The Late Permian herbivore *Suminia* and the early evolution of arboreality in terrestrial vertebrate ecosystems

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Vertebrates have repeatedly filled and partitioned the terrestrial ecosystem, and have been able to occupy new, previously unexplored habitats throughout their history on land. The arboreal ecospace is particularly important in vertebrate evolution because it provides new food resources and protection from large ground-dwelling predators. We investigated the skeletal anatomy of the Late Permian (approx. 260 Ma) herbivorous synapsid *Suminia getmanovi* and performed a morphometric analysis of the phalangeal proportions of a great variety of extant and extinct terrestrial and arboreal tetrapods to discern locomotor function and habitat preference in fossil taxa, with special reference to *Suminia*. The postcranial anatomy of *Suminia* provides the earliest skeletal evidence for prehensile abilities and arboreality in vertebrates, as indicated by its elongate limbs, intrinsic phalangeal proportions, a divergent first digit and potentially prehensile tail. The morphometric analysis further suggests a differentiation between grasping and clinging morphotypes among arboreal vertebrates, the former displaying elongated proximal phalanges and the latter showing an elongation of the penultimate phalanges. The fossil assemblage that includes *Suminia* demonstrates that arboreality and resource partitioning occurred shortly after the initial establishment of the modern type of terrestrial vertebrate ecosystems, with a large number of primary consumers and few top predators.

Keywords: Synapsida; Anomodontia; arboreality; terrestrial ecosystem; evolution

1. INTRODUCTION

Arboreal vertebrates are a major component of terrestrial ecosystems. Small and medium-sized vertebrates, among them several lineages of reptiles, including birds, and several lineages of synapsids, including mammals, have repeatedly and independently invaded this ecospace. Although adaptations to life in trees evolved through convergent evolution, most vertebrates share similar mechanisms, including grasping, clinging, hooking, arm swinging and adhering (Hildebrand & Goslow 2001). As a result, there are readily recognizable ecomorphological adaptations for similar arboreal behaviours. While some of these mechanisms are restricted to certain groups (e.g. arm swinging being limited to primates and adhering being unique to animals of very small body size), grasping is much more widespread and well known in extant primates, other placental mammals, marsupials, chameleons and perching birds (Hildebrand & Goslow 2001). Grasping and clinging can also be readily recognized in the fossil record because it has clear osteological correlates (e.g. Hopson 2001; Bloch & Boyer 2002; Luo *et al.* 2003).

New material of the basal anomodont *Suminia getmanovi* (Ivakhnenko 1994) that was recently excavated at the Upper Permian Kotel'nich locality in the Kirov region of Russia consists of more than a dozen mostly

complete and articulated skeletons on a single large block (figure 1). The skeletal anatomy of *Suminia* displays numerous features that are associated with an arboreal lifestyle, documenting the earliest evidence for arboreality in the fossil record of vertebrates. Anomodontia is an extinct clade of non-mammalian synapsids from the Permian and Triassic, and possibly the Cretaceous (Thulborn & Turner 2003), representing the dominant herbivores of particularly Late Permian terrestrial vertebrate ecosystems (Hotton 1986; DiMichele *et al.* 1992). As a clade, anomodonts obtained a cosmopolitan distribution and, in terms of number of taxa, as well as variety of body forms, they are one of the most diverse groups of terrestrial tetrapods of their time (e.g. Fröbisch 2008, 2009). The new material of *Suminia* comprises an ontogenetic span ranging from mostly subadult (femur length 59.20 mm) to adult (femur length 80.87 mm) individuals, providing one of the most complete pictures of the postcranial anatomy of any Palaeozoic synapsid. The well-preserved skeletons show no evidence of weathering, predation or scavenging, indicating rapid burial, possibly as a result of a catastrophic event. Discrete disarticulation of some skeletons suggests that minor transportation might also have occurred.

