As in Anarosaurus, Dactylosaurus, and Keichousaurus, the cheek is deeply embayed. There are no clear supratemporal fenestrae, and it appears they have been very much reduced. Possible fragmentary traces of these openings occur in the posterolateral corners of the parietal table, but there are no clear margins, and they could even be completely absent. Scleral ossicles appear to be absent in the better-preserved right orbit; these are variably present in other pachypleurosaurs. The pineal foramen is located in the centre of the parietal skull table, as is typical for pachypleurosaurs.

In the axial skeleton CMLV_1 exhibits the individual cervical vertebrae more clearly than YDBGLV_4, but unfortunately the series runs along the edge of the block and only traces of each of the anterior cervicals remain. In YDBGLV_4 the outline of the neck is more intact but there is a significant gap between the posterior margin (occiput) of the skull and the mid cervical series, which renders it difficult to obtain more than an approximate cervical count. Moreover, in both specimens it is difficult to demarcate the cervical series from the first dorsal vertebra, but we consider there to be at least 20 cervical vertebrae, and perhaps as many as 24. These numbers are within the range of variation known in other pachypleurosaurs, although tending towards the higher end (e.g., 25–26 Keichousaurus; 20 Dianopachysaurus; 17 Dactylosaurus; 15–18 Serpianosaurus; 17 Neusticosaurus edwardsii; 18–20 Neusticosaurus pusillus; Carroll and Gaskill 1985; Rieppel and Lin 1995; Sues and Carroll 1985; Sander 1989; Lin and Rieppel 1998; Liu et al. 2011).

There are at least 16 left dorsal ribs. This would correspond to an unusually low number of dorsal vertebrae for a pachypleurosaur, although not too dissimilar to Keichousaurus (18–19) and Dianopachysaurus (19). Other members of the group have more dorsal vertebrae, with, for example, 22–24 in

Table 1. Key measurements (in mm) of unidentified pachypleurosaurs from Myanmar (after Sander 1989). Standard length is defined as the length of the four posterior dorsal centra; na, not available (as the specimen is incomplete).

<table>
<thead>
<tr>
<th></th>
<th>CMLV_1</th>
<th>YDBGLV_4</th>
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<tbody>
<tr>
<td>skull</td>
<td>51</td>
<td>50</td>
</tr>
<tr>
<td>neck length</td>
<td>151</td>
<td>127</td>
</tr>
<tr>
<td>neck length</td>
<td>165</td>
<td>112</td>
</tr>
<tr>
<td>standard length</td>
<td>na</td>
<td>27</td>
</tr>
<tr>
<td>incomplete tail</td>
<td>na</td>
<td>42</td>
</tr>
<tr>
<td>humerus</td>
<td>46</td>
<td>37</td>
</tr>
<tr>
<td>radius</td>
<td>2.7</td>
<td>22</td>
</tr>
<tr>
<td>ulna</td>
<td>29</td>
<td>23</td>
</tr>
<tr>
<td>femur</td>
<td>na</td>
<td>38</td>
</tr>
<tr>
<td>fibula</td>
<td>na</td>
<td>22</td>
</tr>
<tr>
<td>tibia</td>
<td>na</td>
<td>23</td>
</tr>
<tr>
<td>snout-vent length</td>
<td>–</td>
<td>315</td>
</tr>
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Neusticosaurus pusillus and as many as 25–26 in Anarosaurus (Sander 1989; Rieppel and Lin 1995; Lin and Rieppel 1998). It is possible that two vertebrae in the cervical/dorsal transitional zone are not cervicals but dorsals, meaning that there would be approximately 22 cervicals and approximately 18 dorsals in YDBGLV_4. There are three sacral vertebrae, as in other pachypleurosaurs except for Keichousaurus, which has 2 or 3 (Lin and Rieppel 1998). The neural arches of the dorsal vertebrae are compressed, and apparently pachyostotic. Pachyostosis is conspicuously absent, however, in the dorsal ribs. The delicate gastralia are numerous in number, and there are at least two per vertebral segment in the posterior trunk region.

