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A new species of *Macrocnemus* from the Middle Triassic of the eastern Swiss Alps

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Abstract A new species of *Macrocnemus* is described on the basis of two incomplete specimens from the Lower Ladinian Prosanto Formation of southeastern Switzerland. The new form can be distinguished by its gracile limb elements and having a noticeably longer tibia than either *Macrocnemus bassanii* or *Macrocnemus fuyuanensis*. One of the new specimens exhibits soft part preservation in the region of the pelvic girdle. The hind part of this individual is preserved fully articulated and allows a complete count of the caudal vertebrae to be made for the first time with 52 caudals. It is postulated that this specimen was predated upon and that the anterior part of the animal was consumed by a large predator such as a nothosaurid reptile or the actinopterygian fish *Saurichthys*.

Keywords Protorosaur · Europe · Triassic · Tethys

Institutional abbreviations

PIMUZ	Paläontologisches Institut und Museum, University of Zürich, Zürich, Switzerland
IVPP	Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China
GMPKU	Geological Museum, Peking University, Beijing, China

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1 Introduction

The protorosaur *Macrocnemus* is well known from the Besano Formation (Grenzbitumenzone) of the southern Alps (Monte San Giorgio area in southern Switzerland and northern Italy). It was first described by Nopcsa (1930) as *Macrochemus* on the basis of a rather poorly preserved specimen then held in the Museo Civico di Storia Naturale in Milano. Unfortunately, this specimen was destroyed during World War II. The name *Macrocnemus* was first used by F. Bassani on the original specimen label (Peyer 1937; Nopcsa 1930). Peyer's subsequent excavations in the Besano Formation of Monte San Giorgio resulted in the recovery of much more material and provided the basis of a monographic study of a single species, *Macrocnemus bassanii* (Peyer 1937). The description relied heavily on one particular specimen, PIMUZ T 4822, which was actually recovered from the somewhat younger Cassina beds of the Meride Formation. Shortly after publication of the monograph another beautifully preserved specimen was excavated. This specimen, PIMUZ T 2472, was described by Kuhn-Schnyder (1962), although his description centred only on the skull, which is surprising given the state of completeness of the specimen. Rieppel and Gronowski (1981), Rieppel (1989), and Renesto and Avanzini (2002) added further detail to the original descriptions.

Recently, a second species was described from the Middle Triassic of southern China (Li et al. 2007; Jiang et al. 2011). Despite the great distance between the two regions, it is perhaps surprising that very little distinction can be made between the Chinese and European forms. The Chinese form has been largely diagnosed as a new species on the basis of the

proportions of the forelimb. *Macrocnemus fuyuanensis* from China has a humerus that is distinctly longer than the radius. It is also possible that *M. fuyuanensis* is a little larger than *M. bassanii* and that it possesses one more presacral vertebra (Li et al. 2007), but this remains to be corroborated. Here we describe a third species of *Macrocnemus* on the basis of two specimens from the Prosanto Formation of the eastern Alps in southeastern Switzerland. The new form differs from the other two species of *Macrocnemus* in having a tibia significantly longer than the femur and also in its markedly more gracile hind limb elements.

2 Geology and stratigraphy

The Prosanto Formation of the eastern Swiss Alps comprises a sequence of dark limestones, shales and dolomites ranging from 100 to 200 m in thickness (Fig. 1). It extends for more than 20 km as a lenticular intercalation in shallow water dolomites (overlying the Vallatscha and underlying the Altein Formations) of the strongly deformed sediments of the Austroalpine Silvretta Nappe (Bürgin et al. 1991; Furrer et al. 1992). Systematic excavations in the upper part of the Prosanto Formation at an altitude between 2,600 and 2,800 m near Davos have yielded a rich assemblage of sauropterygian reptiles, fishes, molluscs, crustaceans and terrestrial plant fragments (e.g. Furrer 1995, 2009). These share many similarities with the classic latest Anisian/Early Ladinian beds of the Monte San Giorgio area in the southern Alps (Besano and Meride Formations). Recent U/Pb zircon ages of 240.91 ± 0.26 Ma from a volcanic ash layer in the fossiliferous beds of the Upper Prosanto Formation (Furrer et al. 2008) suggest a good time correlation with the vertebrate horizons in the Lower Meride Formation (Gredleri Zone, Early Ladinian; Mundil et al. 2010; Stockar et al. 2012).