The current study presents a preliminary account on the postcranial anatomy of the basal anomodont *S. getmanovi*, which will be described in more detail elsewhere. This study further investigates the variety of phalangeal proportions in extant as well as extinct tetrapods and aims to enable the identification of locomotor behaviour in fossil tetrapods, with special reference to

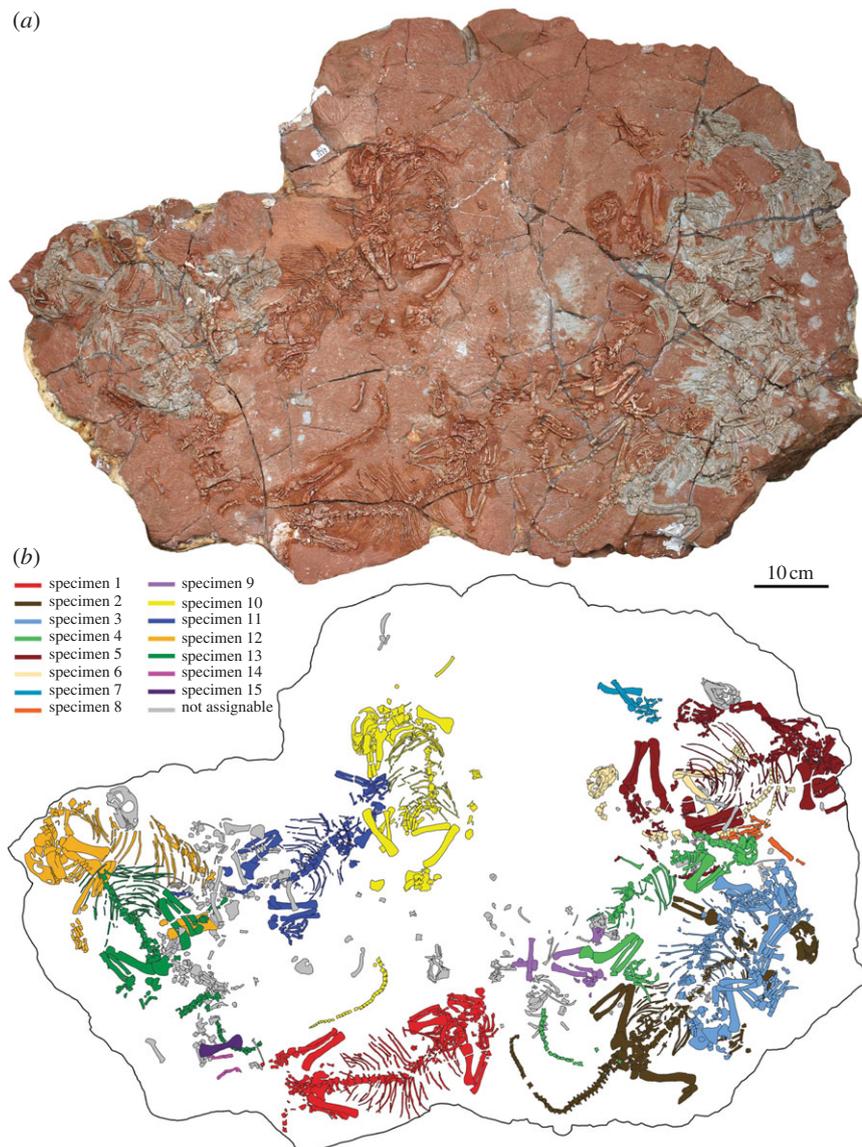* Author for correspondence (jfrobisch@fieldmuseum.org).

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Figure 1. *Suminia getmanovi*, large block with articulated skeletons. (*a*) Photograph and (*b*) colour-coded outline drawing of PIN 2212/116, showing the presence of at least 15 specimens.

Suminia, based on the phalangeal proportions. Moreover, the vertebrate fauna of the Kotel'nich locality represents an excellent example of Late Permian terrestrial vertebrate communities and provides new insights into the evolution of arboreality in terrestrial vertebrate ecosystems.

