

# A new species of *Macrocnemus* (Reptilia: Protorosauria) from the Middle Triassic of southwestern China and its palaeogeographical implication

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**A new species of the terrestrial protosaur *Macrocnemus* is briefly described and named *Macrocnemus fuyuanensis* sp. nov. The specimen was found from the marine Triassic of Yunnan Province, southwestern China. It differs from the type species *M. bassanii* in having the following characters: (1) 17 or 18 dorsal vertebrae; (2) relatively long humerus; and (3) femur longer than tibia. *M. fuyuanensis* is the only record of the genus outside Monte San Giorgio area and the first definite terrestrial reptile found from the marine Triassic of China. The age of the fossil-bearing Zhuganpo Member of the Falang Formation is believed to be the Ladinian based on associated vertebrate fauna. The existence of *Macrocnemus* in the limestone suggests the presence of a terrestrial ecosystem which probably originated from the Anisian and well developed in the Ladinian in this region. The island system along the north-coast of Tethyan during the Triassic was probably an important route for the exchanges of reptiles, especially the terrestrial reptiles between the west and east.**

Protorosauria, Middle Triassic, Ladinian, Yunnan, terrestrial reptile

The Middle Triassic Zhuganpo Member of the Falang Formation in Yunnan and Guizhou provinces, southwestern China has yielded abundant vertebrate fossils, including fishes and marine reptiles<sup>[1-7]</sup>. This fossil vertebrate fauna, which is generally called “Xingyi Fauna” according to the biggest city of the region, shows a clear affinity to the Monte San Giorgio Fauna, where the terrestrial reptile fossils such as *Ticinosuchus*<sup>[8]</sup> and *Macrocnemus*<sup>[9]</sup> were found in marine deposits. The Monte San Giorgio basin was bordered by reef structures during the deposition of the Middle Triassic<sup>[10]</sup>, but so far no such information has been known from the Xingyi Fauna. Since 2005, several terrestrial reptile fossils, mainly the protosaurids, were excavated from the limestone Zhuganpo Member of Fuyuan, Yunnan Province. Most of the specimens are complete and articulated skeletons, suggesting a terrestrial environment nearby. Besides the new material described here, two marine

protosaurid genera have been reported from China, they are *Dinocephalosaurus*<sup>[11,12]</sup> and *Tanystropheus*<sup>[7]</sup>. *Prolacertoides jimusarensis*<sup>[13]</sup> is known from the terrestrial deposits of early Triassic in Xinjiang, northwestern China, but its phylogenetic position is still in debate.

## 1 Systematic paleontology

Class Reptilia Linnaeus, 1758

Protorosauria Huxley, 1871

Prolacertidae Parrington, 1935

*Macrocnemus* Nopcsa, 1930

*Macrocnemus fuyuanensis* sp. nov.

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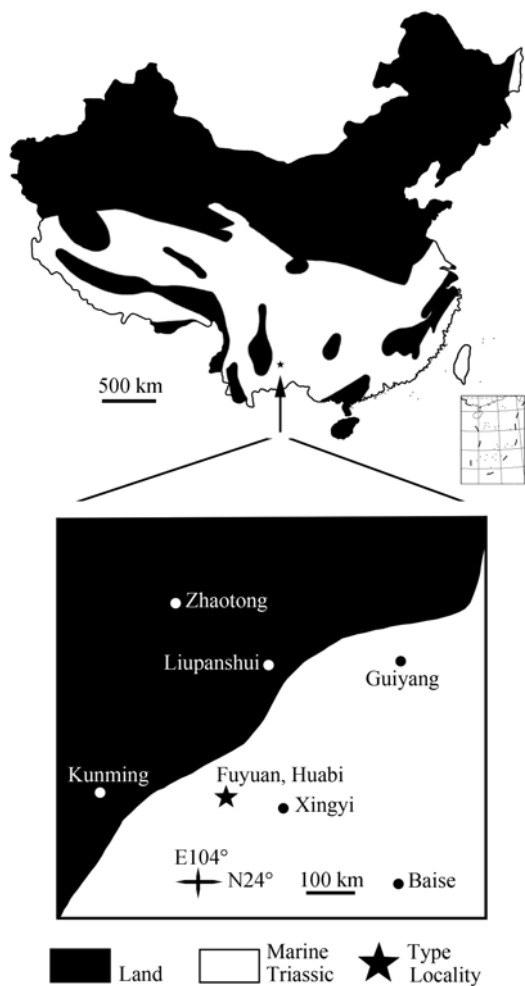
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**Etymology.** The species name refers to the type locality.

