

variations in upwelling rate above the plume stem, which lead to unrealistically large crustal thickness variations (>200 km). Most of the variation is confined to the plume stem and prominent V-shaped ridges fail to form. Secondly, the depth of the dehydration boundary does not increase significantly away from the ridge axis (Fig. 2a). This prevents the formation of a rheological groove from the off-axis thickening of a thermally controlled lithosphere, which could otherwise channel plume material along the ridge axis for very-low-viscosity plumes²⁴. Flow away from the plume stem is therefore nearly radial. This model thus demonstrates how a radially expanding and pulsing plume can generate Reykjanes V-shaped ridges as well as similar sea-floor age-transgressive ridges south of the Azores hotspot^{25,26}. The possibility of a high-viscosity dehydration layer at other plume-ridge systems has broad implications for the fundamental dynamics of plume-ridge interaction as well as asthenosphere-lithosphere interaction in general. □

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Earliest evidence for efficient oral processing in a terrestrial herbivore

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Herbivores can increase their digestion rate by mechanically reducing particle size through oral trituration¹. Groups of terrestrial vertebrates with the greatest capacity to reduce tough plant foods orally are also the most abundant and diverse, as exemplified by ornithomimid dinosaurs during the Mesozoic and extant artiodactyl and perissodactyl mammals². Thus, the effective oral processing of high-fibre plant material seems to represent an evolutionary innovation of both functional and macroevolutionary significance. However, evidence for oral processing is poorly documented in the fossil record, especially during the initial stages of terrestrial vertebrate diversification^{3,4}. Here we report on the basal anomodont *Suminia getmanovi*, the only known Palaeozoic vertebrate in which unequivocal specializations in its cranium and teeth for high-fibre herbivory are well preserved. We propose that the capacity to comminute tough plant foods was critical to the diversification of anomodonts, the most diverse, widely dispersed and abundant group of Palaeozoic terrestrial vertebrates, and to the onset of modern terrestrial ecosystems.

One of the most significant evolutionary events in the history of life on land is the development of the modern pyramidal trophic structure in which terrestrial plants support a large number of herbivores, which in turn supports a relatively small number of predators⁴. Among vertebrates, this trophic organization was not fully developed until the Upper Permian (260 Myr ago) of the

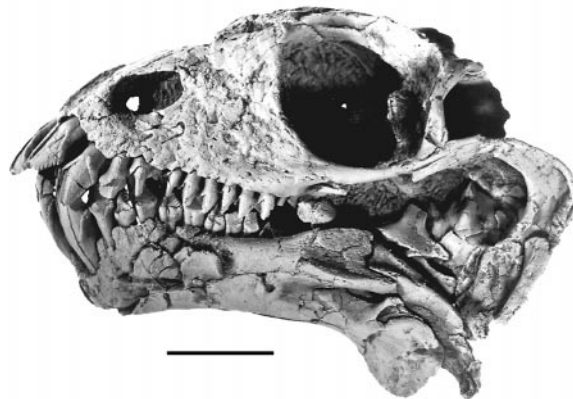


Figure 1 Skull of *Suminia getmanovi*, PIN 2212/62. Scale, 1 cm.

Palaeozoic when the primary consumer base was largely formed by the enormously abundant and diverse anomodonts⁵⁻⁷.

The majority of anomodonts belong to the Dicynodontia, a diverse group characterized by striking cranial specializations including a short snout, an expanded temporal region for adductor musculature, an anteroposteriorly sliding jaw joint (permitting proplinal, or fore-aft, movement, and a beak. This suite of traits has traditionally been thought to have facilitated the processing of plant matter^{8,9}, but they do not provide good evidence of herbivory. For example, birds and turtles, the living beaked vertebrates, both possess herbivorous and non-herbivorous forms, and among turtles both herbivorous and non-herbivorous forms show proplinity². Thus, the presence of beaks and proplinity cannot be directly correlated with herbivory and extensive oral processing. Moreover, it is difficult to infer the relative capacity of dicynodonts to process food orally because their beaks are not preserved in the fossil record and there is no dental occlusion in the few dicynodont taxa that have retained teeth.