The rich and well-preserved actinopterygian fish fauna suggest a deposition in stagnant abiotic, probably anoxic bottom water conditions of a small intraplatform basin (Furrer 1995). Small plankton feeding, and larger predatory fishes, together with sauropterygian reptiles probably lived in the surface water. Medium sized fish feeding on hard-shelled bivalves, crustaceans, and calcareous algae must have lived at the border of the basin in a shallow water environment. Terrestrial plants, a few insects, and a fragment of a rauisuchian reptile (Grauvogel-Stamm et al. 2003; Furrer 2009; Scheyer and Desojo 2011) were probably washed in by storms. An isolated articulated foot and the articulated rear end of a skeleton represent the remains of another terrestrial tetrapod, *Macrocnemus*, which are described here.

3 Material

PIMUZ A/III 1467 from Ducanfurgga, Davos, Canton Graubünden, Switzerland. It comprises the posterior region of the dorsal vertebral series together with much of both hindlimbs and the tail in complete articulation (Fig. 2). The specimen was discovered in 2009 by Christian Obrist during a bed-by-bed excavation in a fossiliferous level of the Upper Prosanto Formation (bed no. 45, Early Ladinian, Middle Triassic), directed by one of us (HF). When PIMUZ A/III 1467 was first discovered it was on the underside of a large slab and the thin layers containing the fossil had to be painstakingly collected piece by piece and then re-assembled. During this process a section of the left tibia and part of the right ankle and a short section of tail were particularly fragmentary and could not be recovered. At the same time the beds below and above the specimen were carefully split anterior to the sacral region, but no more of the skeleton was found.

PIMUZ A/III 722 from the scree west of the mountain Gletscher Ducan, Davos, Canton Grisons, Switzerland. The articulated right pes exposed in dorsal view and missing phalanges 4 and 5 on digit IV. The specimen was discovered in 1991 by one of us (HF) during systematic fossil collection in the scree of the same fossiliferous level in the Upper Prosanto Formation.

4 Systematic palaeontology

Order Protorosauria Huxley 1871
Genus *Macrocnemus* Nopcsa 1930

Macrocnemus obristi sp. nov. (Figs. 2, 3)

Diagnosis. Species of *Macrocnemus* with gracile limb elements and a tibia and fibula at least 20 % longer than the femur.

Type locality. Ducanfurgga, Davos, Canton Graubünden, Switzerland.

Type level. Prosanto Formation, Early Ladinian, Middle Triassic.

Holotype. PIMUZ A/III 1467 (Figs. 2, 3). PIMUZ A/III 1467 consists of an incomplete and compressed hind section of an articulated skeleton preserved in dorsal view (Fig. 2). The posterior region of the dorsal series is partially preserved along with the sacrum, both hind limbs and most of the tail apart from a short section in the mid anterior region. The distal end of the tail is complete.

Referred specimen. PIMUZ A/III 722 (Fig. 5). PIMUZ A/III 722 comprises a right tarsus exposed in dorsal view.

Etymology. Named for Christian Obrist who discovered, collected and then fully prepared the holotype.

