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The Middle Triassic (Anisian) Otter Sandstone biota (Devon, UK): review, recent discoveries and ways ahead.

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ABSTRACT

The Middle Triassic (Anisian) Otter Sandstone was laid down mostly by braided rivers in a desert environment and is now well exposed along the south-east Devon coast in south-west England, part of the 'Jurassic Coast' World Heritage Site. It yields uncommon and generally fragmentary fossils, principally of vertebrates, including fish, temnospondyl amphibians and reptiles such as rhynchosaurs, predatory archosaurs, and small superficially lizard-like forms. These provide important information about a freshwater and terrestrial ecosystem that marks recovery from the end-Permian mass extinction, but pre-dated the appearance of dinosaurs and mammals. The constantly eroding Otter Sandstone exposures continue to reveal new taxa (for example, freshwater sharks). Furthermore, microvertebrate material obtained by sieving bone-bearing levels has the potential to further expand the faunal list. Newly discovered associated and articulated vertebrate remains, including small tetrapods, improve knowledge of whole-body anatomy and facilitate systematic work. Invertebrate burrows and reptile footprints provide information on ecological interactions and detailed bed-by-bed collecting casts light on taphonomic processes and faunal changes over time.

Keywords: fluvial; temnospondyls; rhynchosaurs; rauisuchians; trace fossils; *Chirotherium*

ABBREVIATED TITLE: Middle Triassic vertebrates

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1. Introduction

Continental red beds deposited during the Permian and Triassic, between approximately 300 and 200 million years ago, are well exposed along the south-east Devon coast, southern England. During that time, the continents were united as the supercontinent Pangea, and what is now Devon was located towards the hot and arid continental interior. Like today, such desert environments supported little life and the Devon red beds are mostly unfossiliferous. There was, however, a Middle Triassic interval during which an extensive network of braided to meandering rivers, the ‘Budleighensis’ river system of Wills (1956, 1970), flowed generally northwards from what is now northern France, up through southern and central England and into the East Irish Sea Basin. These river channels provided life-supporting water, and the associated sediments contain the remains of organisms. In Devon, this rock sequence is termed the Otter Sandstone. The Otter Sandstone previously had formation status, but has recently been subsumed by the British Geological Survey within the Helsby Sandstone Formation, along with other sandstone formations of similar age throughout southern Britain (Ambrose et al., 2014). Reaching a total inland thickness of around 210 m (although thinner on the coast), the Otter Sandstone comprises mostly reddish-hued fine-grained sandstones with subordinate conglomerates and mudstones (Edwards and Gallois, 2004). It is magnificently exposed, although often difficult to access, along approximately 10 km of sea cliffs and intertidal foreshore ledges extending eastwards from the coastal town of Budleigh Salterton to just east of Sidmouth (Fig. 1) (National Grid References SY 0807 8212 to SY 1297 8730), forming part of the Dorset and East Devon Coast World Heritage Site (popularly known as the ‘Jurassic Coast’).

Magnetostratigraphic data indicate that the Otter Sandstone encompasses most of the Anisian stage of the Middle Triassic, with the top of the sequence lying close to the Anisian-Ladinian boundary (Hounslow and McIntosh, 2003). It therefore represents an age range of approximately 247 – 242 Myr (Cohen et al., 2013).

The Otter Sandstone fossil remains, although generally fragmentary and uncommon, indicate a moderately diverse biota comprising plants, arthropods, fish, temnospondyl amphibians, rhynchosaurs, archosaurs and small, superficially lizard-like reptiles (e.g. see Milner et al., 1990; Benton et al., 1994). Invertebrate and vertebrate trace fossils also occur (Gallois, 2013; Coram and Radley, 2015).

The recorded vertebrates indicate a broadly Anisian age for these beds, supporting the magnetostratigraphic data (Benton et al., 2002) and corresponding to the Perovkan landvertebrate faunachron of Lucas (1998, 2010). Anisian terrestrial vertebrate sites are uncommon worldwide, and especially so in Europe, which was largely submerged beneath the Muschelkalk sea (Benton, 1997). The Otter Sandstone, and coeval fossiliferous deposits in the English Midlands, therefore make an extremely valuable contribution to knowledge of the mid Triassic non-marine biota. This was an important time for terrestrial vertebrate evolution; reptiles in particular were recovering and diversifying 10 Myr or less after the end-Permian mass extinction, the most severe in the planet's history. Among these vertebrates were the ancestors of dinosaurs, pterosaurs and mammals, which appeared later in the Triassic.

Research on Otter Sandstone fossils commenced in the latter part of the 19th century, with the discovery of a rhynchosaur bone on the bank of the River Otter, near Budleigh Salterton (Whitaker, 1869). Subsequent finds were made along the coast further east between High Peak and Sidmouth (e.g. Lavis, 1876). Following a long period of relative inactivity, an extensive and well-studied collection of vertebrate material was made in the late 20th Century, by P.S. Spencer and others, mostly from coastal exposures either side of Sidmouth (e.g. Milner et al., 1990; Benton and Gower, 1997; Spencer and Storrs, 2002; Hone and Benton, 2008).

Collecting activity and palaeontological research has continued to the present. The coastal sections are still actively eroding and producing new vertebrate material, some of it exceptionally preserved and/or representing previously unrecorded taxa, which are currently under study and will be formally described elsewhere. Additionally, new information is being provided by vertebrate and invertebrate trace fossils that have until recently received little attention. This article summarises and discusses some of this new material, and outlines recent research that is improving our knowledge of the Otter Sandstone fauna and palaeoenvironment, and contributing to a better understanding of the global Anisian non-marine biota. It will also suggest further potentially profitable areas of investigation. Figured vertebrate fossils were collected by RAC; deposited specimens are housed in the collections of the University of Bristol (prefix BRSUG).

2. Palaeoenvironments

The lowermost part of the Otter Sandstone has been interpreted as aeolian in origin, and the remainder as predominantly braidplain deposits (Benton et al., 2002; McKie and Williams, 2009; Barton et al., 2011). It was laid down under a hot, seasonally semi-arid climate, and comprises a cyclical series of mostly ochre-red sandstone units typically around 2 m thick. These are sometimes separated by generally thin red lacustrine mudstones, especially towards the top of the sequence (Fig. 2). The cycles reflect the migration of river channels across the landscape, the sand bars deposited by them often eventually becoming subaerially exposed, supporting terrestrial plant and animal life, before being buried beneath mudstone or sandstone to initiate the next sedimentary cycle (Benton et al., 1994).

Historically, most of the Otter Sandstone vertebrate remains have been collected from intraformational conglomerates which often form the base of, and fine up into, the main sandstone beds (Spencer and Isaac, 1983). These are interpreted as channel lags deposited by energetic migrating river channels that partly eroded and reworked the underlying braidplain sandstones and mudstones, as well as collecting subaerially exposed debris including animal remains. In addition to bone material, intraclasts typically include red rip-up mudstone clasts and reworked carbonate nodules including fragments of rhizocretions.

The Otter Sandstone palaeoenvironment would have included a range of aquatic habitats: braided river channels, river-fed ponds and small lakes and generally larger, more isolated and less hospitable ephemeral water bodies. Terrestrial habitats were primarily life-supporting vegetated channel borders and interfluves, which would have been periodically inundated by river floods and buried beneath fresh sediment delivered by migrating channels. Beyond the influence of the Budleighensis river system, there would have been generally more elevated terrain such as the Cornubian Massif occupying present-day Cornwall and west Devon, similarly subjected to long arid phases punctuated by heavy rainfall.

There would have been some biological overlap between aquatic and terrestrial habitats, for example, temnospondyl amphibians and certain insects would have been aquatic when immature but spent at least some of their adult lives out of the water.

3. Aquatic biota

3.1. Invertebrates

Various invertebrates would have inhabited the braided rivers and associated braidplain water bodies, but fossil evidence for these is presently meagre. Conchostracans (*Euestheria* and *Lioestheria*) have been recorded from lacustrine facies (Benton, 1997) and may indicate ephemeral conditions by analogy with recent taxa (Scholze and Schneider, 2015). Additionally, the channel sandstones preserve a variety of invertebrate trace fossils similar to those produced by various extant aquatic annelid worms and arthropods. These have received little research attention despite providing an insight into ecological interactions and revealing the presence of organisms, albeit poorly identified, that are not known from body fossils. Gallois (2013) figured some pencil-shaped (and roughly pencil-sized) burrows, which he interpreted as possibly produced by deposit feeding insects or crustaceans. Sometimes similar burrows are exposed in profusion on the foreshore to the west of Sidmouth (Fig. 3).

3.2. Fish

In contrast to invertebrates, body fossils of fish are reasonably common in the channel sandstones and their basal lags, although in these lithofacies they are invariably disarticulated to a greater or lesser extent. Historical records of fish are sparse, and they have received little study (Milner et al., 1990; Dineley and Metcalf, 1999). Recent collecting, however, has revealed a moderately diverse fish fauna with hitherto unrecognised taxa. These include relatively large forms which probably preyed on smaller fish, such as freshwater sharks (Fig. 4A) and an undescribed pike-sized predator represented by a jaw (Fig. 4B). These augment knowledge not only of aquatic faunal diversity but also of aquatic food chains. Recent sieving trials of known bone-bearing sandstone horizons by one of us (RAC) have also yielded identifiable microvertebrate remains, principally of fish (Fig. 5), offering potential for the recovery of further new taxa.

Rare more intact fish fossils also occur in the Otter Sandstone, collected from lithofacies other than channel sandstones. Articulated, although headless, examples of the small deep-bodied perleidiform *Dipteronotus* have previously been recorded from a presumably lacustrine mudstone near Sidmouth (Milner et al., 1990). More recently, further articulated specimens of this fish have been recovered, which provide additional morphological details, especially regarding the head (Fig. 6). The remains are usually found clustered in what were evidently pools occupying hollows on the exposed surfaces of channel bars. These subsequently became rapidly filled by an influx of fine river sand which presumably killed the fish and preserved them (Fig. 7). Whether the fish were perennial inhabitants of the bar-surface pools, or were stranded by retreating river waters, and then perhaps concentrated as pools dried out and reduced in size, is unknown.