**Holotype.** IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences) V15001. A nearly complete skeleton.

**Type locality and horizon.** Huabi of Fuyuan, Yunnan Province, southwestern China. Zhuganpo Member of the Falang Formation. Ladinian, Middle Triassic.

**Diagnosis.** Differs from *M. bassanii* by the characters: (1) tibia shorter than femur; (2) humerus significantly longer than radius (see description and comparison below); and (3) 17 or 18 dorsal vertebrae.



**Figure 1** Type locality of *Macrocnemus fuyuanensis* sp. nov., the Chinese palaeogeographic map is derived from Ma<sup>[14]</sup>.

## 2 Description and comparison

The size of the type species *M. bassanii* varies from 35 to 86 cm<sup>[15]</sup>. Rieppel<sup>[16]</sup> suggested a large size when describing the materials from the Palaeontological Institute

of the University of Zürich, but it is difficult to give the absolute measurement of the animal because none of the known specimens preserved a complete tail. With 4 breaks at the tail region, V15001 has no missing caudal vertebra and the total length is about 116.5 cm.

The skull and the mandible: The skull is broken and exposed in its ventral view. Except the gracile pterygoid with dense tiny teeth, no other bone can be identified clearly. The lower jaws are complete and articulated with each other by a short symphysis. The length of the jaw is 9.1 cm and the length of the mandibular fossa is 2.2 cm. The homodont dentition includes 24 chisel-shaped teeth on each side, while the reconstructed number of the teeth in lower jaw would be 45–50 in total.

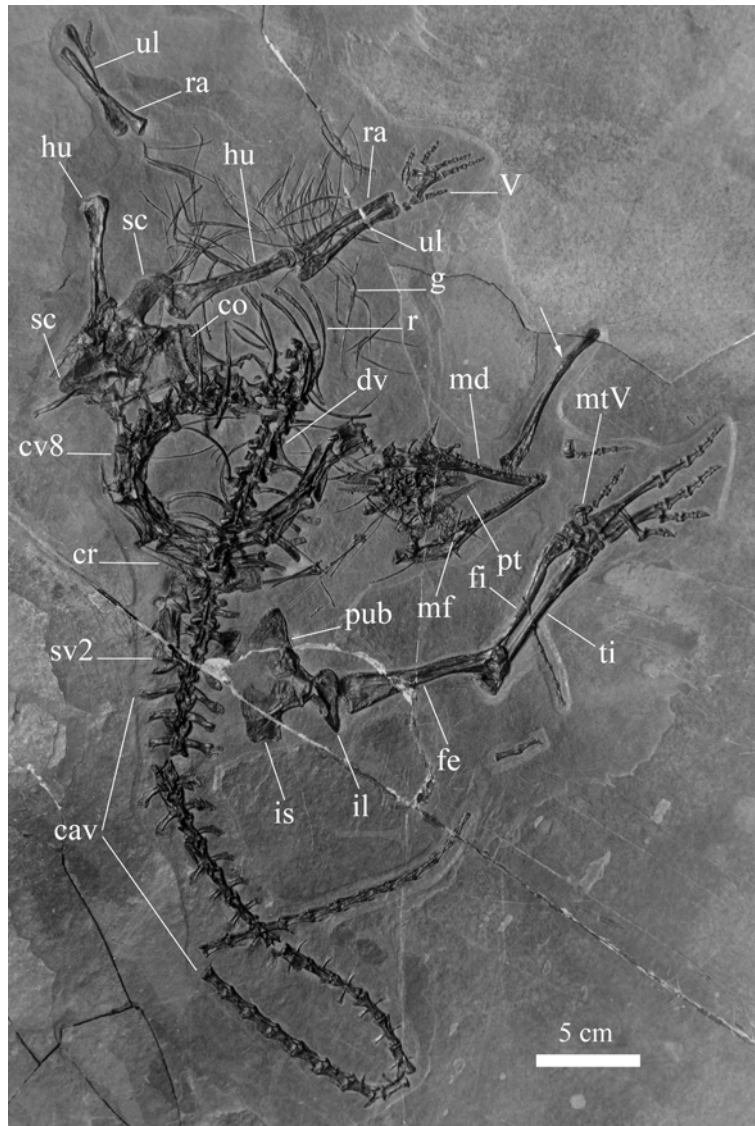
The axial skeleton: The cervical vertebrae of *M. bassanii* were counted from 7 to 9 by different authors<sup>[15–19]</sup>. Besides the atlas which might be missing or hidden below the skull, V15001 bears 7 moderately elongated cervical vertebrae, thus the total number of cervicals should be 8. As in *M. bassanii*, the length of cervical vertebrae (Table 1) increase from front to the middle of the neck (C4 and C5) and decreases thereafter.