2. MATERIAL AND METHODS

The length of the metacarpal, proximal phalanx and penultimate phalanx of the third digit was measured in selected fossil synapsids, as well as in arboreal and non-arboreal members of a great variety of extant tetrapods, using digital callipers (table S1 in the electronic supplementary material). Individuals were measured only once. The sampled fossil synapsids include members of every major clade of basal synapsids and non-mammalian therapsids. Measurements of extant tetrapods were taken from chamaeleonids, agamids and iguanids among reptiles, and several groups of mammals, including Primates, Dermoptera, Chiroptera and didelphimorphian Marsupialia. In addition, data for diprotodontian marsupials, rodents and selected primates and lacertids were obtained from the literature (Arnold 1998; Hamrick

2001; Weisbecker & Warton 2006; Weisbecker & Schmid 2007). All measurements were plotted on ternary diagrams using the software package PAST v. 1.78 (Hammer *et al*. 2001).

3. RESULTS
(a) *Discrete evidence for an arboreal lifestyle in* Suminia

The newly available material of the small anomondont *Suminia* (body length approx. 50 cm), known for its unique dentition (Rybczynski & Reisz 2001), reveals numerous autapomorphic features in its postcranium, most of which are associated with an arboreal lifestyle. These include an elongated neck with unusually broad cervical vertebrae, a long tail, a slender, tall scapular blade and elongated limbs (figures 1 and 2). In particular, the proportions of the manus are unusual, measuring 40 per cent of the length of the entire forelimb. Additional autapomorphic characters are displayed in the manus and pes, and comprise an enlarged, phalangiform distal carpal 1 and tarsal 1, elongated penultimate phalangeal
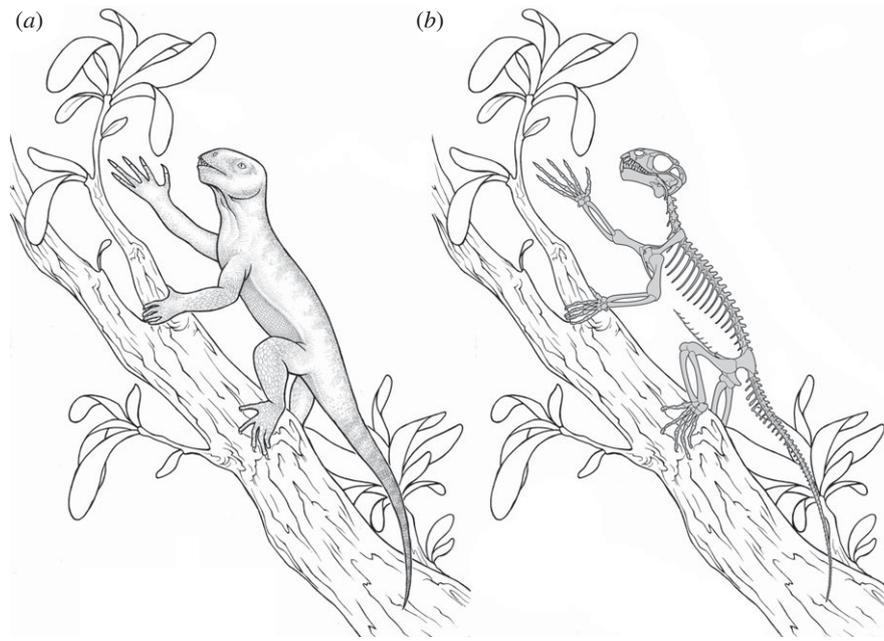
Figure 2. Reconstruction of the basal anomodont *Suminia getmanovi*. (*a*) Flesh and (*b*) skeletal reconstruction.