3.3. Coprolites

Generally ovoid coprolites (fossilised droppings) up to *c*. 60 mm long are frequently encountered in the Otter Sandstone channel lags. Such structures were unlikely to have been able to withstand extended transport and so were probably produced by local aquatic vertebrates, most likely fish. Some coprolites are packed with scales and bones, mostly or all from smaller fish. Such concentrations may offer potential for the recovery of informative microvertebrate material and facilitate the reconstruction of food webs, although confidently associating particular coprolites with their producers is not easy. Some clues are provided by their structure; for example, spiral coprolites such as that in Figure 8 are likely to have been produced by sharks (Duffin, 1979).

4. Terrestrial biota

4.1. Plants and invertebrates

As the Budleighensis river channels migrated across the landscape, the sand bars often became subaerially exposed, as indicated by gypsum moulds and occasional desiccation cracks. Most conspicuously, the roots of conifer trees are preserved as calcareous cylindrical rhizocretions (Purvis and Wright, 1991) and can often be observed in spectacular abundance in cliff faces and within foreshore sections. Channel bar surfaces thus often remained exposed long enough for the establishment of presumably extensive groves and woodlands of conifers. Other types of vegetation would have been present as well, but other than occasional portions of equisetalean (horsetail) stems, first reported by Hutchinson (1879), these have not been documented. Similarly, miospores, which would greatly assist dating within the sequence, have so far not been detected (Benton, 1997).

The plants would have supported organisms including insects and other terrestrial arthropods such as scorpions, which are known from rare and fragmentary body fossils (Benton, 1997), and possible trace fossils. Rhizocretions sometimes bear on their surfaces small (1–2 mm) diameter burrows attributed by Gallois (2013) to *Taenidium* isp. (Fig. 9) and which may have been produced by sap-sucking insects.

4.2. Large tetrapods

Most of the Otter Sandstone tetrapod remains are found in channel-lag conglomerates. The bones are almost invariably disarticulated, and often broken or worn, indicative of fluvial transport and burial in a relatively high energy and abrasive environment (Spencer and Isaac, 1983). Since this material is transported, it can say little about the original life habitats of the taxa, their living abundance and the extent to which they coexisted and interacted.

The commonest vertebrate fossils encountered in the channel sandstones are those of squat, herbivorous archosauromorph rhynchosaurs (Fig. 10), accounting for approximately half of identifiable specimens (Benton et al., 1994; pers. obs. RAC). This suggests that they were common animals on the local floodplains, perhaps forming herds, although the general sturdiness of their bones no doubt favoured their preservation. Rhynchosaurs are also, unusually for the larger tetrapods, known from somewhat more complete remains. Partial or intact skulls from two named genera, *Fodonyx* and *Bentonyx*, have been recovered (Langer et al., 2010), as well as associated body portions, most notably a partial headless skeleton from Ladram Bay, to the southwest of Sidmouth (Benton et al., 1993; Hone and Benton, 2008). Found in an otherwise barren red channel sandstone, the latter is interpreted as a recently dead carcass that was washed into a river, or even fell in whilst alive (Hart, 2014).

Isolated bones, teeth and rarer jaw portions attributable to several predatory archosaur reptile taxa have also been recovered from the channel-lag conglomerates (Fig. 11). Notable previous finds include a toothed lower jaw possibly of the poposauroid *Bromsgroveia*, remains of which are known from the English Midlands (Benton, 2011), and an enigmatic elongate bone that may be a neural spine of a ‘sail-backed’ poposauroid (Milner et al., 1990; Benton and Gower, 1997).

The larger Otter Sandstone archosaurs also left trace fossils (Coram and Radley, 2013, 2015). Figure 12 shows an abandoned channel bar surface temporarily exposed on the foreshore to the west of Sidmouth. Accompanying scattered rhizocretions, there is a right hind footprint attributed to *Chirotherium*. Such tracks, first found in Germany almost 200 years ago, derive their name from the Greek for ‘hand beast’ because of the blunt outward-pointing digit that superficially resembles a human thumb (Kaup, 1835). There was much Victorian speculation regarding what could have produced these footprints, with giant frog-like amphibians (what are now recognised as temnospondyls) and even bizarre marsupials being mooted as candidates (e.g. Owen, 1842). They are now thought to have been generated by terrestrial predatory crocodile-line ‘rauisuchians’, a paraphyletic group of taxa known from all continents that includes mainly quadrupeds, but also some bipedal forms that might have looked superficially like theropod dinosaurs (Gower, 2000; Nesbitt, 2011). With a length of about 280 mm, the footprint in Figure 12 would have belonged to an animal approximately 4 m in length, based on calculations provided by Coram and Radley (2013).

Chirotheriid footprints are now known from several levels in the higher part of the Otter Sandstone, mostly in reddened lacustrine lithofacies that are virtually lacking in body fossils (Coram and Radley, 2013, 2015). The footprints can occur in large densities and in a range of sizes, suggesting herding behaviour.

The rare body fossils found in association with the footprints may furnish clues to the trackmakers' lives. Figure 13 shows a block bearing a tooth adjacent to a partial chirotheriid footprint. Blade-shaped and with serrated edges, the tooth is evidently that of a predatory archosaur. Theropod dinosaurs regularly shed their teeth when they became worn, as do modern crocodiles (Poole, 1961). The worn extremity of this tooth, which would have compromised its slicing and piercing function, indicates that it too was probably shed by a living animal. Although it may have been fortuitously washed up next to a chirotheriid footprint, in the near absence of other tooth or bone material at this level, it may well instead have been derived from one of the trackmakers, conceivably the actual individual that produced the adjacent print. Such isolated large, serrated teeth attributed to rauisuchians have already been reported as being reasonably common in the Otter Sandstone (Benton and Gower, 1997).

Also rarely found at footprint-bearing levels are small clusters of bone fragments (Fig. 14A). Again, these could be chance associations, but their close proximity to footprints and apparent absence from otherwise similar mudstones suggests, alternatively, that they are the remains of trackmaker meals, indigestible remnants that were either regurgitated or defecated by the wandering animals. The fragment enlarged in Figure 14B bears a surface groove commensurate with bite damage by a serrated archosaur tooth (Fig. 14C). All bone material found in association with chirotheriid footprints pertains to superficially crocodile-like temnospondyls, recognisable from the distinctively pitted ornamentation, suggesting that these were favoured prey of the trackmakers. Presumed rauisuchian predation damage to temnospondyl bones has also recently been reported from the Middle Triassic of Germany (Schoch and Seegis, 2016).

Temnospondyl bones are also frequently encountered in Otter Sandstone channel-lag conglomerates (Fig. 15), outnumbered only by rhynchosaur fossils. Past material has been referred to *Mastodonsaurus*, *Eocyclotosaurus* and an unnamed taxon (Milner et al., 1990), although Damiani (2001) considered the *Mastodonsaurus* remains to be indeterminate. Being amphibians, the temnospondyls almost certainly returned to water to breed, and were probably semi-aquatic at other times. This inference, however, is presently not supported by preservational context, since their invariably fragmentary remains cannot be distinguished taphonomically from those of the presumably primarily or exclusively terrestrial rhynchosaurs and archosaurs. Their conical pointed teeth indicate that they were predatory, perhaps mostly feeding on fish. Like modern crocodiles, the larger individuals, probably reaching lengths in excess of 5 m, may also have been ambush predators of terrestrial animals, perhaps including rauisuchians, that approached too close to the water.

4.3. Small tetrapods

Several taxa of small superficially lizard-like reptiles have previously been recognised, on the basis of uncommon jaw and skull material derived mostly from sandstone channel lags. These include the possible lepidosauromorph *Coartaredens* (Spencer and Storrs, 2002) and a tooth resembling that of the long-necked archosauromorph protorosaurian *Tanystropheus* (Milner et al., 1990). Also known are several procolophonid parareptiles, one assigned to *Kapes*, a genus known from Russia and helping to confirm the Anisian age of the Otter Sandstone fauna (Spencer and Storrs, 2002). Another taxon, known from a single lower jaw, shows similarities to the Central European genus *Sclerosaurus* (Spencer and Storrs, 2002), although Sues and Reisz (2008) considered it too poorly preserved for positive identification. A number of further procolophonid skulls, including a leptopleuronine, have been collected over the years, and these are currently under study by other researchers, including Angela and Andrew Milner at the Natural History Museum, London.

As well as within channel lags, bones of large and small terrestrial tetrapods are sometimes preserved on the very tops of channel bar sandstones, but these are often too fragmented or worn for confident identification. Such bones would have undergone extended transport and/or prolonged exposure, along with possible scavenging, on the exposed sandbar surfaces prior to burial.

In total contrast, such surfaces have recently yielded a small number of exquisitely preserved small tetrapods. These were evidently residents of the exposed surfaces that were alive or only recently dead when overwhelmed by sudden influxes of fine alluvial sand. Their small size facilitated rapid burial, meaning that the skeletons show variable, but sometimes good, articulation.

Figure 16 shows a small diapsid reptile, possibly, pending systematic study, a basal lepidosaur or a protorosaurian. This new Devon specimen is well articulated, although lacking tail and hindlegs, mostly or entirely due to recent coastal erosion. The life habits of small Middle Triassic diapsids are somewhat equivocal. The protorosaurian *Macrocnemus,* known from Central Europe and China (Rieppel, 1989; Jiang et al., 2011) is inferred from the limb structure to have been predominantly terrestrial, and perhaps a facultative biped when running at speed (Rieppel, 1989). The gracile build and sharp conical teeth suggest an active hunting lifestyle, probably of insects and other arthropods, along with smaller vertebrates, but the fine preservation of many of the European and Chinese specimens in marine sediments suggests at least a littoral lifestyle, and maybe even semi-aquatic, although probably not fully aquatic, habits, along with perhaps a more piscivorous diet (Fraser, 2006). The Otter Sandstone small diapsids may therefore similarly have frequented the margins of water bodies and perhaps ventured into them.