*Suminia getmanovi*¹⁰ is a Late Permian (Upper Tatarian) basal anomodont from Kotelnich, in the Vjatka region of Central Russia. Represented by several well preserved skulls (Fig. 1) and four partial skeletons, *Suminia* was a small animal with large eyes, a short, high skull, and long limbs. Its skull is similar to that of dicynodonts, and also possessed an expanded temporal region and sliding jaw joint¹¹.

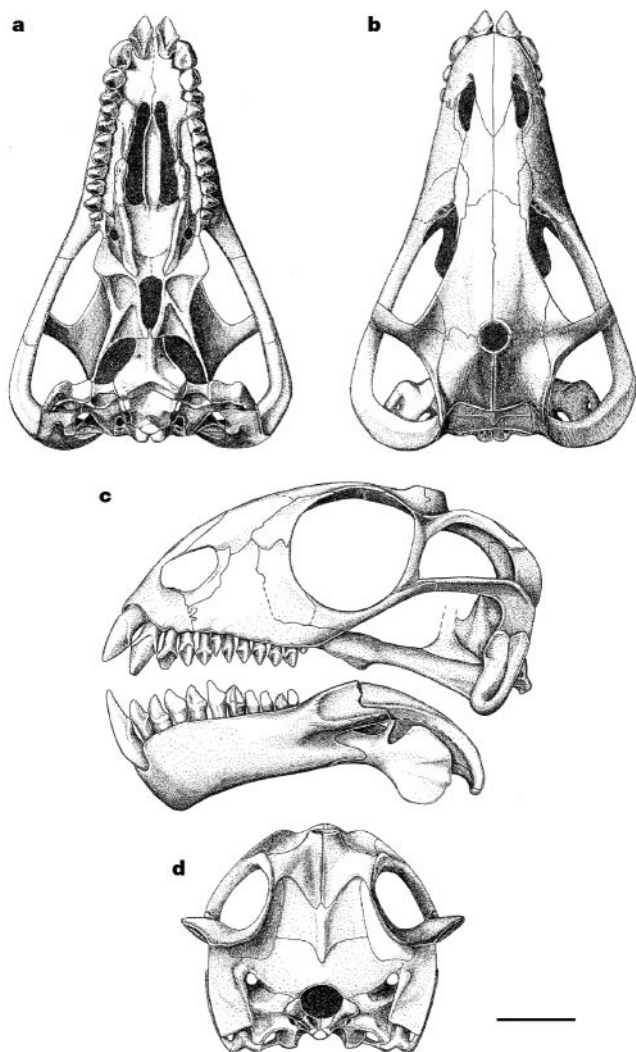


Figure 2 Skull restoration of *Suminia getmanovi*. Based largely on PIN 2212/62, in ventral (a), dorsal (b), lateral (c) and occipital (d) views. Scale, 1 cm.

Instead of a beak, it possessed a complete marginal dentition of 'leaf-shaped' teeth, which are labiolingually compressed with a widened base, and coarse serrations along anterior and posterior edges that are oriented at 45° or less from the margin of the tooth¹². Such teeth have evolved convergently in at least five independent lineages of terrestrial herbivores: iguanid lizards, ornithischian and prosauropod dinosaurs, pareiasaurs and caseid synapsids^{4,6,12}. In *Suminia*, the teeth are closely packed and oriented in echelon so that the serrated edges of the teeth are angled obliquely relative to the long axis of the tooth row. A similar condition is seen in iguanas, ornithischian dinosaurs and prosauropod dinosaurs¹².

The overall pattern of tooth shape and wear in *Suminia* is entirely consistent with herbivory. The enlarged anterior incisiform teeth were probably used to detach portions of plants for ingestion, in a manner similar to the herbivorous lizard *Uromastix*¹³. The presence of anterior teeth specialized for cropping is indicative of an herbivorous diet because herbivores must be able to detach portions