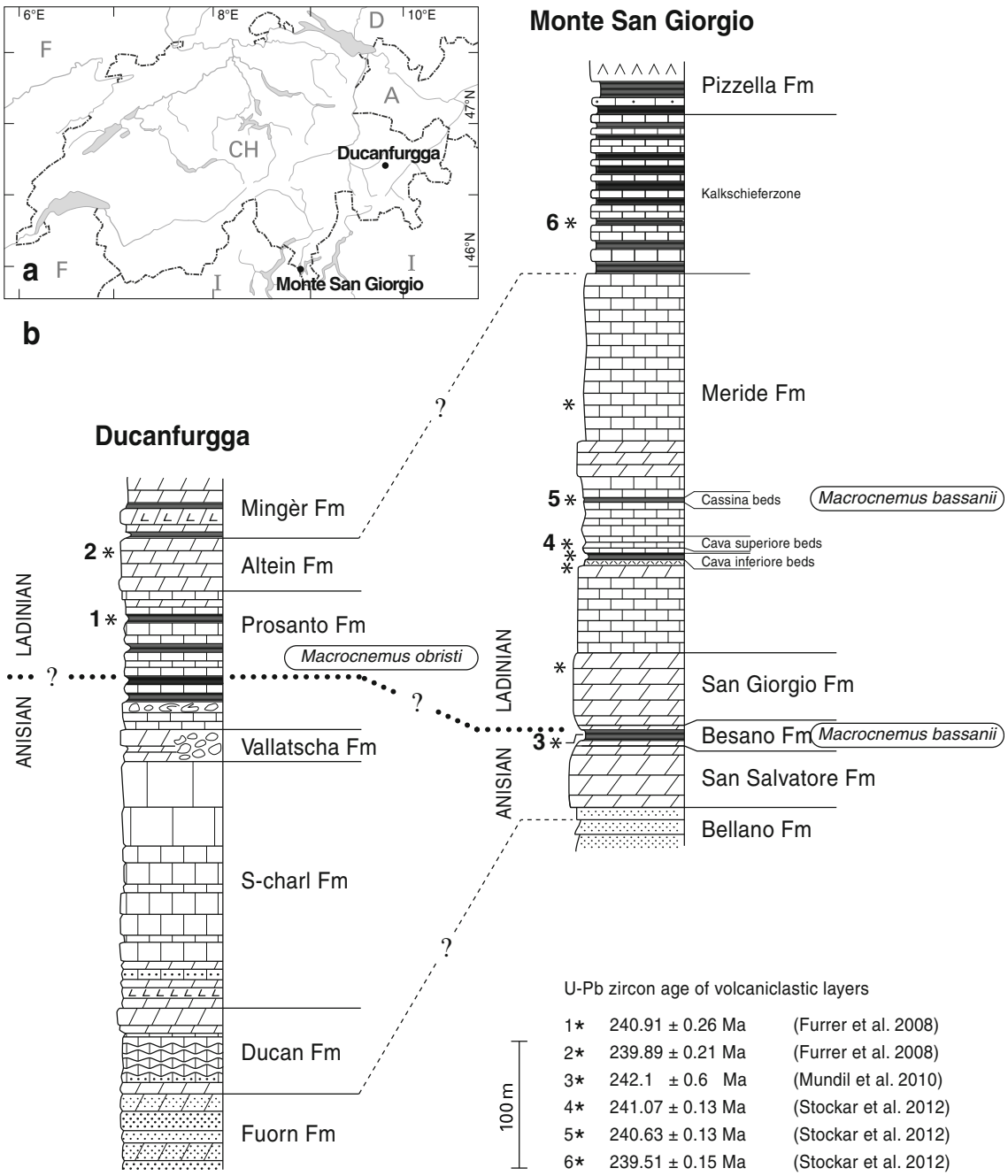

Fig. 1 **a** Locality map showing the Ducanfurgga locality relative to the classical vertebrate site of Monte San Giorgio. **b** Correlation of the Middle Triassic section at Ducanfurgga (Upper Austroalpine Silvretta Nappe, eastern Switzerland) with Monte San Giorgio (southern Alps, southern Switzerland). Note the stratigraphic position of the finds of the *Macrocnemus* species

4.1 PIMUZ A/III 1467

4.1.1 Dorsal vertebrae series

The fragmentary remains of nine dorsal vertebrae are preserved. The first comprises only the posterior end of the centrum and the posteriormost part of the neural spine. The next preserved dorsal is the most complete with a centrum 7.3 mm long. At the mid-point, measured to the dorsal most edge of the elongate neural spine, it has a height of 8.1 mm. Very little more of the dorsal series is preserved, but judging from what remains of the neural spines the subsequent dorsal vertebrae were progressively shorter.