The small articulated procolophonid in Figure 17 was likely to have been similarly overwhelmed and buried largely intact. It has subsequently lost the tail and hindlimbs to recent erosion. Procolophonids were probably predominantly herbivorous and almost certainly terrestrial, exhibiting no aquatic adaptations. It has been inferred from histological and morphological evidence that at least some were fossorial (Botha-Brink and Smith, 2012). The excessively long cranial spines of the newly recovered specimen (which probably bore keratinous sheaths that would have extended them even further in life; Cisneros, 2008) are likely to have impeded burrowing activity, so this life mode cannot be inferred here.

Histological study of the Otter procolophonid and other small tetrapod material could provide further information about their life modes, and the more intact fossils offer scope for investigative techniques that were not applicable, or less applicable, in the past. These include computed tomography (CT) scanning to reveal bones and osteological details still obscured by matrix, currently being undertaken by MJB at the University of Bristol (Fig. 17B,C).

5. Faunal changes through time

The fluvial Otter Sandstone has been subdivided by Gallois (2004, 2013) into three members (Fig. 18). In succession, these are: the Otterton Point Sandstone Member, probably in excess of 100 m thick (although interrupted by faults on the coast) and principally exposed in the western part of the coastal section; the Ladram Bay Sandstone Member, *c*. 55 m thick and most accessible at Ladram Bay midway along the section; and the *c*. 15 m thick Pennington Point Member, exposed at shore level at the eastern end of the section, on either side of the town of Sidmouth.

Although vertebrate skeletal material has been recorded throughout the fluvial Otter Sandstone, there is a noticeable increase in abundance above the Otterton Point Sandstone Member, peaking near the top of the succession within the Pennington Point Member (Benton et al., 1994; pers. obs. RAC). This increase in richness is, however, exaggerated by collecting bias because the higher beds, exposed on either side of Sidmouth and in Ladram

Bay, are the most accessible, whereas much of the lower part of the Otter Sandstone can only be reached with difficulty at low tide, or by boat.

Otter Sandstone deposition is likely to have spanned most or all of the Anisian Stage (Hounslow and McIntosh, 2003), equating to approximately 5 Myr of time (Cohen et al., 2013). Temporal changes in palaeoenvironment, biotic composition and diversity are to be expected, as well as evolutionary changes in specific lineages.

In lower parts of the fluvial succession, the abundant rhizocretions are usually vertically oriented, and evidently represent tap-roots that extended to several metres down to the water table (Purvis and Wright, 1991). Higher in the succession, immediately above the top of the Otterton Point Sandstone Member, the orientation of the rhizocretions changes quite abruptly to predominantly subhorizontal, indicating a higher water table, likely linked to an increase in rainfall (Coram and Radley, 2015). Preserved channel widths also increase from <10 m to <100 m at this level (Gallois, 2013), suggesting increased discharge. The observed upward increase in frequency of vertebrate fossils mentioned above similarly accords with a transition to a more benign, and perhaps less seasonally arid, climate.

Gallois (2013) figured and discussed large putative burrows in the Otter Sandstone and, on the basis of their size and structure, speculated that they could have been produced by therapsid synapsids (‘mammal-like reptiles’). Interestingly, these structures have only been noted at the very top of the Otterton Point Sandstone Member (Fig. 18), which, if confirmed as therapsid burrows, could reflect short-term conditions suitable for these creatures that are otherwise unknown from the British Middle Triassic, and very rare in western Europe in general, favouring more temperate palaeolatitudes (Parrish et al., 1986; Maisch et al., 2009). While previously reported burrows in Permo-Triassic sandstones of the South African Karoo have frequently been identified as those of therapsids, and certain examples contain skeletons of basal cynodonts (e.g. Jasinoski and Abdala, 2017), one contained a temnospondyl and others contain procolophonids (Abdala et al., 2006). Therefore, a therapsid burrow-maker is plausible by comparison with previously described examples of large burrows and their inhabitants, but the absence of therapsid fossils in the Devon Triassic might suggest another maker, presumably one of the taxa represented by body fossils. So far, no-one has described diagnostic morphological features of burrows constructed by these different tetrapod groups.

Red lacustrine mudstone bands become more conspicuous in the higher part of the Otter Sandstone sequence, particularly in the Pennington Point Member. These are virtually lacking in body fossils, testifying to inimical conditions for life, perhaps due to high or rapidly fluctuating temperatures and/or salinity, as well as possible isolation from more favourable environments such as active river channels. Towards the top of the Otter Sandstone sequence, the braided river channels and their associated sandstones become less dominant as rivers disappeared from the landscape with a return to more arid conditions (Mader and Laming, 1985). *In situ* rhizocretions are absent from the topmost sandstones, suggesting an absence of local tree cover. The sandstones are eventually replaced almost entirely by red mudstones of the overlying Sidmouth Mudstone Formation of the Mercia Mudstone Group (Gallois, 2001). This was deposited mostly in playa palaeoenvironments with little fluvial input (Hounslow and Ruffell, 2006; Barton et al., 2011) and is virtually unfossiliferous.

Vertebrate body fossils disappear with the last of the thick fluvial sandstones, but the overlying mudstones immediately beneath the junction with the Sidmouth Mudstone Formation contain a thin zone rich in chirotheriid footprints. This footprint level is evident in foreshore sections both to the east and west of Sidmouth, approximately 2 km apart, indicating that it is extensive (Fig. 19). As in other track-bearing mudstones in the Pennington Point Member (Coram and Radley, 2015), the footprints are associated with traces of presumed rootlets, indicative of water levels low enough for plant growth and terrestrial archosaur activity. It is not known why these animals were aggregating in what had evidently become an increasingly forbidding landscape, in which fresh water and animal prey were likely scarce; possibly they were migrating between more suitable habitats. Despite the occurrence of lithologically similar rootlet-bearing horizons in the overlying Sidmouth Mudstone Formation (pers. obs. RAC), definitive chirotheriid footprints have not been recognised at these levels, suggesting that the archosaur trackmakers were no longer present in the area.

6. Conclusions and further research

Based on the fossil evidence obtained to date, it is possible to make a basic reconstruction of the local palaeoenvironment and elucidate some of the more likely trophic interactions (Fig. 20). The rate of recovery of new material, particularly of vertebrates, indicates that many taxa await discovery, perhaps representing as yet unrecognised life modes, for example arboreal or even gliding. Additional undescribed specimens probably reside in private collections and further prospecting of the constantly eroding coastal outcrops, particularly the poorly sampled lower horizons at less accessible sites, will no doubt be rewarding. Historically, most Otter Sandstone fossils have been collected from fallen beach blocks of imprecisely known stratigraphic provenance, and bed-by-bed collecting of *in situ* macrofossils, as well as further sampling for microfossils, will provided the opportunity to investigate finer-level faunal changes.

In addition to vertebrates, effort should be made to improve knowledge of the poorly documented plant and invertebrate fossils. Although the generally coarse-grained sandstone lithologies making up most of the sequence are not conducive to the preservation of delicate structures such as plant foliage, conchostracans and insect wings, further investigation of the fine-grained, laminated mudstone and siltstone facies that also occur has the potential to yield more important material. Conchostracan remains, in particular, are likely to assist more accurate dating of the sequence.

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Figure captions

Fig. 1. Geological sketch map of the coast between Budleigh Salterton and Sidmouth, Devon, south-west England, showing surface outcrop of Otter Sandstone (also exposed at shore level between High Peak and Peak Hill).

Fig. 2. Otter Sandstone exposed at Pennington Point, east of Sidmouth.

Fig. 3. Invertebrate trace fossils exposed on foreshore below Peak Hill, west of Sidmouth. Width of hammer head 220 mm.

Fig. 4. (A) Fin spine of freshwater shark, BRSUG 29950-1. Scale in mm. (B) Lower jaw of predatory bony fish, BRSUG 29950-2.

Fig. 5. Selected microvertebrate remains sieved from *c*. 20kg sample of a sandstone bed exposed near Sidmouth. Fish scales (a), teeth of fish (b-h) and possible temnospondyl (i,j), and indeterminate jaw portion (k).

Fig. 6. Intact perleidiform fish *Dipteronotus*, BRSUG 29950-3, in lateral view.

Fig. 7. Fish-bearing sandstone (A) infilling hollow on surface of channel bar sandstone (B), exposed west of Sidmouth. Hammer length 300 mm. Photo taken in 2013 and outcrop since removed by coastal erosion.

Fig. 8. Coprolite, BRSUG 29950-4, perhaps from a shark, showing spiral cross-section. Scale in mm.

Fig. 9. Rhizocretion in channel sandstone showing associated thread-like burrows of cf. *Taenidium* (enlarged in inset). Width of hammer head 220 mm.

Fig. 10. Rhynchosaur remains: (A) humerus (upper arm bone), BRSUG 29950-5, in channel lag conglomerate matrix; (B) lower jaws, BRSUG 29950-6, viewed from above.

Fig. 11. Archosaur remains: (A) vertebra, BRSUG 29950-7, in side view; (B) upper jaw and associated skull elements of small form, BRSUG 29950-8.

Fig. 12. Exposed surface of channel bar showing rhizocretions (e.g. A) and chirotheriid footprint (B), enlarged in inset. Digits I and II are incompletely preserved, III and IV show the clawed terminations, V is the blunt, outwardly-projecting ‘thumb’. Hammer length 300 mm.

Fig. 13. Partial chirotheriid footprint (A) with associated archosaur tooth (B), BRSUG 29950-9, tooth enlarged in inset (scale in mm).

Fig. 14. (A) Chirotheriid footprint with associated temnospondyl bone fragments, largest shown in inset. Width of hammer head 220 mm. (B) Detail of same bone showing presumed biting damage. (C) Tooth of predatory archosaur from a different horizon showing serrated margin. Scale in mm.

Fig. 15. Temnospondyl remains: (A) partial skull, BRSUG 29950-10, orbits indicated by X; (B) clavicle (collarbone), BRSUG 29950-11.

Fig. 16. Articulated skeleton of small diapsid reptile, BRSUG 29950-12.

Fig. 17. Procolophonid skull with partial skeleton, BRSUG 29950-13. (A) Partially prepared in matrix; (B,C) computed tomography scan of fossil showing ventral (B) and dorsal (C) aspects.