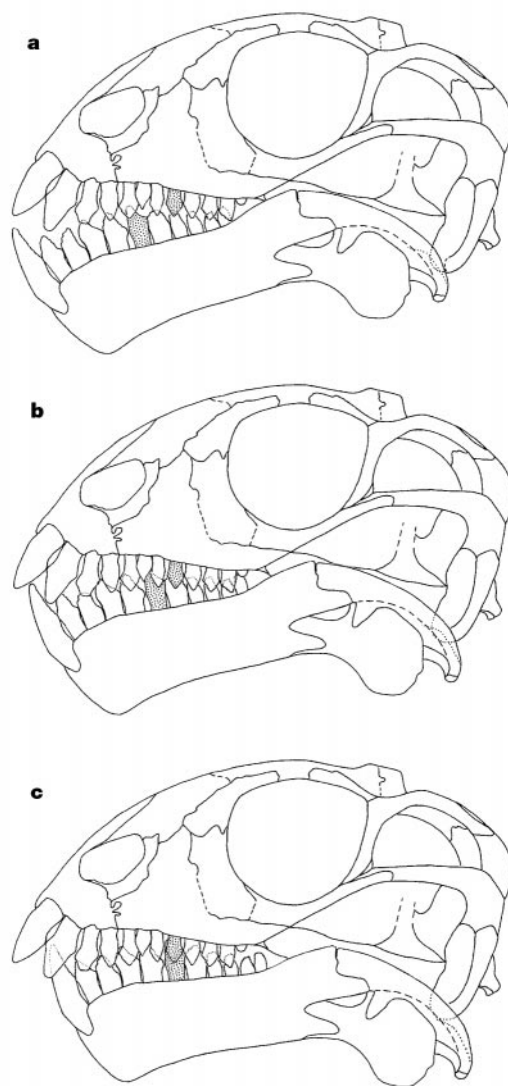


Figure 3 Reconstructed power stroke in *Suminia*. Stippled teeth in the upper jaw and dentary bones are U8 and L6, respectively. The power stroke can be divided into three major stages. **a**, In the earliest phase of occlusion the lower teeth move along the lingual surface of the upper teeth in a motion that combines elevation and retraction. **b**, In the second stage the direction of movement of the lower teeth becomes increasingly longitudinal. **c**, In the last stage of the power stroke the jaw motion is nearly parallel with the tooth row.

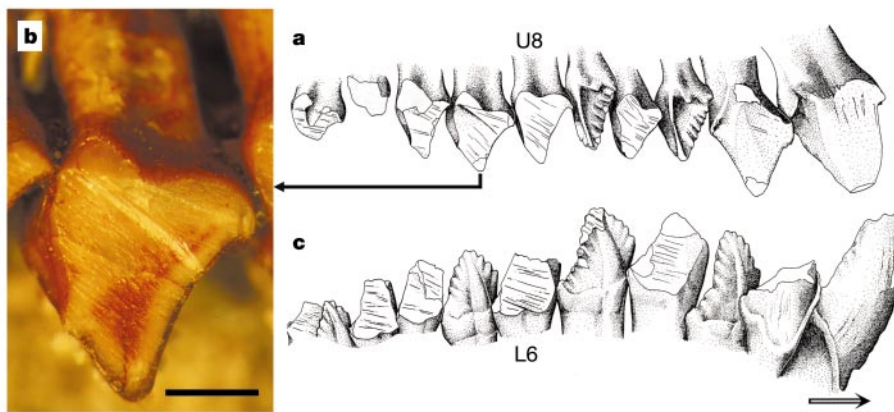


Figure 4 Lingual surface of the right upper tooth row and buccal surface of the right lower tooth row of *Suminia* (PIN 2212/62) and photomicrograph image of U8 tooth. **a**, The upper tooth row and **b**, **c**, U8 are shown in mirror-image so that they may be compared directly to those of the lower tooth row. The wear facet of U8 is characterized by a large ventral region of steeply-angled ($50 \pm 5^\circ$) striations and a smaller region of shallower-angled features ($20 \pm 5^\circ$). These two regions are separated by a step, with the ventral region

being recessed. The dorsal striations were created by L6 whereas the ventral striations were created by the more laterally positioned L8. The step between the two regions is the result of L8 being more laterally positioned than L6. L7 is newly erupted, non-occluding lower tooth that accounts for the step seen in U8. The arrow with double-lined shaft indicates the anterior direction on the dentition. Scale, 1 mm.

of plants before ingestion. *Suminia*'s posterior teeth processed ingested food materials, and the upper and lower posterior tooth rows have wear facets on the labial and lingual aspects of the teeth, respectively. These wear facets are distinct and evidently derived from precise, tooth-to-tooth occlusion, rather than tooth-to-food wear¹⁴.