elements, as well as a plesiomorphic phalangeal formula for amniotes: 2-3-4-5-3 in the hand (manus) and 2-3-4-5-4 in the foot (pes). Moreover, the penultimate phalanges possess a robust proximal end, which becomes progressively more slender towards the distal end of the element. A round distal articular surface for the terminal (ungual) phalanx, not seen in other Palaeozoic vertebrates, permits a greater mobility of the terminal phalanx. The terminal phalanges of *Suminia* are strongly curved and laterally compressed, resulting in a claw-like morphology, which is known to be indicative of clinging abilities in arboreal tetrapods (e.g. Feduccia 1993). These features are particularly conspicuous when compared with other Palaeozoic anomodonts (figure 3*a,c*). Overall, the skeleton of *S. getmanovi* is characterized by its distinct slenderness and a flexible vertebral column, indicated by the elongated cervical region and the lack of fusion between the vertebral centra and neural arches in the dorsal region. The latter feature does not appear to be related to body size and thus ontogenetic age, as some large individuals (e.g. specimens 2 and 3 on the block, Paleontological Institute, Russian Academy of Science, Moscow, Russia—PIN 2212/116) show this lack of fusion, while other smaller individuals display well co-ossified centra and neural arches in this region (e.g. specimen 1 of PIN 2212/116 and Kotel'nich Paleontological Museum, Kotel'nich, Russia—KPM 173).

The most striking features of the postcranial skeleton of *Suminia* are its extremely elongated penultimate phalanges on the large hand and long forelimb, indicating an arboreal lifestyle (see below). There are two ways in which strong elongation of the penultimate phalanx is achieved in *Suminia*: the obvious increase in length, and the addition of phalangeal elements to the penultimate phalanx in digits III and IV, and digit V in the pes. The latter is unexpected because reduction of the phalangeal count from the primitive amniote condition of 2-3-4-5-3 in the manus and 2-3-4-5-4 in the pes to the mammalian phalangeal formula of 2-3-3-3-3 in manus and pes is a

general, well-documented evolutionary trend within non-mammalian synapsids (Hopson 1995). This reduction is achieved by a loss in both manus and pes of one or more elements, preceded by a shortening of the respective elements to disc-like bones. None of the known anomodonts show the primitive condition but rather the derived mammalian phalangeal count, including the basal taxa *Patranomodon*, *Galeops* and *Eodicynodon* (Brinkman 1981; Rubidge *et al.* 1994; Rubidge & Hopson 1996). Only *Suminia* shows the intermediate condition of having one disc-like phalangeal element in digit III, two in digit IV and one in the pedal digit V. Optimization of this character on current cladograms of anomodonts results in divergent patterns. Previous phylogenetic analyses suggest that the condition in *Suminia* represents an evolutionary reversal (e.g. Fröbisch 2007), whereas a recently published phylogeny of basal anomodonts implies a more basal position of *Suminia* than *Patranomodon* and *Galeops* (Liu *et al.* in press), which would explain the phalangeal formula in *Suminia* as intermediate condition. It is these disc-shaped elements that contribute further to the elongation by being tightly attached to the penultimate phalanx in subadults, and co-ossified in the manus of the largest known specimens. Thus, the fusion of these elements combined with the elongated penultimate phalanges has provided a means to greatly enlarge the phalangeal proportion of the autopodium of *Suminia*.