Fig. 18. The Otter Sandstone succession of east Devon, adapted from Gallois (2013), showing the vertical distribution of biogenic features discussed in the text.

Fig. 19. Chirotheriid footprint horizon close to top of Otter Sandstone. Note upward transition to unfossiliferous playa mudstones of overlying Sidmouth Mudstone Formation. (A) Foreshore beneath Peak Hill. Right hind footprint in inset. (B) Foreshore east of Pennington Point. Two incompletely preserved hind footprints in inset. Hammer length 300 mm.

Fig. 20. Preserved biota and inferred trophic interactions on the Otter Sandstone braidplain. FPOM is fine particulate organic matter.

Figure

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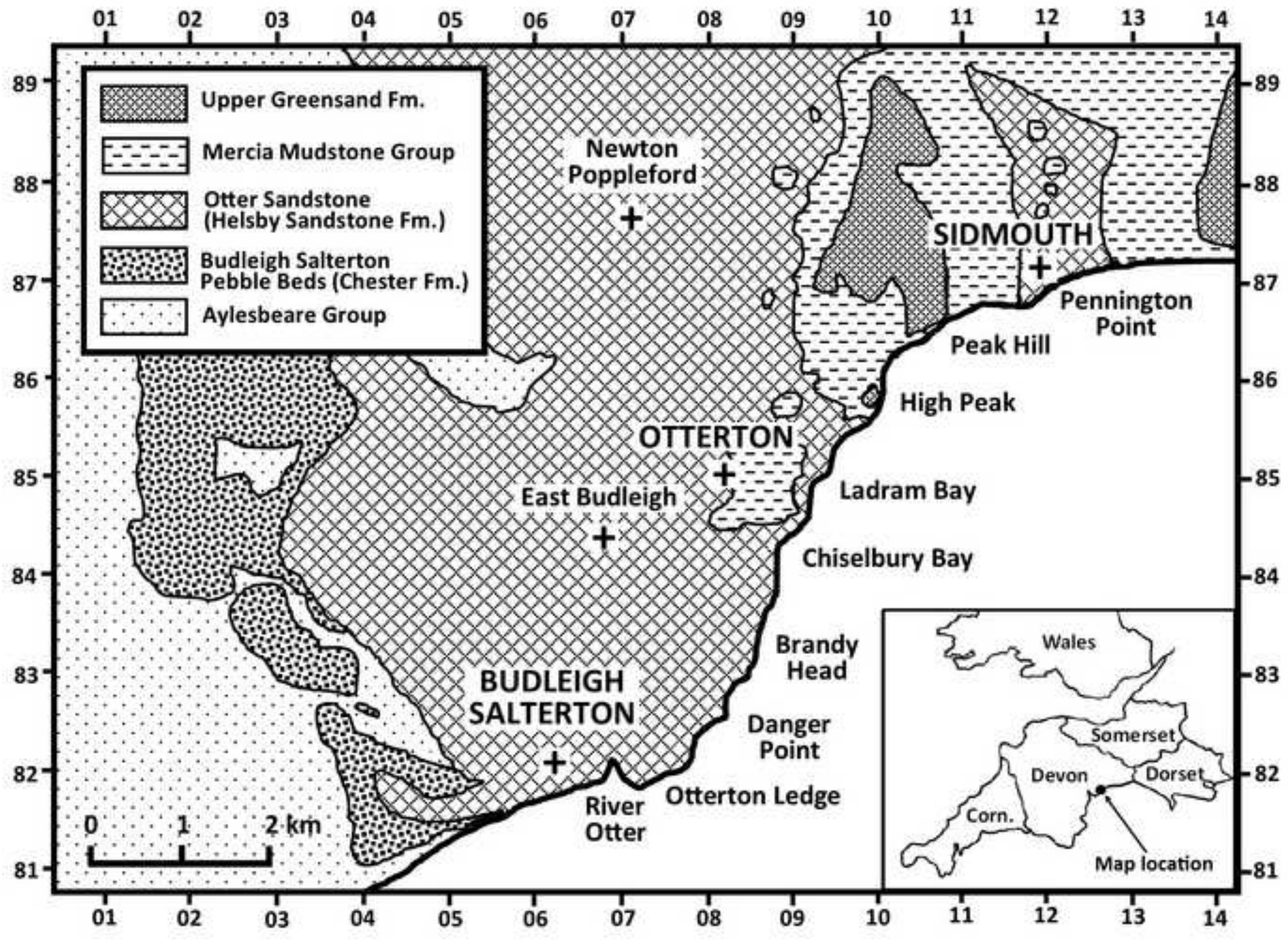