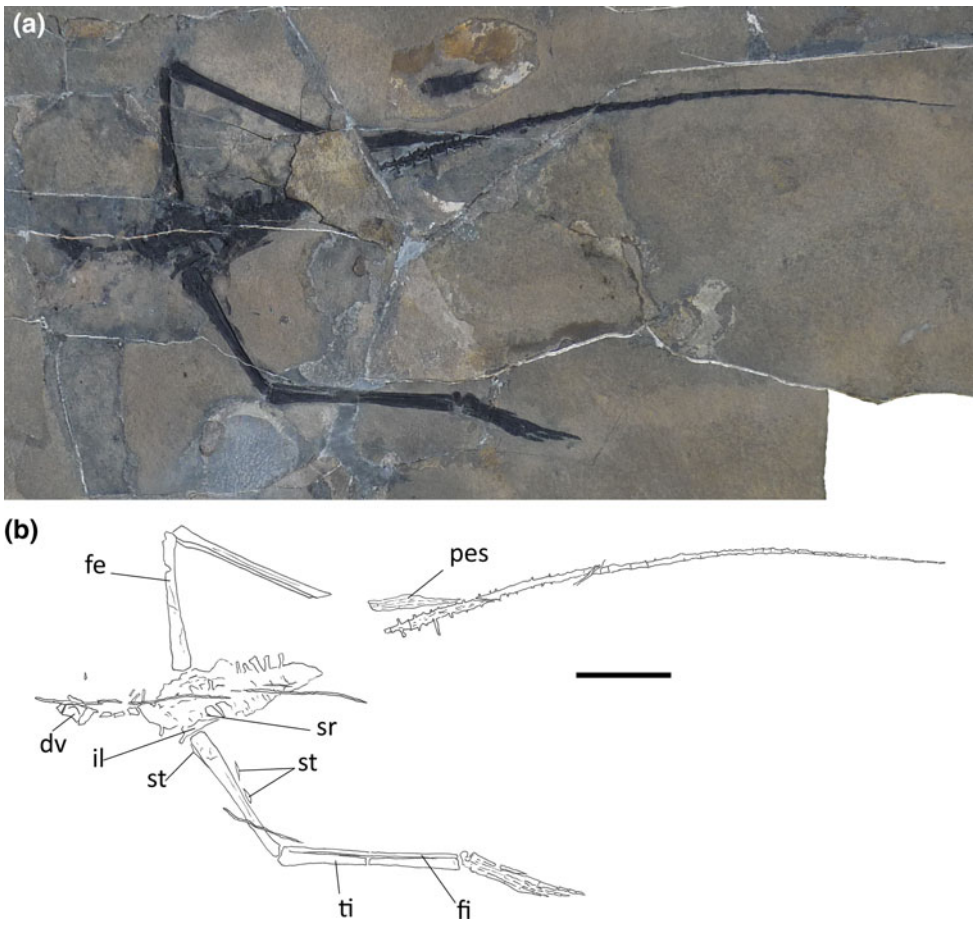

Fig. 2 *Macrocnemus obristi*. The holotype PIMUZ A/III 1467 in dorsal view. **a** photograph view. **b** line drawing. *Scale bar* equals 40 mm. *dv* dorsal vertebra, *fe* femur, *fi* fibula, *il* lium, *sr* sacral rib, *st* soft tissue, *ti* tibia

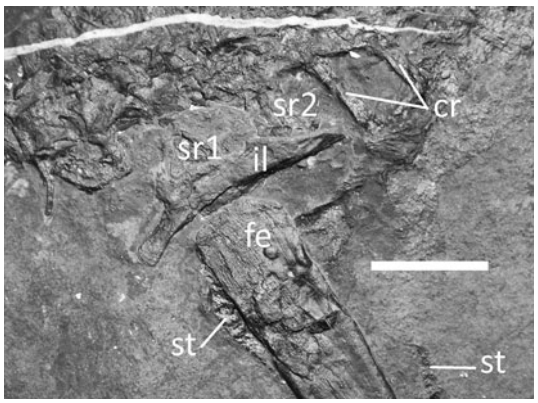

Fig. 3 The pelvic region of the holotype PIMUZ A/III 1467. *Scale bar* equals 10 mm. *cr* caudal ribs, *fe* femur, *il* ilium, *sr* sacral rib, *st* soft tissue

4.1.2 Sacrum

There are two sacral vertebrae with sacral ribs articulating with the ilium. On the left side the sacral rib can be clearly seen to bifurcate distally (Fig. 3), with the posterior spur lacking an articulation with the pelvis.