Additional and diagnostic features for arboreality, unseen in any other Palaeozoic vertebrate, include the widely divergent first digit with an angle of approximately 30–40° to the remaining digits of the manus and pes (figures 2 and 3). Distal carpal 1 in the manus and tarsal 1 in the pes are enlarged and phalangiform, and metapodial I is massive and short, and does not contact the other metapodials. The articular surfaces of the carpal and tarsal of the first digit indicate an ability to flex ventrally as well as to abduct and adduct relative to the rest of the manus and pes. This indicates that the
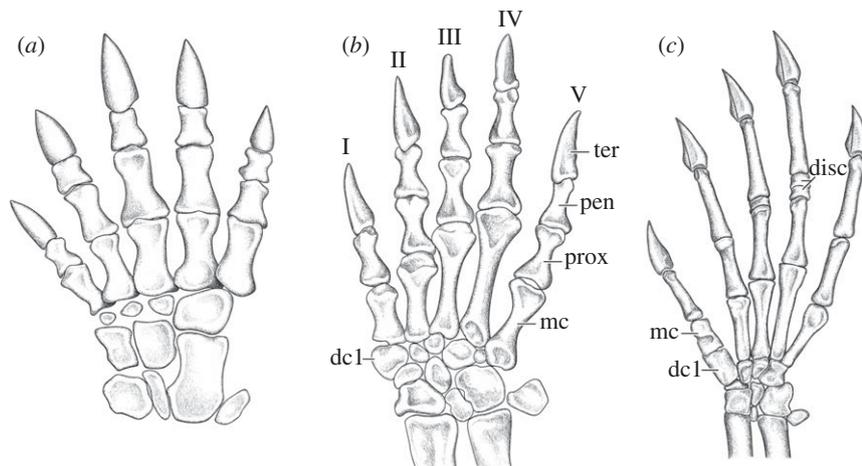
Figure 3. Reconstructions of the manus in anomodonts. (*a*) The dicynodont anomodont *Robertia* (terrestrial, redrawn from Hopson 1995), and the basal anomodonts (*b*) *Galechirus* (terrestrial) and (*c*) *Suminia* (inferred arboreal, morphotype (ii)). dc, distal carpal; disc, disc-like phalangeal element; mc, metcarpal; pen, penultimate phalanx; prox, proximal phalanx; ter, terminal phalanx. Not to scale.

first digit may have been used as an opposable, proximally robust 'thumb'. At the same time, metapodials II–V have very narrow proximal ends that contact each other, forming a very tight complex that allows for little more than flexion and extension along the distal edge of the carpus and tarsus.

A further potential specialization for arboreality is the modified tail. Although *Suminia* shows the plesiomorphic condition of having a very long tail, at least 120 per cent of the precaudal region, the proximal 22 caudal vertebrae bear prominent transverse processes that are fused to comparably long caudal ribs, and the spinous processes retain much of the length of those in the posterior dorsal region. Among anomodonts, these features are seen only in *Suminia*. These characteristics indicate a relative expansion of the anterior region of the tail and are probably related to a hypertrophy of the musculoskeletal system along the proximal part of the tail in order to enable balancing and potentially prehensile abilities in this small synapsid (German 1982; Jenkins & Krause 1983; Rose 1987; Youlatos 2003).

(b) Morphometric evidence for an arboreal lifestyle in Suminia

Phalangeal proportions have previously been used to describe and infer an arboreal lifestyle in other tetrapods, including various mammals (Van Valkenburgh 1985; Lemelin 1999; Hamrick 2001; Bloch & Boyer 2002; Luo *et al*. 2003; Weisbecker & Warton 2006; Weisbecker & Schmid 2007; Kirk *et al*. 2008), lizards (Arnold 1998), pterosaurs (Clark *et al*. 1998) and birds (Hopson 2001). We investigated the phalangeal proportions in the manus of extinct non-mammalian synapsids and various clades of extant tetrapods, including members of reptilian and synapsid amniotes, in a comparative morphometric analysis (figure 4; table S1 in the electronic supplementary material). The results strongly support a general trend in arboreal tetrapods towards an increased phalangeal index, which is the combined length of the proximal and penultimate phalanges as a percentage of their respective metapodial element. Thus, a typical terrestrial