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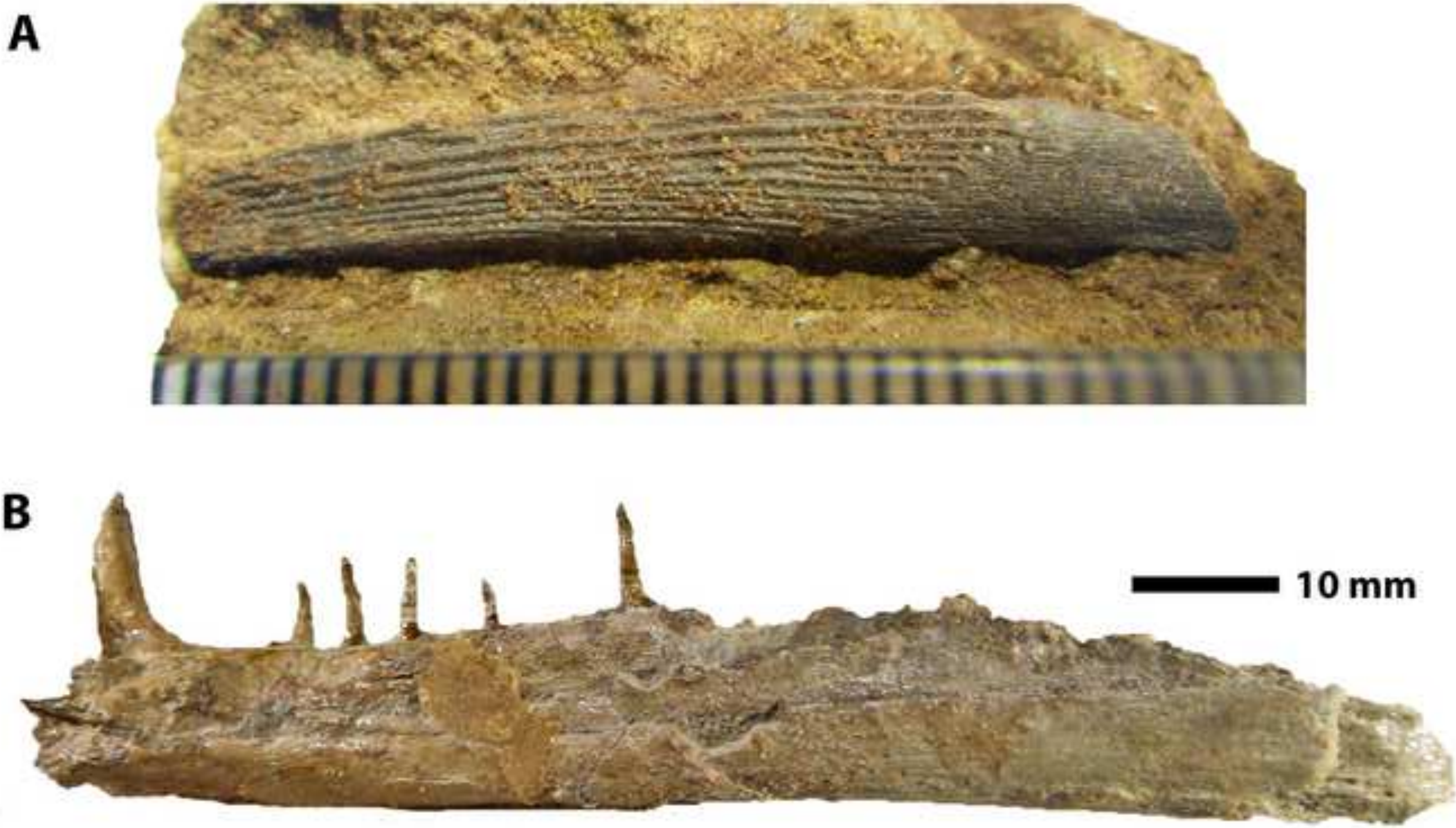
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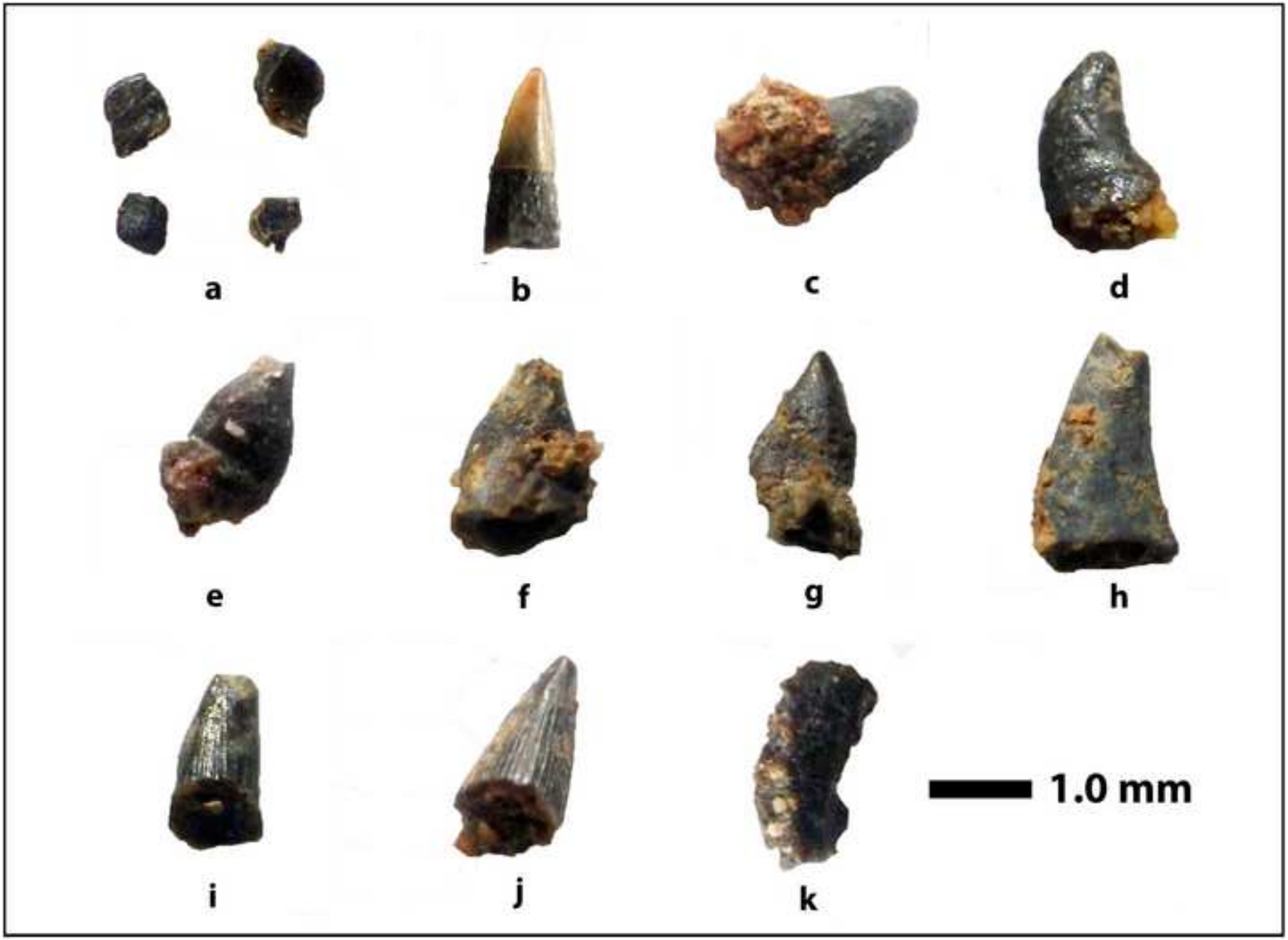
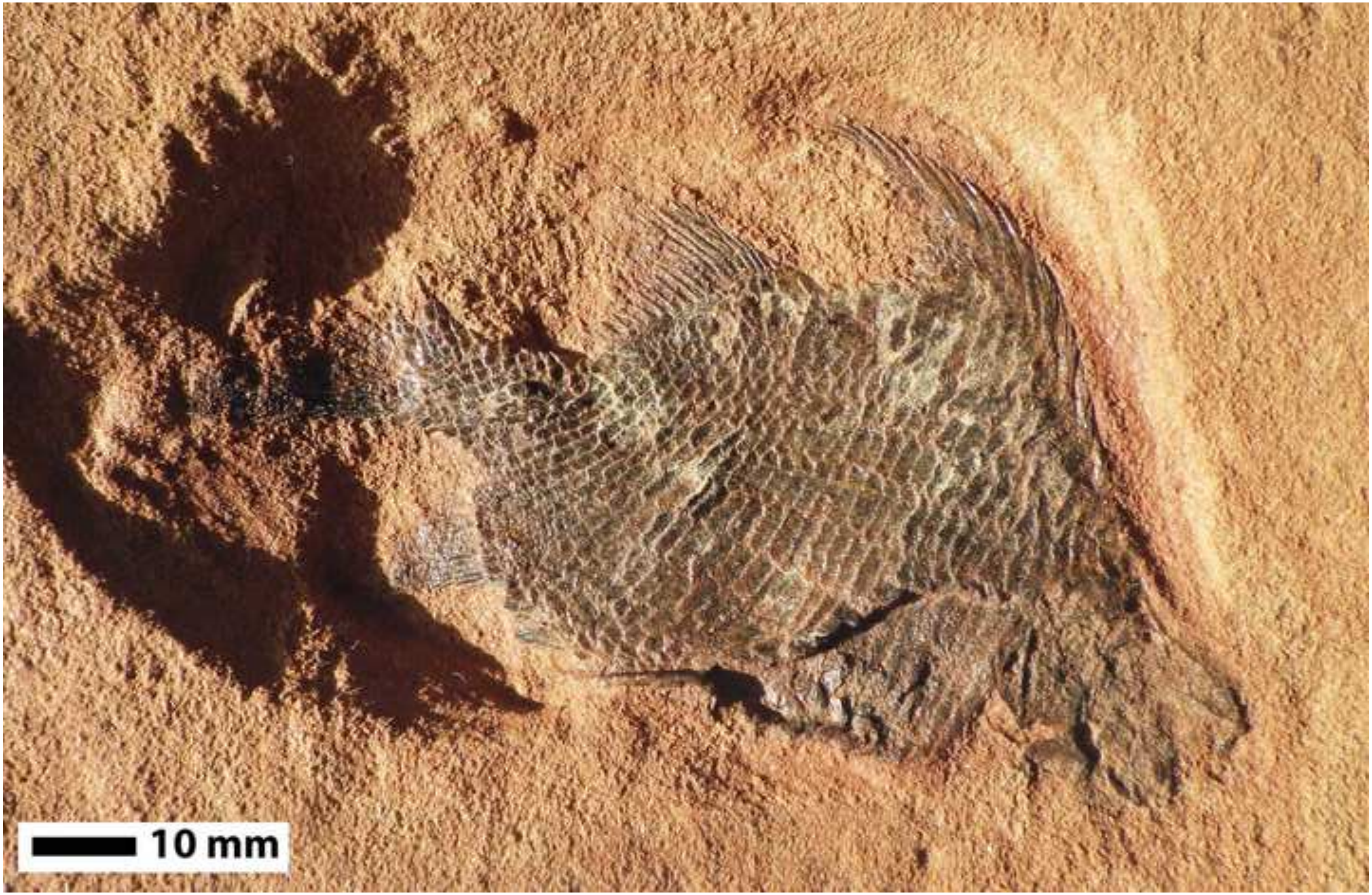
Figure