4.1.3 Caudal vertebrae

Posterior to the sacrum, there are seven caudals that are relatively complete. Following behind these a small piece of matrix, that was occupied by a short section of the tail together with the left ankle and part of the pes, is missing and was not recovered during the excavation. This is then followed by a further 41 caudals that are positioned in a direct line with the first seven caudals. Apart from a very slight break between vertebrae 34 and 35 of this section of the caudal series, the tail appears to be in complete articulation. The gap between the two sections of the tail is 34.8 mm long. Given that the centrum of caudal seven measures 7.3 mm and the centrum of the most proximal complete vertebra in the second caudal section is 6.9 mm long it is reasonable to assume that only four or possibly five complete vertebrae could have been accommodated in the gap. This would give a full count of 52 or 53 caudals. The last one is little more than a tiny undifferentiated piece of bone.

The first 7 caudals as well as caudals 12–20 are exposed in dorsal view. In the region of caudal 9–13 they have twisted onto their dorso-left lateral sides. Transverse

Table 1 Lengths (mm) of femora and tibiae in selected specimens of *Macrocnemus*

Specimen	PIMUZ A/III 1467	PIMUZ T 4822	PIMUZ T 4355	PIMUZ T 2472	MSNM BES SC111	IVPP V15001 *Macrocnemus fuyuanensis*
Left femur	62.75	46.91	–	72.02	34.27	
Left tibia	78.92	45.01	–	75.91	37.82	
Right femur	57.94	47.58[a]	65.95	70.00	34.40[b]	90.0
Right tibia	73.28	44.53	72.75	75.83	37.14	87.5
Tibia:femur ratio	1.26	0.96	1.10	1.07	1.10	

[a] Partially reconstructed

[b] Estimated as proximal end is partially covered by the ilium

processes occur on the first 27 vertebrae of the caudal series, although on 25 and 26 they are minimally developed. In the 7 proximal vertebrae the transverse processes are pronounced and expand slightly towards their distal extremities. In preserved caudals 10 and 11, the transverse processes are shorter, yet still exhibit some distal expansion. Such expansion of the transverse processes is not typically seen in specimens of *M. bassanii* (e.g. PIMUZ T 2477). Caudals 28 and 29 appear to lack anything other than a very faint, rounded swelling in the region of the transverse processes. Chevron bones cannot be seen on the last ten caudals, but a very short and delicate chevron can still be seen on caudal 42.

Very tiny circular excrescences are randomly distributed across the surface of some of the caudals. These are particularly prominent in the posterior region, for example on vertebrae 41 of the caudal series (Fig. 3). It is not clear what these may represent, but they appear to be some kind of pathological condition—possibly arthritis.

4.1.4 Left limb

The femur is long and slender, tapering slightly from its proximal end. The squared-off proximal head is still in direct articulation with the pelvis (Fig. 3). The femur measures 62.8 mm long, 7.9 mm wide at the proximal end and 6.7 mm wide across the distal head. The tibia, at 78.9 mm, is distinctly longer than the femur. The proximal head measures 7.1 mm across and the distal head 6.7 mm. The fibula is slightly shorter than the tibia at 75.0 mm long. A comparison with the femora and tibiae of other specimens of *Macrocnemus* (Table 1) indicates that they are noticeably more slender in PIMUZ A/III 1467.