tetrapod is characterized by a long metapodium and short phalanges, whereas a typical arboreal tetrapod shows a short metapodium and long phalanges. In addition, we recognized for the first time two distinct patterns of skeletal specialization within arboreal tetrapods: (i) an elongate proximal phalanx and (ii) an elongate penultimate phalanx. The first morphotype (i) is typically found in primates, including 'plesiadapiforms' (Hamrick 2001; Bloch & Boyer 2002; Kirk *et al*. 2008), and other mammals, including diprotodontian marsupials (e.g. possums, kangaroos, wallabies, wombats; Weisbecker & Warton 2006) and didelphid marsupials (opossums; Lemelin 1999; Luo *et al*. 2003), carnivorans (Van Valkenburgh 1985) and rodents (Weisbecker & Schmid 2007), as well as chameleons (J. Fröbisch 2008, personal observation), and probably represents grasping adaptations using opposable digits. The second morphotype (ii) is known from dermopterans (colugos or 'flying lemurs'; Hamrick 2001; Luo *et al*. 2003) and megachiropterans (megabats; Hamrick 2001) among mammals, as well as iguanid and lacertid lizards (J. Fröbisch 2008, personal observation; Arnold 1998), and the pes of pterosaurs (Clark *et al*. 1998) and birds (Hopson 2001), and appears to be related to clinging behaviour. This latter morphotype (ii) is also clearly developed in the basal therapsid *Suminia*, demonstrating the early evolution of this ecomorphological adaptation for clinging in tetrapods. The position of *Suminia* in the ternary diagram (figure 4) reflects similar phalangeal proportions to extant tetrapods that display not only an arboreal lifestyle but are further capable of gliding (e.g. Dermoptera, Megachiroptera and the lacertid lizard *Holaspis*). However, the skeletal anatomy of *Suminia* shows no further indication that this taxon was a glider, and is therefore conservatively considered to be arboreal only. In addition, Boyer & Bloch (2008) recently suggested that the elongation of penultimate phalanges in dermopterans, megachiropterans and sloths indicates suspensory behaviour rather than gliding adaptations, as has previously been proposed for dermopterans (Beard 1990). While this potentially holds true for mammals, this observation is not supported in reptilian tetrapods with elongated penultimate phalanges. Instead, the
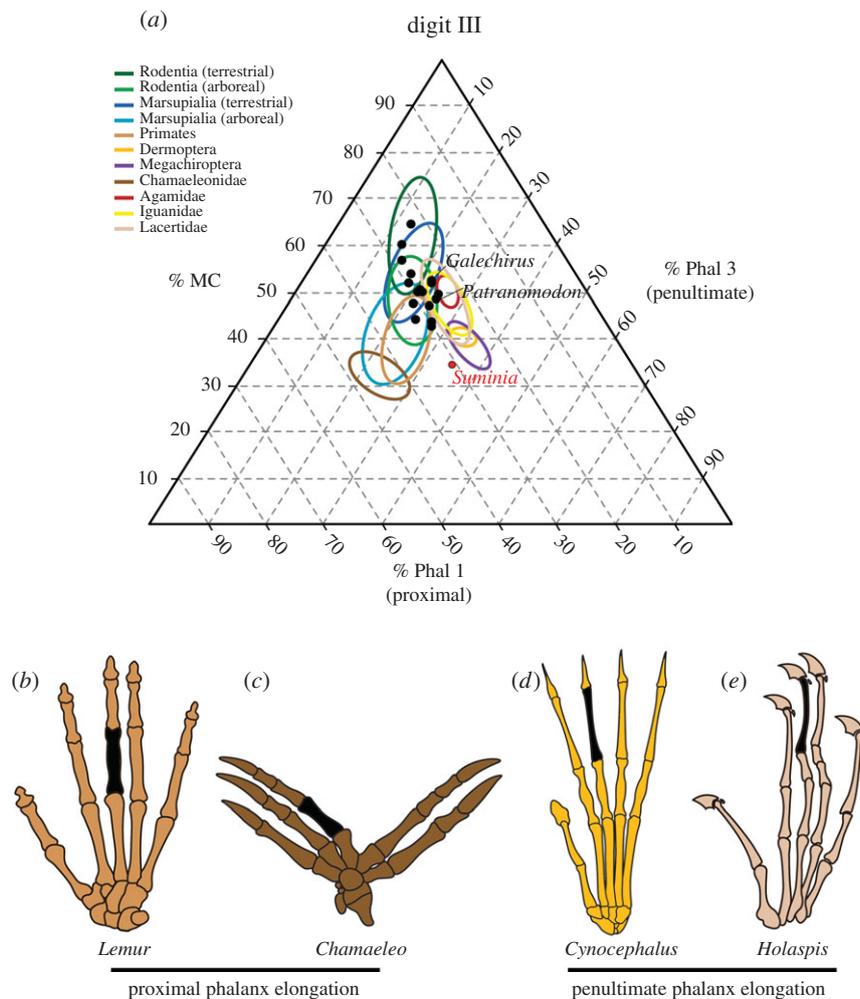
Figure 4. Digital proportions of selected extinct and extant tetrapods. (*a*) Ternary diagram depicting the digital proportions of digit III (MC, metacarpal; Phal 1, phalanx 1; Phal 3, phalanx 3) in selected extinct fossil synapsids and a variety of extant tetrapods. Data points of fossil synapsids are illustrated as black dots, including the basal anomodonts *Galechirus* and *Patranomodon*, with *Suminia* indicated in red. Various clades of extant tetrapods are shown as coloured ellipses. Note the distinct reduction of the metacarpal length in all arboreal taxa, and the clear distinction between the two morphotypes described with an elongated proximal phalanx ((i), bottom left) on the one hand and an elongated penultimate phalanx ((ii), bottom right) on the other hand (see text for details). Reconstructions of the manus in (*b*) the primate *Lemur* (arboreal, morphotype (i), after Böker 1935), (*c*) the chamaeleonid *Chamaeleo* (arboreal, morphotype (i), after Romer 1956), (*d*) the dermopteran *Cynocephalus* (arboreal, morphotype (ii), after Bloch *et al.* 2007) and (*e*) the lacertid *Holaspis* (arboreal, morphotype (ii), after Arnold 1998). Not to scale.