In the appendicular skeleton, the coracoid is elongate, plate-like, and biconcave, as is standard for pachypleurosaurs. The scapula is difficult to discern in detail, but appears unremarkable for a pachypleurosaur, and the interclavicle is indistinct. The most salient feature of the appendicular skeleton is the distinctly and evenly curved humerus, as in CMLV_1. This differs from other (mature) pachypleurosaurs, but is a feature the Myanmar pachypleurosaur shares with Dianopachysaurus (Liu et al. 2011). The entepicondylar foramen seems to be absent, an unusual character state otherwise known only in Keichousaurus amongst pachypleurosaurs. The ulna is distinctly broadened proximally, more so than in most other pachypleurosaurs, but not overall as broad as in
Keichousaurus. The number and morphology of the carpal ossifications and phalanges in the manus are difficult to observe. The pelvis is also difficult to describe, but the femur is slender, weakly sigmoidally curved, and longer than the humerus. This latter feature is again shared with Dianopachysaurus (Liu et al. 2011), and also with Anarosaurus, where the femur length exceeds humerus length to an even greater degree (Rieppel and Lin 1995; Klein 2012). In other pachypleurosaurs known from a larger number of specimens (Neusticosaurus, Serpianosaurus, Carroll and Gaskill 1985; Rieppel 1989; Sander 1989), the ratio of humerus to femur length is subject to ontogenetic variation as well as sexual dimorphism (Rieppel 1993: fig. 8). The metatarsals of the right foot are well preserved; the first metatarsal is much shorter than the others, as is standard for pachypleurosaurs.

Concluding remarks
The two new specimens from Myanmar, CMLV_1 and YDBGLV_4, can both be assigned to Pachypleurosauria because they possess several diagnostic features of the clade, including: preorbital region of the skull longer or subequal in length to postorbital region; upper temporal fenestra much smaller than the orbit; pre- and postzygapophyses pachyostotic; sacral ribs not expanded distally. The two specimens most likely belong to the same lower-level taxon, due to their shared presence of an evenly and distinctly curved humerus, which is unknown in other pachypleurosaurs except Dianopachysaurus (Liu et al. 2011), and apparently similar cervical and dorsal vertebral numbers. Obliteration of the upper temporal fenestrae would be an important autapomorphy of a new taxon, but the
specimens are too poorly preserved to allow an unequivocal as-
ssessment of this trait. We also are unable to confidently include
the Myanmar specimens in a phylogenetic analysis at this time,
as we feel we do not yet have enough morphological informa-
tion from the limited fossils to render such an analysis informa-
tive. Preferring a phylogenetic approach to species delimitation,
we therefore refrain from diagnosing a new species, due to
the incompleteness of the specimens and the potential for finding
new fossils with additional fieldwork. There has recently been a
flourishing of phylogenetic studies of basal eosauropterygian
relationships, some of which have questioned the monophyly of
Pachypleurosauria and other traditional clades (e.g., Rieppel et
al. 2002; Holmes et al. 2008; Liu et al. 2011; Shang et al. 2011,
Shang and Li 2015; Cheng et al. 2016). Addressing this debate
is outside the scope of this paper, but additional material of the
Myanmar pachypleurosaur, analysed in a phylogenetic context,
may contribute important new insights in the future.

The presence of pachypleurosaurians in Myanmar is impor-
tant for several reasons. First, these reptiles are known only
from the Triassic, so they are a key piece of evidence that the
Nwabangyi Dolomite Formation and coeval rocks in northern
Shan State, whose ages have long been the subject of uncer-
tainty, are Triassic in age. Second, there is a possibility that the
Myanmar specimens may be among the oldest pachypleu-
rosaurians in the world, which might give insight into the origins
of the group and potentially help untangle the thorny phylo-
genetic relationships of basal eosauropterygians. The current
oldest unequivocal pachypleurosaurians are Anisan (Liu et al.
2011), but if the Nwabangyi Dolomite Formation is indeed cor-
related with the Thigunthaung Limestone of southern Shan
State, then it is possible that the Myanmar taxon is anywhere
from Induan to Anisan in age. Third, if the Myanmar taxon is
among the oldest pachypleurosaurians, it might corroborate the
often-discussed hypothesis of an eastern Tethyan origin for the
group (e.g., Rieppel 1999, 2000; Rieppel and Hagdorn 1997),
or alternatively, pending its inclusion in a phylogenetic analy-
sis, hint that the fossil record is currently too poor to strongly
support any biogeographic scenario.

Finally, the discovery of articulated reptilian material in the
Triassic of Myanmar, although currently limited to these two
specimens, suggests that fine preservation of aquatic and near-
shore reptiles may be common in particular units, but has gone
unrecognized due to limited collecting. The fossil-bearing
Burmesic rocks are not particularly far geographically from the
Lagerstätten (conservation deposits) of Guizhou and Yunnan
in southwestern China, which over the past two decades have
yielded a wealth of spectacularly preserved Triassic reptiles
(e.g., Wang et al. 2008; Zhang et al. 2008). There may be po-
tential for similar Lagerstätten in Myanmar.

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