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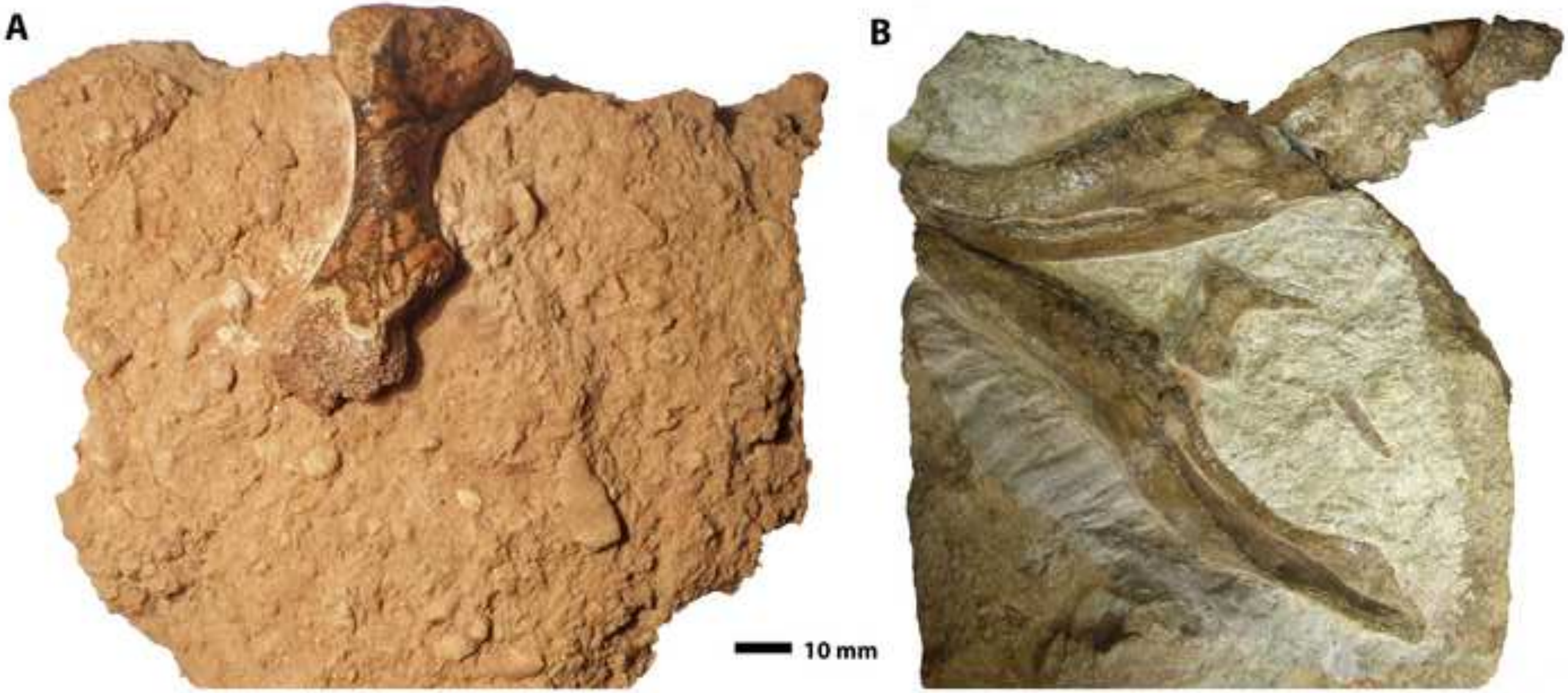
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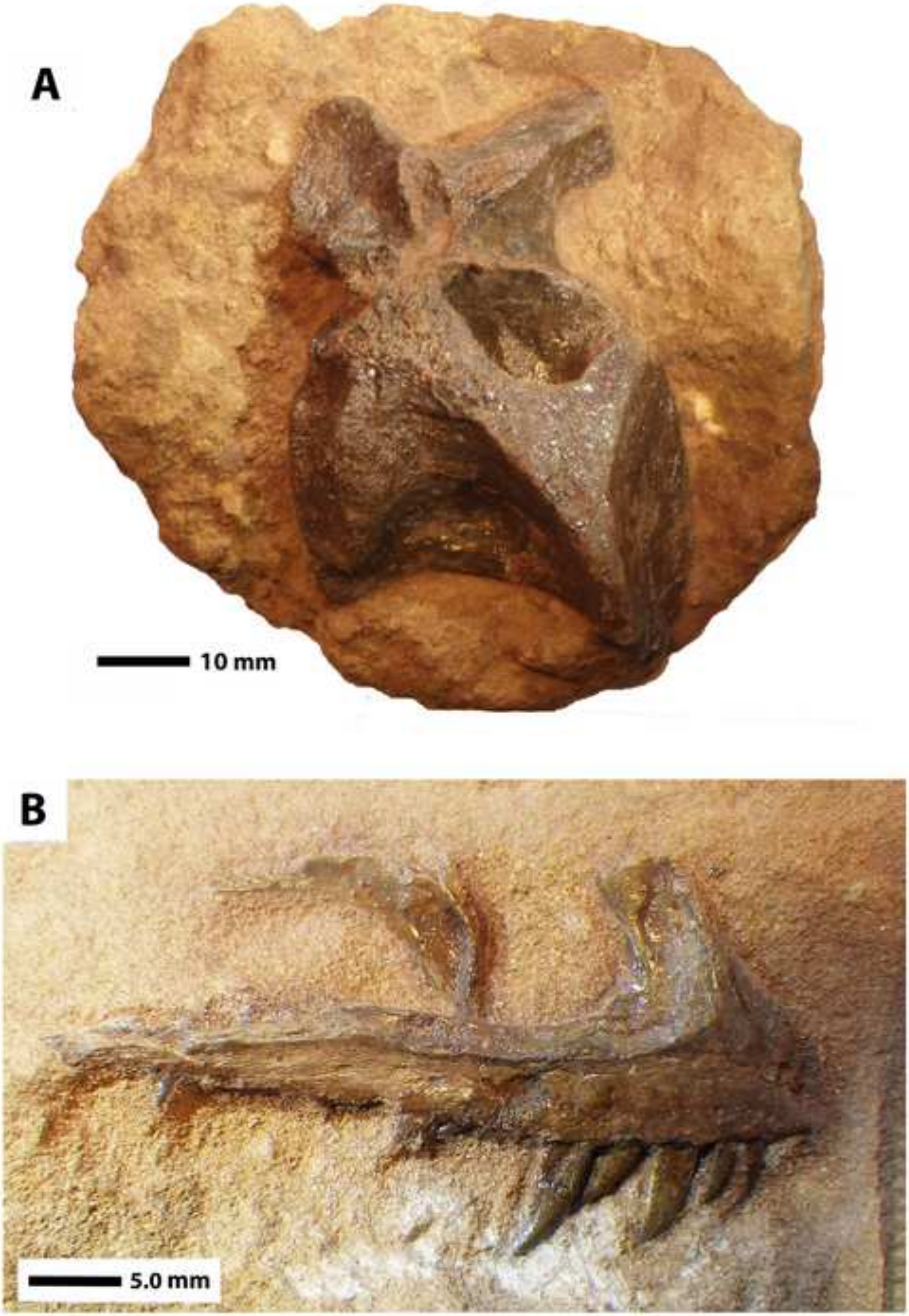
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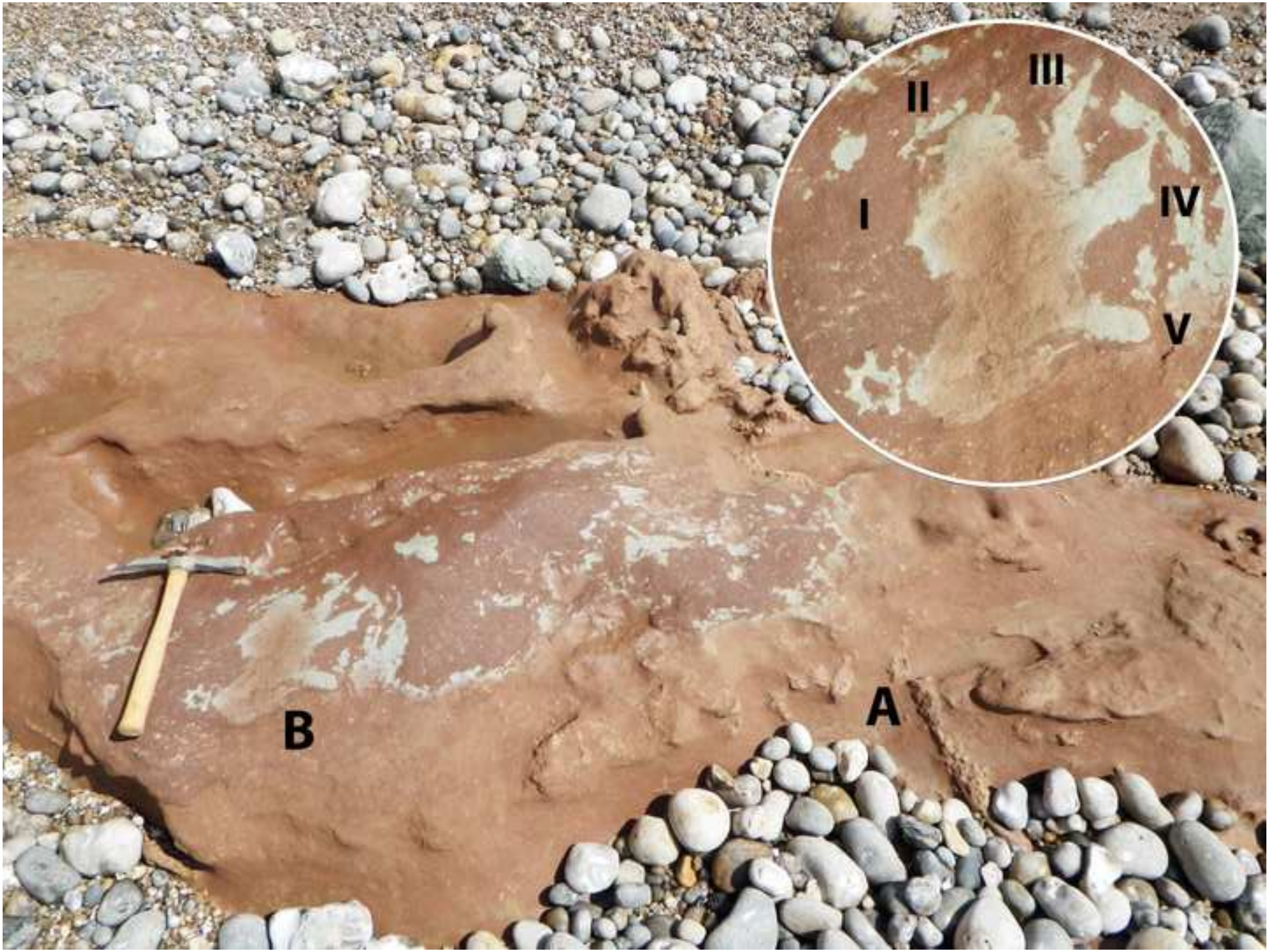