The jaw action that processes food within the oral cavity is the power stroke (Fig. 3). In *Suminia*, the high angle of the occlusal plane (about $7.0 \pm 5^\circ$ from the plane of the jaws) and the presence of roughly parallel striations over the entire surface of the wear facets (Fig. 4) indicate that food particles were reduced with a precise, shearing power stroke (as opposed to crushing). Such an occluding, leaf-shaped dentition with a shearing power stroke is not seen again until it appears convergently in the Mesozoic with the appearance of ornithischian dinosaurs.

The superb preservation of the skull and dentition of *Suminia* (Figs 1, 2) made it possible to infer the pattern of tooth occlusion during the power stroke, the first such reconstruction for a Palaeozoic tetrapod. The shape of the jaw joint and the steeply angled wear facets indicate that jaw movement during the power stroke was constrained to the sagittal plane. The direction of the power stroke was inferred from a combination of evidence including: (1) the posteriorly oriented external adductor musculature; (2) the wear profiles across the enamel–dentine interfaces¹⁵; (3) the concave curvature of the anterior blade edges of the upper teeth and posterior blade edges of the lower teeth and the occurrence of thickened enamel on the anterior edge of the upper tooth blades^{16,17}. All evidence is consistent with a retractive power stroke.

The pattern of tooth occlusion during the power stroke was reconstructed from microwear striations on the tooth wear facets (Fig. 4). The power stroke would have involved roughly the posterior two-thirds of the tooth row, the jaw would have retracted for about 20% of the total tooth row length, and each of the occluding lower teeth would have contacted two or three upper teeth (Fig. 3). Consequently, during a single power stroke the blade edge of each lower tooth would have occluded with several upper teeth (and vice versa). This contrasts with an orthal power stroke in which each blade edge functions once per power stroke. Thus, the retractive power stroke in *Suminia* permitted an enhanced capacity to reduce mechanically tough plant material.

In summary, the dentition of *Suminia* is clearly more specialized for high-fibre herbivory than any other known Palaeozoic tetrapod,

and the combined cranial and dental anatomy provides conclusive evidence that extensive oral processing took place in this anomodont. This finding is significant not only because it is the oldest known such example in the evolutionary history of terrestrial vertebrates, but also because it indicates an association between the evolution of the anomodont/dicynodont-type cranial architecture and the extensive oral processing of high-fibre plant materials. Specifically, *Suminia* is a basal member of Anomodontia¹¹, and this suggests that the capacity to process orally tough plant material may have been a basal 'innovation' within anomodonts. In conclusion, effective oral processing of high-fibre plant materials appears to have been an important factor in the evolution and diversification of the anomodonts, the largest herbivorous group that was associated with the onset of the modern terrestrial ecosystem. □

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Effects of macrophyte species richness on wetland ecosystem functioning and services

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Wetlands provide many important ecosystem services to human society^{1–5}, which may depend on how plant diversity influences biomass production and nutrient retention^{4,6–8}. Vascular aquatic plant diversity may not necessarily enhance wetland ecosystem functioning, however, because competition among these plant species can be strong, often resulting in the local dominance of a single species^{4,9}. Here we have manipulated the species richness of rooted, submerged aquatic plant (macrophyte) communities in experimental wetland mesocosms. We found higher algal and total plant (algal plus macrophyte) biomass, as well as lower loss of total phosphorus, in mesocosms with a greater richness of macrophyte species. Greater plant biomass resulted from a sampling effect; that is, the increased chance in species mixtures that algal production would be facilitated by the presence of a less competitive species—in this case, crisped pondweed. Lower losses of total phosphorus resulted from the greater chance in species mixtures of a high algal biomass and the presence of sago pondweed, which physically filter particulate phosphorus from the water^{2,10,11}. These indirect and direct effects of macrophyte species richness on algal production, total plant biomass and phosphorus loss suggest that management practices that maintain macrophyte diversity may enhance the functioning and associated services of wetland ecosystems.