The completely intact tarsus and pes are well preserved in dorsal view with a phalangeal formula of 2:3:4:5:4 which is the same as the other described species of *Macrocnemus* (Table 2; Fig. 5). The proximal tarsus preserves a well-rounded calcaneum and pillar like astragalus that are slightly disarticulated. Nevertheless, it is clear they were perforated by a foramen when in articulation (Fig. 4). Two

Table 2 PIMUZ A/III 1467

Digit	I	II	III	IV	V
Metatarsal	17.7	22.9	25.9	28.9	6.4
Phalanx 1	5.8	6.1	6.9	8.2	6.4
Phalanx 2	3.0[a]	3.7	3.6	3.9	3.3
Phalanx 3		3.0[a]	2.9	3.0	2.7
Phalanx 4			2.8[a]	2.4	2.2[a]
Phalanx 5				2.4[a]	

Lengths (mm) of the metatarsals and phalanges on the left pes

[a] Ungual phalanx

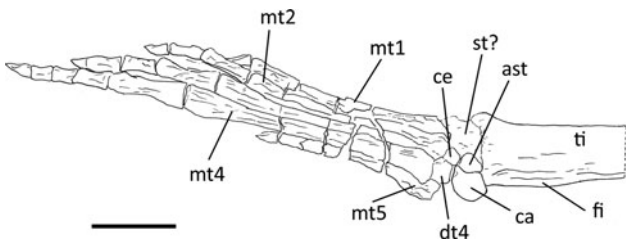

Fig. 4 *Macrocnemus obristi*. The left pes of the holotype PIMUZ A/III 1467 in dorsal view. *Scale bar* equals 10 mm. *ast* astragalus, *ca* calcaneum, *ce* centrale, *dt* distal tarsal, *fi* fibula, *mt* metatarsal, *st?* possible soft tissue, *ti* tibia

other approximately equal sized ossifications are preserved which are presumed to be the centrale and distal tarsal 4. Both are sub-rhomboidal in shape. There is a large gap between the tibia and the metatarsals of digits I and II and no evidence of any additional distal tarsals. However, there is some dark staining in this area that could possibly represent some kind of soft tissue. The proximal articular ends of the metatarsals are particularly rugose and the tarsals also appear almost fused together in places. Again this is suggestive of some kind of pathology such as arthritic joints.

The fifth metatarsal is distinctly hooked and is followed by four clearly preserved phalanges. Ratios of metatarsal lengths to widths indicate that these elements are quite

slender (see "Discussion" below). This is almost certainly not an artifact of bone width being exaggerated by the severe compression in the Besano Formation fossils, since the new fossils are also equally crushed.

4.1.5 Right hindlimb

The femur is complete and measures 57.9 mm long and is 9.3 mm wide across the proximal head. Since a significant part of the distal epipodials and the proximal tarsus is missing it has not been possible to provide meaningful measurements of these elements.

The distal tarsus is positioned extending alongside part of the tail, but the fourth digit is quite badly deformed. This section of the tail is also quite markedly more crushed than the adjoining caudals (Fig. 2). It is clear that this area was subjected to additional trauma, possibly a bite. At the same time we would have expected such an incident to have resulted in at least some realignment of the tail which is not the case.

In the region of the pelvis and also in the vicinity of the proximal left femur there are clear blackened areas that display a uniform mottled pattern and with a distinct margin on the left side of the proximal tail (Fig. 2). These almost certainly represent skin and other soft tissue remains.

4.2 PIMUZ A/III 722

The extreme tip of the fibula is present together with a hint of the latero-distal corner of the tibia where it contacts the astragalus. The calcaneum is a large rounded ossification with a medial excavation contributing to the astragalocalcaneum foramen. The astragalus is a fairly short columnar bone with the lateral margin emarginated by the astragalocalcaneum foramen. Two other approximately equal-sized ossifications are present: the centrale and distal tarsal 4. The centrale lies at the end of the astragalus and above the second digit. An additional very small ossification is squeezed in between distal tarsal 4 and metatarsals II and III, and must therefore represent either distal tarsal 2 or 3. Digit IV is incomplete, missing the distal end of phalanx 3 and all of phalanges 4 and 5. The remainder of the foot is preserved in complete articulation with the digits all closely opposed, particularly along the lengths of the metatarsals. The proportions of the pedal elements closely match those of PIMUZ A/III 1467 (Tables 2, 3, 4, 5).