presence of such distinct phalangeal proportions as seen in *Suminia* seem to be associated with large and strongly recurved, claw-shaped terminal phalanges, indicating effective clinging behaviour such as is observable in modern lizards and birds (Arnold 1998; Hopson 2001).

4. DISCUSSION

Arboreal vertebrates are known from all major clades of terrestrial tetrapods, including several lineages among amphibians, reptiles (comprising birds) and mammals. As a result of parallel evolution, arboreal vertebrates independently evolved similar mechanisms as adaptations to an arboreal lifestyle, including grasping, clinging, hooking, arm swinging and adhering (Hildebrand & Goslow 2001). Very small vertebrates (less than 10 cm body length) primarily use adhesive mechanisms, such as capillary adhesion in tree-climbing frogs and salamanders versus dry adhesion in arboreal lizards, such as geckos, some anoline iguanids and

skinks (Cartmill 1985). In contrast, larger vertebrates and in particular mammalian synapsids exploit rather different mechanisms, including skin friction, hooking, clinging and prehensile extremities for grasping. Among them, grasping is one of the most prominent mechanisms that is also clearly recognizable in the fossil record (e.g. Hopson 2001; Bloch & Boyer 2002; Luo *et al.* 2003). While prehensile tails are characterized by a number of characteristics (German 1982; Youlatos 2003), autopodial specializations are expressed in either one or two digits being markedly divergent from the remaining digits in the manus and pes. Such a pattern is well known in extant primates and other placental mammals, as well as marsupials, chameleons, certain tree frogs and perching birds (Cartmill 1985; Hildebrand & Goslow 2001). Moreover, arboreal vertebrates with grasping hands and feet display distinct phalangeal proportions when compared with non-arboreal relatives (Hopson 2001; Bloch & Boyer 2002; Weisbecker & Warton 2006; Weisbecker & Schmid 2007).

Arboreal vertebrates are frequently known from the fossil record and include taxa from the reptilian as well as synapsid lineages of amniotes. Among synapsids, prominent examples of inferred arboreal taxa comprise the Late Jurassic crown-group mammal *Henkelotherium* (Krebs 1991), selected Early Cretaceous crown-group mammals (e.g. *Eomaia* and *Sinodelphis*; Ji *et al*. 2002; Luo *et al*. 2003), members of the extinct mammalian clades Multituberculata and Apatemyidae (Jenkins & Krause 1983; Koenigswald & Schierning 1987), as well as fossil euprimates and 'plesiadapiforms' (Hamrick 2001; Bloch & Boyer 2002; Kirk *et al*. 2008). Among reptiles, specializations for an arboreal lifestyle have been described for a number of taxa, including the Triassic drepanosaurids (e.g. *Megalancosaurus*; Renesto 1994), the Late Triassic archosauromorph *Trilophosaurus* (Spielmann *et al*. 2005), at least selected members of pterosaurs (Wang *et al*. 2008), the Middle Triassic lepidosauromorph *Megachirella* (Renesto & Posenato 2003), the Early Cretaceous lepidosaur *Scandensia* (Evans & Barbadillo 1998) and the Early Eocene gecko *Yantarogekko* (Bauer *et al*. 2005). In addition, an arboreal lifestyle of primitive birds and closely related non-avian theropods has been extensively debated regarding the origin of avian flight ('ground up' versus 'trees down'; for a critical review see Hutchinson & Allen 2009).