A critical question in environmental biology is whether macrophyte diversity in wetlands determines the effectiveness of the well-known services of wetlands to society, such as the sustainable production of food, recreational opportunities, and water purification by retention of pollutants and sediments. These services probably depend on how well wetlands perform certain ecosystem functions, such as nutrient retention^{1,2,12} and primary production^{1,13,14}. Work in grasslands has suggested that greater plant species richness leads to more efficient uptake of nutrients and greater productivity^{15–18}; however, local environments in wetlands are typically dominated by a single vascular plant species^{4,9}. Thus, vascular plant diversity in wetlands may not affect ecosystem functioning positively, or even by the same mechanisms operating in grassland systems, and therefore biodiversity may not positively affect ecosystem functioning ubiquitously. For these reasons, we investigated whether the diversity of submerged, rooted freshwater

aquatic vascular plants can affect wetland biomass production and phosphorus retention—two ecosystem processes closely related to wetland ecosystem services^{1,2}.

We manipulated species richness of four submerged aquatic macrophyte species, sago pondweed (*Potamogeton pectinatus*), long-leaved pondweed (*Potamogeton nodosus*), crisped pondweed (*Potamogeton crispus*) and horned pondweed (*Zannichellia palustris*), in experimental mesocosms. The species are functionally and morphologically different, for example in their use of space and resources in soil, water and air.

Aboveground biomass of macrophytes ('shoot biomass') was measured to understand how macrophyte biomass is correlated with macrophyte species richness. Periphyton, which were present predominantly as green filamentous algae and hereafter are referred to as 'algae', were also measured because the macrophyte species differed in how well they supported algae, and because algae are an important structural and functional component of wetlands^{11,19}. Phytoplankton were not measured owing to their relatively low biomass compared with the biomass produced by filamentous algae.

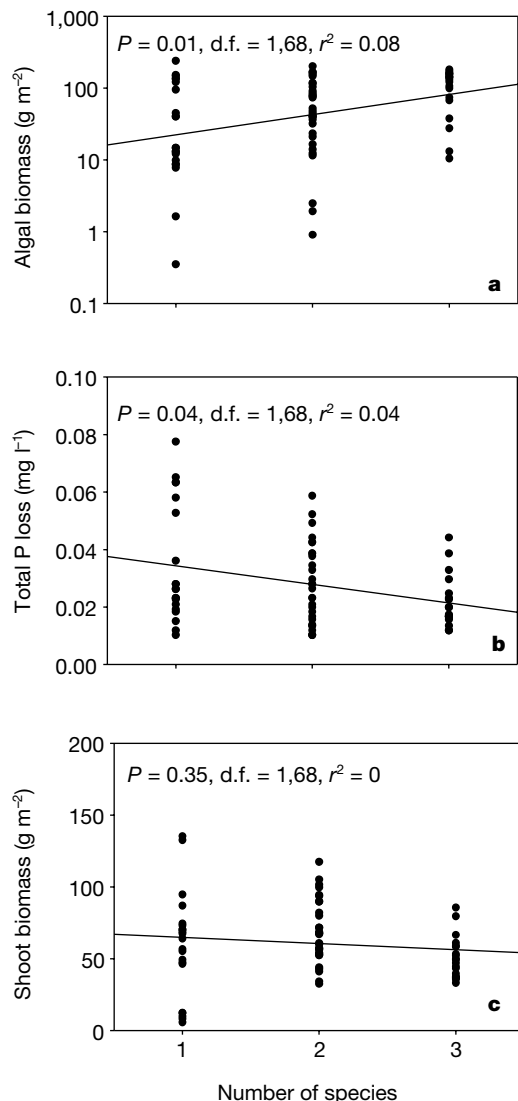


Figure 1 The effect of species richness on algal biomass (a), nutrient retention (b) and above-ground macrophyte biomass (c) (mean \pm s.e.). Solid line is regression of biomass or total P versus species richness. Algal biomass is periphyton biomass that is mostly composed of green filamentous algae. Nutrient retention was inferred from measured total phosphorus (P) loss from the outflow of each mesocosm. Shoot biomass is aboveground biomass of submerged aquatic macrophytes.

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