5 Discussion

While the two new specimens described do not preserve any of the skull or cervical vertebral series that are so characteristic of *Macrocnemus*, they can be confidently referred to *Macrocnemus*. Terrestrial tetrapods are relatively rare in the Middle Triassic of Alpine Europe. The nature of the ankle, complete with a hooked fifth metatarsal, together with the elongate limb elements and tarsal elements possessing well-ossified proximal and distal ends are features consistent with protorosaurs and in particular a terrestrial form. Within the approximately penecontemporaneous marine sediments of the western Tethys, only two protorosaur genera are known: *Tanystropheus* and *Macrocnemus*. Importantly they can be readily distinguished from each other on the basis of the pes. In *Macrocnemus* the proximal phalanx on digit V is relatively short whereas in *Tanystropheus* this proximal phalanx shows the derived condition of being distinctly elongate and consistent in length with metatarsals I through IV (e.g., Fraser and Rieppel 2006). Both of the new specimens possess a short proximal phalanx on digit V (Figs. 4, 5). Although not known from the Besano Formation, it is worth noting that two other European protorosaurs, *Amotosaurus* (Fraser and Rieppel 2006) and *Langobardisaurus* (Renesto 1994;

Table 3 PIMUZ A/III 722

Digit	I	II	III	IV	V
Metatarsal	13.1	17.4	21.3	24.5	5.4
Phalanx 1	4.6	5.2	5.6	5.9	4.9
Phalanx 2	2.5[a]	2.8	3.0	3.3	3.0
Phalanx 3		2.4[a]	2.5	2.4[b]	2.2
Phalanx 4			2.6[a]	–	1.8[a]
Phalanx 5				–	

Lengths (mm) of the metatarsals and phalanges on the right pes (mm)

[a] Ungual phalanx

[b] Incomplete distally

Table 4 PIMUZ A/III 1467

	I	II	III	IV	V
Proximal	1.5	[a]	[a]	2.8	2.9
Minimum	1.1	0.9	0.9	1.7	1.7
Distal	2.1	1.9	1.9	2.6	1.7

Width (mm) of the left metatarsals

[a] Overlapping metatarsals obscure the distal width

Table 5 PIMUZ A/III 722

	I	II	III	IV	V
Proximal	1.1	1.3	1.3	1.9	3.1
Minimum	0.9	0.6	0.9	1.0	1.5
Distal	1.5	1.5	1.7	1.9	1.5

Width (mm) of the metatarsals

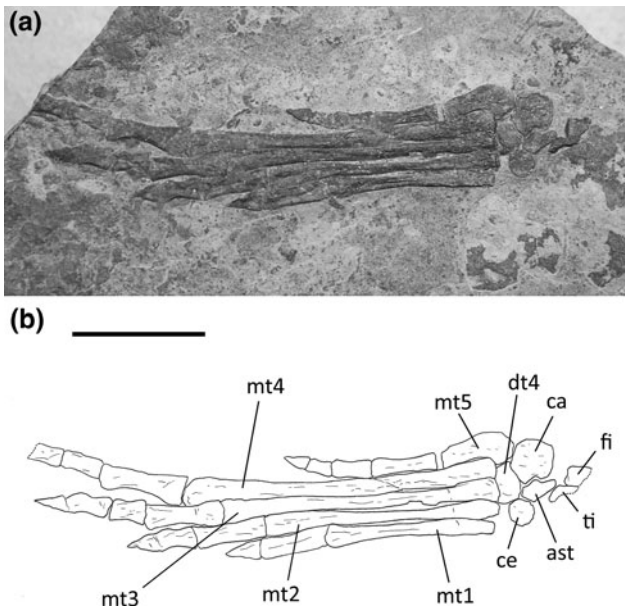

Fig. 5 *Macrocnemus obristi*. Referred specimen PIMUZ A/III 722. **a** in dorsal view and **b** line drawing. *Scale bar* equals 10 mm. *ast* astragalus, *ca* calcaneum, *ce* centrale, *dt* distal tarsal, *fi* fibula, *mt* metatarsal, *ti* tibia