**Table 1** Length (mm) of the cervical vertebra (centra) in V15001

	C2	C3	C4	C5	C6	C7	C8
Length	17.03	25.39	30.70	30.18	28.72	27.11	25.18

The double headed cervical ribs are elongated and slender, but not as conspicuous as that of the marine protorosaurs *Dinocephalosaurus* and *Tanystropheus*<sup>[12,17]</sup>. They are more similar to the cervical ribs of marine archosaurs<sup>[20]</sup>. The absolute length of neck ribs is difficult to measure, while their length decreases posteriorly. The rib attached to C8 is even shorter than the centra. Compared with the long-necked marine protorosaurid, the relatively short centra and neck ribs well reflect the terrestrial habit of the animal. Besides, V15001 corroborates the opinion of Rieppel<sup>[16]</sup> that no intercentra exist in the neck of *Macrocnemus*.

Different from *M. bassanii*, *M. fuyuanensis* has 17–18 dorsal vertebrae. The length of the centra decreases slightly from front to back. The length of the first dorsal vertebra is about 2 cm and the last one is shorter than 1.5 cm. The neural spines of the dorsals are very low compared with those of the cervical vertebrae. This is an exception of terrestrial characters observed in other parts of the postcranial skeleton.



**Figure 2** *Macrocnemus fuyuanensis* sp. nov. (IVPP V15001). Abbreviations: cav, caudal vertebrae; co, coracoid; cr, cervical rib; cv, cervical vertebra; dv, dorsal vertebra; fe, femur; fi, fibula; g, gastralia; hu, humerus; il, ilium; is, ischium; md, mandible; mf, mandibular fossa; mtV, fifth metatarsal; pt, pterygoid; pub, pubis; ra, radius; rb, rib; sc, scapula; sv, sacral vertebra; ti, tibia; ul, ulna; the arrow shows the scar in the tibia.

As in *M. bassanii*<sup>[16]</sup>, there are two sacral vertebrae in *M. fuyuanensis*. The pleurapophyses are greatly expanded distally, and the 2nd one is bifurcated. Although poorly preserved, it is clear that the distal ends of the pleurapophyses overlap each other and enclose a foreman between them.

With 4 breaks at the tail region, 44 caudal vertebrae are observed. The anterior ones bear very prominent transverse processes, which gradually decreased in size until the 18th caudal vertebra. The broken scar of the transverse process can be observed from caudals 19 to 24. The tiny chevron bones are observed from caudals 24 to 39.