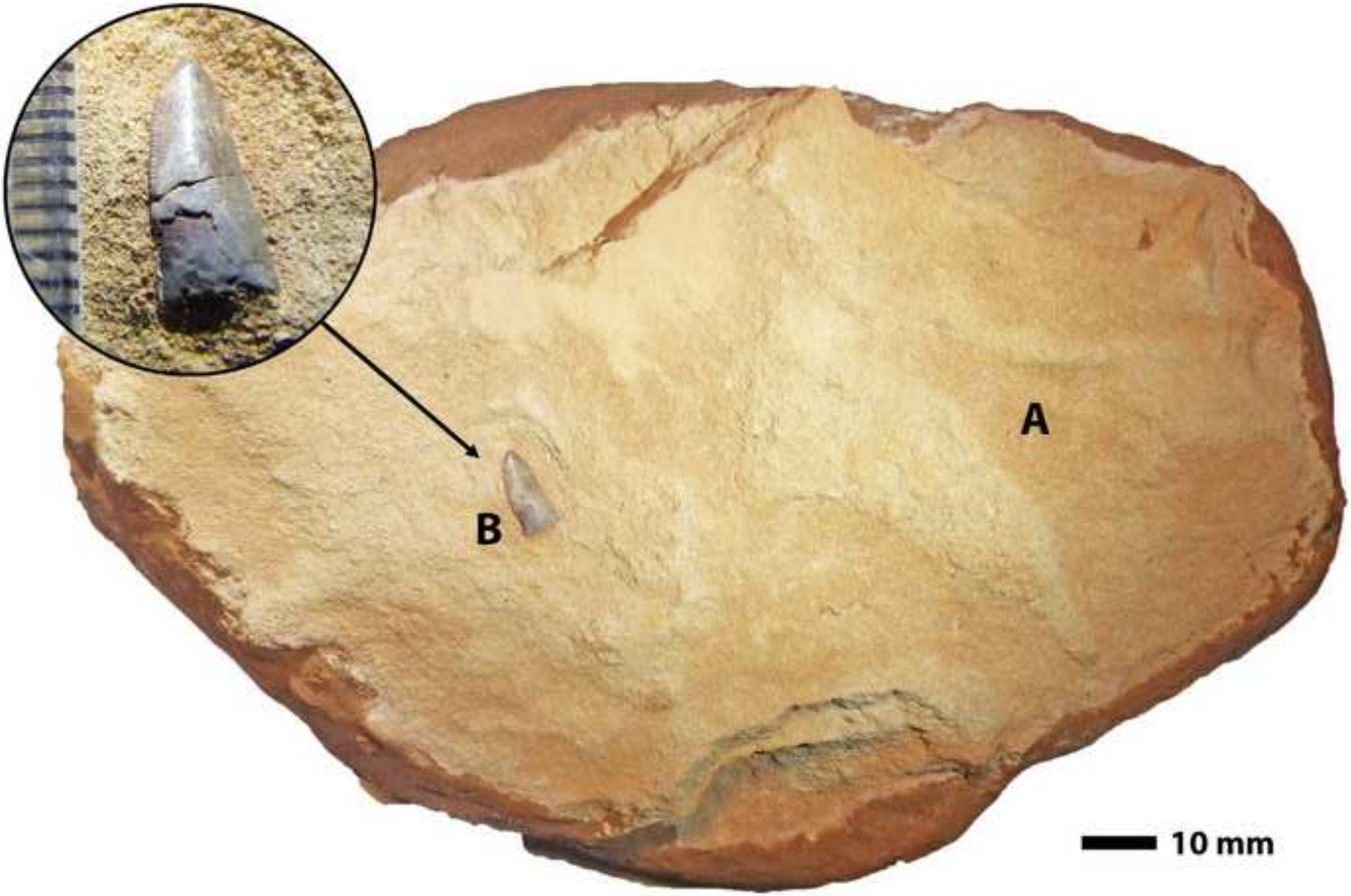
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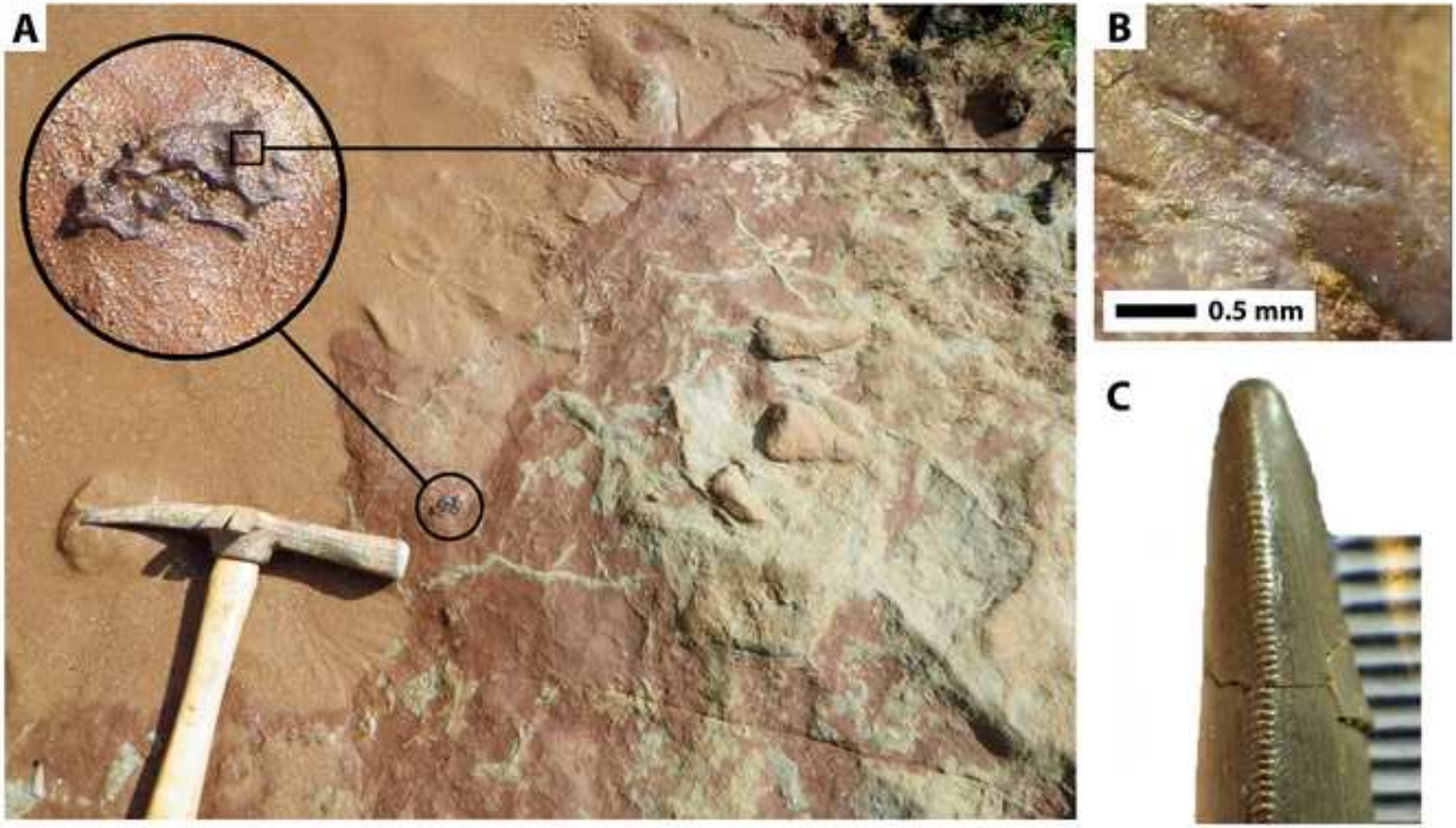
A
B
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C

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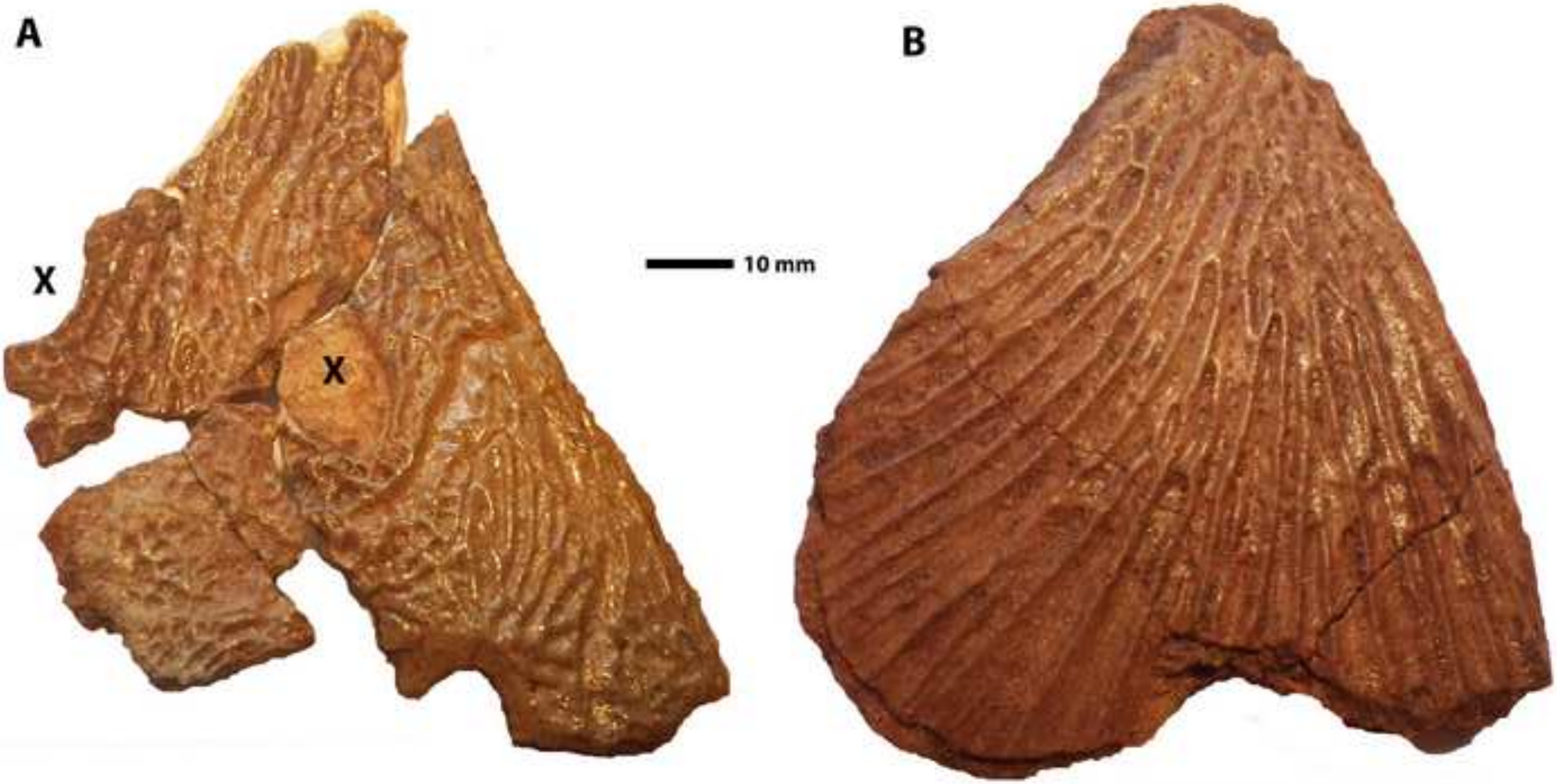