The combination of the morphologically distinct characters (discrete and morphometric) of *Suminia* and its small body size indicates that *Suminia* was an arboreal animal capable of using its manus and pes for grasping and clinging, thus representing the oldest evidence for arboreality in the vertebrate fossil record. This shows that the basal anomodont *Suminia* independently evolved grasping and clinging abilities long before (approx. 30 Ma) the evolution of these characters in any other tetrapod. In addition, the arboreality of *Suminia* further documents a broader pattern in synapsid evolution in which the same ecological role was iteratively occupied by successive bursts of synapsid diversification in non-mammalian and later mammalian therapsids (see Luo 2007). The interpretation of the lifestyle of *Suminia* as an arboreal animal is consistent with its highly specialized feeding behaviour, involving oral processing of high-fibre plant materials such as leaves and fine stems (Rybczynski & Reisz 2001).

The morphometric analysis presented in this study supports a general differentiation between grasping and clinging arboreal tetrapods, with the former showing relatively longer proximal than penultimate phalanges and the latter having elongated penultimate phalangeal elements, when compared with their terrestrial relatives. Thereby, *Suminia* displays the phalangeal proportions representative of the clinging morphotype. This results in the unique combination of morphological features in *Suminia*, showing clinging adaptations on the basis of phalangeal proportions and, in addition, prehensile abilities as a result of the divergent first digits in the manus and pes, as well as the likely prehensile tail.

Late Permian terrestrial vertebrate ecosystems provide the earliest evidence for a modern pattern of trophic interactions, with large numbers of herbivores supporting a relatively small number of top predators (Olson 1966; DiMichele *et al*. 1992; Sues & Reisz 1998). The Kotel'nich locality has yielded a rich, diverse assemblage

of vertebrates, representing a prime example of Late Permian terrestrial vertebrate communities. The evidence for this assemblage has been accumulated through a systematic programme of excavations spanning two decades that has yielded more than 350 articulated and partially articulated skeletons. This large fauna is dominated numerically by herbivores, comprising approximately 83 per cent of the recorded specimens, and small numbers of insectivores (approx. 4%), as well as small (approx. 9%) and large (approx. 4%) carnivores (table S2 in the electronic supplementary material). Among herbivores, large-bodied vertebrates are represented by numerous articulated skeletons of dicynodont anomodonts and pareiasaurian reptiles (approx. 79%), as well as the small-bodied basal anomodont *Suminia* (approx. 21%). Although no stomach contents have been recovered yet, the sediments that have yielded the large block with the *Suminia* skeletons also contain several coprolites with extensive leaf fragments. The size of these coprolites (less than 10 mm) is consistent in their association with *Suminia*. The macroflora and palynology of the Kotel'nich locality is well known (Gomankov 1997; Gomankov *et al*. 1998), and *in situ* preservation of roots indicates the presence of large tree-like plants that exceeded 2.5 m in height, much taller than any contemporaneous ground-dwelling herbivores.

The highly diverse flora and fauna at this locality provides the first evidence of food partitioning between small arboreal and much larger ground-dwelling herbivores shortly after the establishment of the trophic structure of modern terrestrial ecosystems, with large numbers of primary consumers supporting a few top predators (DiMichele *et al*. 1992; Sues & Reisz 1998).

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