The appendicular skeleton: Both of the pectoral and the pelvic girdle are similar to *M. bassanii*, including the short “hooked” fifth metatarsal and the phalangeal formula (2-3-4-5-3 for manus, 2-3-4-5-4 for pes). The most obvious difference between them is the relative length of different parts of their limbs (Table 2). Major difference between *M. fuyuanensis* and the specimens from the Palaeontological Institute of the University of Zürich described by Rieppel<sup>[16]</sup> are listed as follows:

- 1 femur longer than humerus by: 23%–32.4% in *M. bassanii*, 25.7% in *M. fuyuanensis*;
- 2 tibia longer than radius by: 42.7%–48.8% in *M. bassanii*, 47.3% in *M. fuyuanensis*;

3 metatarsal IV longer than metacarpal IV by: 134.2% in *M. bassanii*, 159.2% in *M. fuyuanensis* ;

4 humerus longer than radius by: 4.5%–8.5% in *M. bassanii*, 20.5% in *M. fuyuanensis* ;

5 tibia longer than femur by 1.1%–10.9% in *M. bassanii*, while shorter than femur by 2.8% in *M. fuyuanensis*;

6 the ratio of hindlimb to forelimb is 1.48 in *M. bassanii* (T2472), and 1.50 in *M. fuyuanensis*.

Therefore, as a new species, *M. fuyuanensis* differs from *M. bassanii* mainly by the relatively long femur and humerus. Moreover, the pes in *M. fuyuanensis* is more slender than the hand. As a whole, the new species has longer thigh, upper arm and foot.

**Table 2** Length (mm) of limb bones in *M. bassanii* (from Rieppel<sup>[16]</sup>) and *M. fuyuanensis*

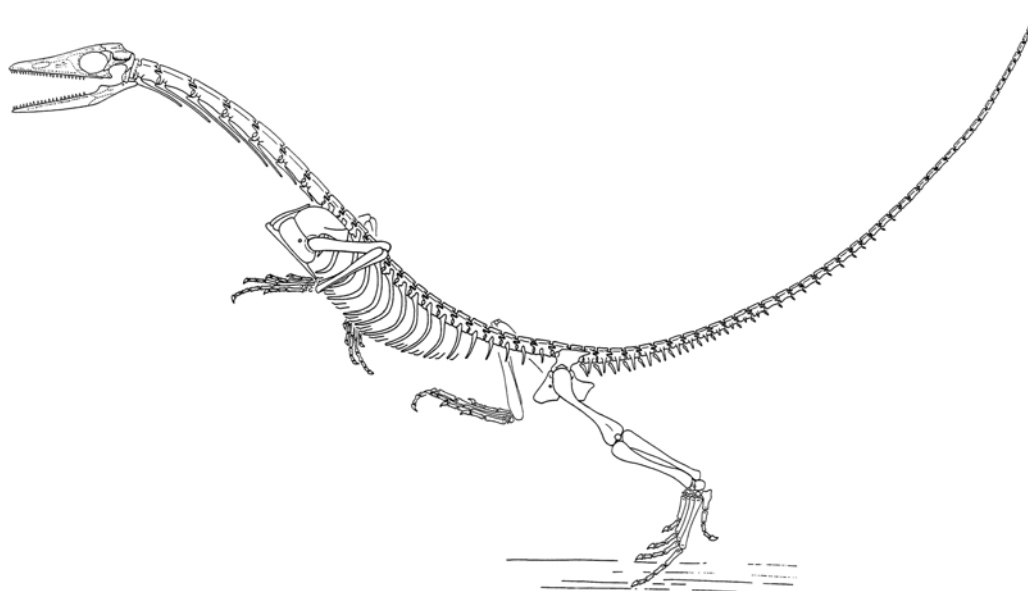
	Humerus	Radius	Mc IV	Femur	Tibia	Mt IV
A III/208				46.8	47.3	24.7
T2473					66.2	28.0
T2477	34.0	32.2		45.0	47.9	24.7
T2816						19.3
T2472	56.2	51.8	15.2	70.4	76.2	35.6
T4355	53.3	51.0		65.6	72.8	32.6
V15001	71.6	59.4	16.9	90.0	87.5	43.8