Table 6 Ratio of width to length of the proximal end of metatarsal IV

	A/III 722	A/III 1467	T 4355	T 2472
Ratio width:length	0.08	0.09	0.18	0.17

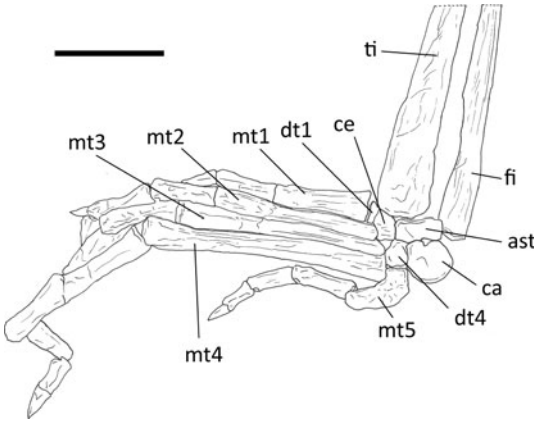

Fig. 6 *Macrocnemus bassanii*. Left pes of PIMUZ T 4822. *Scale bar* equals 10 mm. *ast* astragalus, *ca* calcaneum, *ce* centrale, *dt* distal tarsal, *fi* fibula, *mt* metatarsal, *ti* tibia

Saller et al. 2013) also possess an elongate proximal phalanx on digit V of the pes.

Furthermore the new specimens of *Macrocnemus* can be assigned to a new species distinct from *M. bassanii* on the basis of the following lines of argument. Firstly, a tibia 20 % longer than the femur is markedly longer than any other known individual of *M. bassanii*. Indeed the name *Macrocnemus* alludes to the elongate tibia and so it is particularly apt for the new species. Secondly, the limb elements and metatarsals are relatively more slender as demonstrated by the ratio of width to length of the metatarsals (Table 6). The fact that the isolated tarsus from the same beds exhibits similar gracile proportions of the metatarsals supports the view that PIMUZ A/III 1467 is not just an isolated individual variant of *M. bassanii*. *Macrocnemus bassanii*, as demonstrated by PIMUZ T 4822 has distinctly stouter bones in the pes (Table 6; Fig. 6). Lastly, the upper Prosanto Formation is slightly younger than the Besano Formation (Grenzbitumenzone) from which most of the known specimens of *M. bassanii* were recovered, but a little bit older than the Cassina beds, from where the specimen PIMUZ T 4822 was recovered. By themselves these lines of evidence might not make an unequivocal argument for recognizing a new species, but when taken together they provide a very robust case.

This is the first specimen of *Macrocnemus* described with a completely intact distal caudal series and it can be confidently stated that, at least in this new species, it possessed either 52 or 53 caudal vertebrae.

Although the preservation of soft tissue has been reported previously in *Macrocnemus* (Renesto and Avanzini 2002), it is rare. Thus the preservation of soft tissue in the region of the pelvis and the thigh is notable.

Finally, the holotype of the new species provides an intriguing snapshot of interaction between the inhabitants of the western Tethys. When PIMUZ A/III 1467 was first discovered the beds below and above the specimen were carefully searched yet no more of the skeleton was found. If it had been preserved it would undoubtedly have been readily apparent. In addition, the clear crushing of the right fourth digit and the adjacent caudal vertebrae is also indicative of some kind of trauma, possibly also a bite. Given that the rest of the skeleton remains completely undisturbed we postulate that the animal was predated upon—perhaps in a single bite by a large predator such as a nothosaurid reptile or the actinopterygian fish *Saurichthys*. Several individuals of *Saurichthys* are known from the same site with complete fishes inside their bodies. The largest one (length 100 cm, PIMUZ A/I 3579, Furrer 2009, p. 26) even has stomach contents with pachypleurosaur remains, vividly demonstrating the voracious habits of these predators. Further evidence of similar predation is not uncommon in the Middle Triassic marine sequences of Monte San Giorgio. For example, such a fate may have also befallen one of the large *Tanystropheus* specimens from the Besano Formation (Grenzbitumenzone). PIMUZ T 2819 comprises the anterior part of a *Tanystropheus* skeleton (Wild 1973, Pl. 15, 16) in which cervical vertebra

10 and the associated ribs appear to have been bitten through leaving the anterior half of the neck and skull still intact.

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