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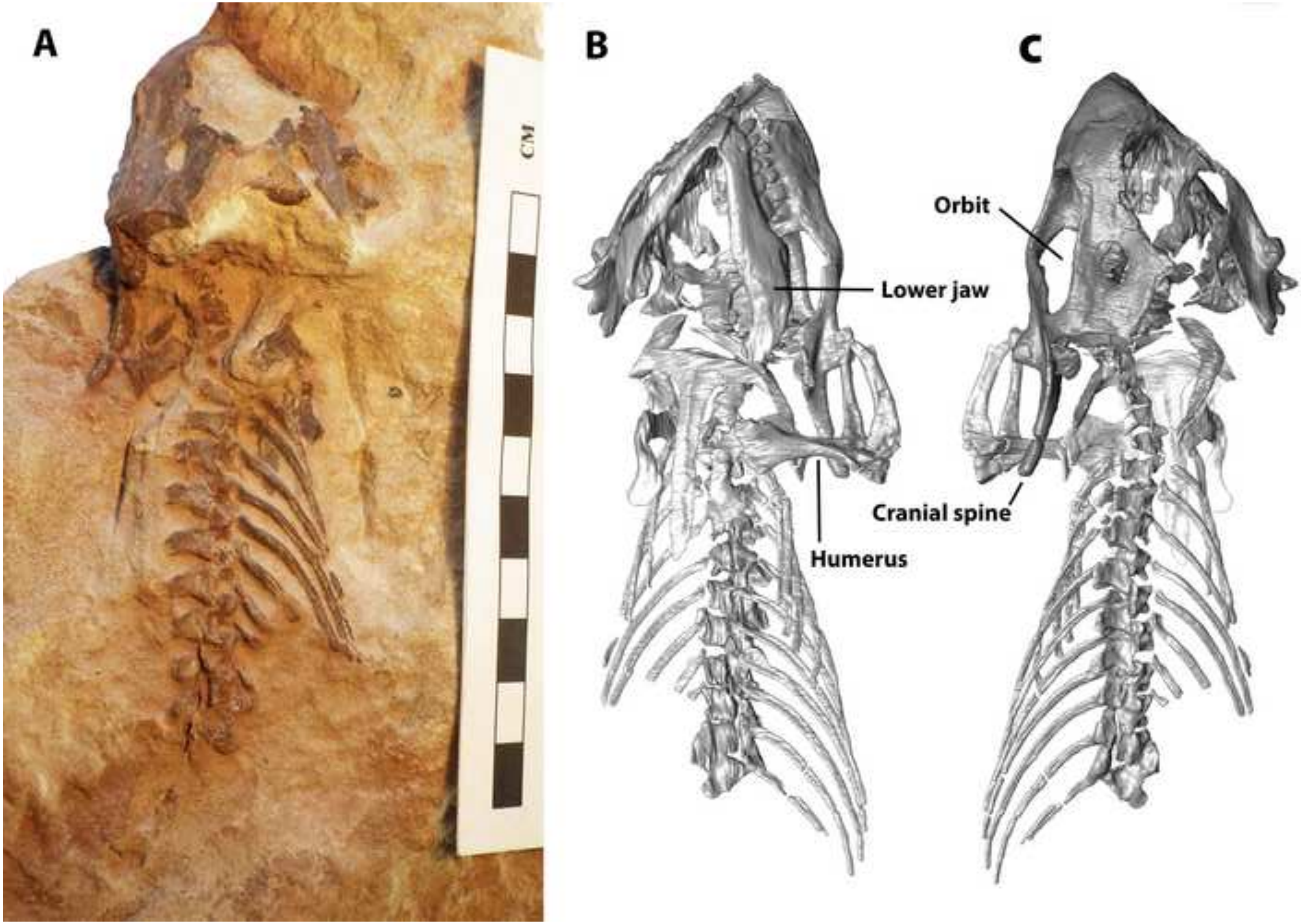

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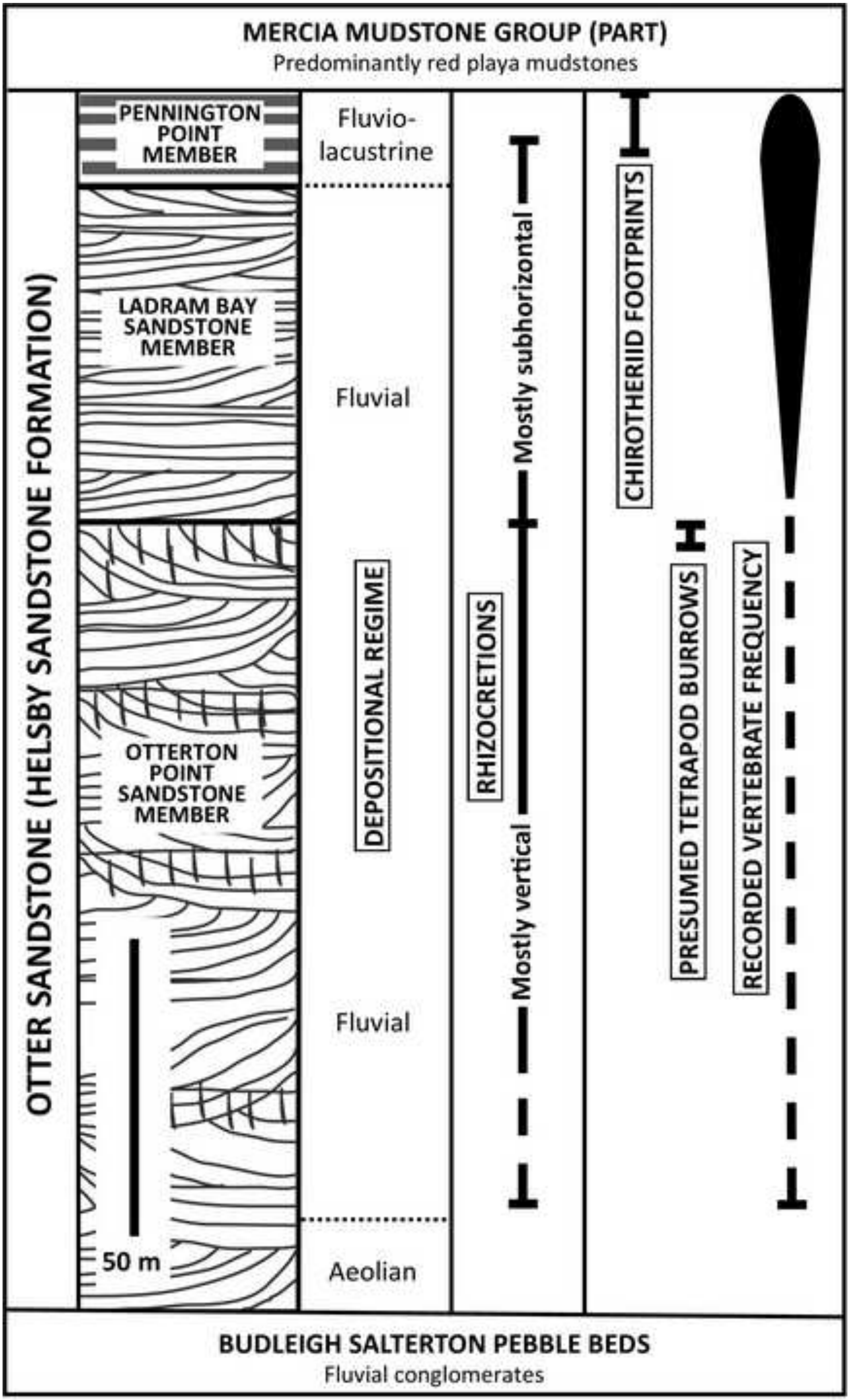

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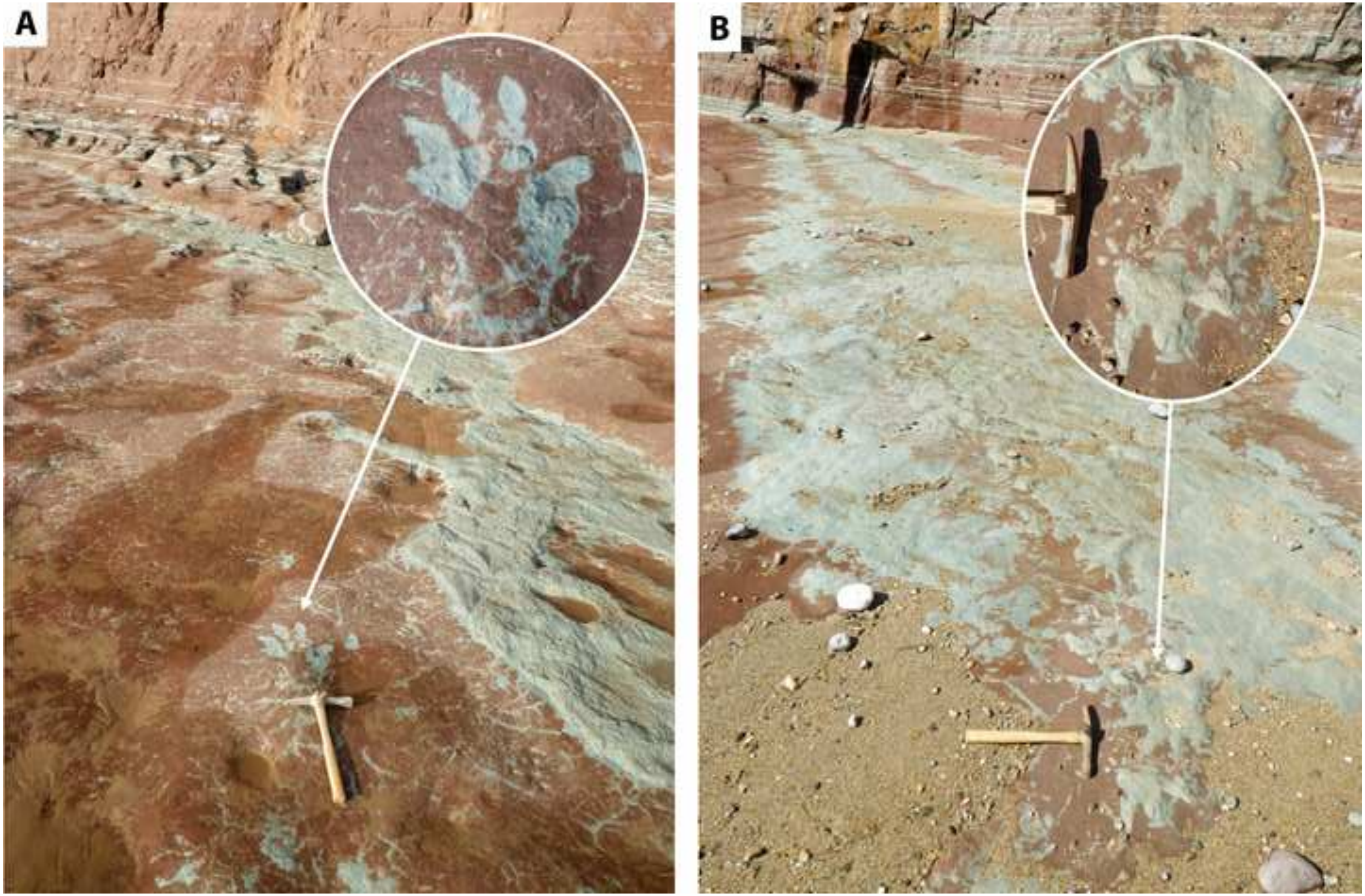

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