V15001 is an adult individual with 6 ossified tarsals. It is also the largest specimen among the known materials of *Macrocnemus*. Although difficult to be compared with the type species *M. bassanii* by the incomplete skull, the new material is referred to *Macrocnemus* for

the following characters: 7 cervical vertebrae (excluding the atlas) moderately elongated; the distal end of the 2nd sacral rib bifurcated; the distal ends of the sacral ribs overlap each other and enclose a foreman; hook-shaped 5th metatarsal and the same phalangeal formula as the type species.

### 3 The age of the Zhuganpo Member of the Falang Formation and the Triassic island in southwestern China

Including another two undescribed materials, all known specimens of *M. fuyuanensis* were found from the same locality in Fuyuan of Yunnan Province, southwestern China. They are all preserved together with *Keichousaurus*, which is the typical fossil for the Zhuganpo Member of the Falang Formation. The age of the Zhuganpo Member has been a controversy for years because of the different opinions worked out from the conodont and the vertebrate fossils. Based on the conodonts, Zhuganpo Member was deposited during the Carnian of the Late Triassic<sup>[21–23]</sup>. It is possible that the age of the Zhuganpo Member spans from Ladinian to Carnian<sup>[24]</sup>, but so far all fossil reptiles such as the pachypleurosaurids<sup>[2]</sup>, *Nothosaurus*<sup>[4]</sup>, *Lariosaurus*<sup>[3]</sup>, *Tanystropheus*<sup>[7]</sup>, pistosaurids<sup>[5]</sup>, askeptosaurids<sup>[6]</sup> and *Macrocnemus* from this horizon show strong resemblance to those of the Ladinian in Europe, confirming a close relationship between eastern and western Tethyan fauna provinces during the Middle Triassic.



**Figure 3** Reconstruction of *Macrocnemus* at high speed. Derived from Rieppel<sup>[16]</sup>.

*Macrocnemus* is believed to be a terrestrial protorosaurid. The structure of the pelvis and the hind limb indicates a sprawling gait, and possibly bipedalism during rapid locomotion like some lizards<sup>[16]</sup>. Besides other terrestrial reptiles such as *Ticinosuchus*<sup>[8]</sup> near the type locality of *M. bassanii*, there is independent evidence that the Monte San Giorgio basin was bordered by reef structures during the deposition of the *Grenzbitumen*-horizon, i.e. Anisian-Ladinian boundary<sup>[10]</sup>. The Ladinian Zhuganpo Member of the Falang Formation has yielded a lot of Triassic marine reptiles<sup>[2-7]</sup>, but so far no terrestrial reptile has been reported from this horizon. *Qianosuchus mixtus*, which was found from the Anisian Guanling Formation in adjacent area is a marine archosaurian with both terrestrial and aquatic characters<sup>[20]</sup>, but all other members found there are marine reptiles and fishes. *M. fuyuanensis* is the first definite terrestrial reptile known from the marine deposits of China, and in company with the specimen described here, a lot of other terrestrial reptile fossils have been

found from the same locality. The tectonic history of the South China Block indicates that the type locality of *M. fuyuanensis* was submerged in marine water at the Ladinian, and the nearest land was about 100 km away (Figure 1). In recent years, several kinds of marine reptiles have been found at this locality, including *Keichousaurus*, cyamodontoids, nothosaurids, askeptosaurids and pistosaurids of more than 5 m. The existence of huge marine reptiles suggests a deep water environment, while the abundant terrestrial reptile fossils represented by articulated skeletons with large or small size suggest the presence of terrestrial ecosystem nearby. This terrestrial environment might be made of islands system and existed there from the Anisian to Ladinian. Triassic reptiles, especially terrestrial reptiles would exchange between the west and east through those islands along the north shore of the Tethyan.

*The specimen is prepared by Ding Jinzhao and photographed by Zhang Jie.*

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