

Osteolepiforms and the ancestry of tetrapods

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Fossil discoveries^{1–7} and improved phylogenies^{3–5,7} have greatly improved our understanding of the origin of tetrapods, making it possible to reconstruct sequences of character change leading to tetrapod morphologies^{5,7} and to tentatively identify the genetic basis for some of these changes^{8,9}. However, progress has centred on the upper part of the Tetrapodomorpha⁵ which is occupied by Devonian tetrapods such as *Acanthostega*^{1,2,5} and *Ichthyostega*¹. Few advances have been made in improving our understanding of the lower, 'fish' part of the group, beyond establishing Elpistostegalia, Osteolepiformes and Rhizodontida as progressively more

primitive constituents^{10–13}. It has not been convincingly confirmed or disproved that the Osteolepiformes, a diverse but structurally uniform group that is central to the debate about tetrapod origins^{14–17}, is monophyletic relative to tetrapods (that is, a single side branch on the tetrapod lineage). The earliest steps of the fish–tetrapod transition have thus remained poorly resolved. Here we present the first detailed analysis of the lower part of the Tetrapodomorpha, based on 99 characters scored for 29 taxa. We show that both the Osteolepiformes as a whole and their constituent group Osteolepididae are paraphyletic to tetrapods (that is, each comprises a section of the tetrapod lineage with several side branches), and that their 'uniting characters' are attributes of the tetrapodomorph stem lineage. The supposedly discredited idea of osteolepiforms as tetrapod ancestors^{14–17} is, in effect, supported by our analysis. Tetrapod-like character complexes evolved three times in parallel within the Tetrapodomorpha.

During much of this century, research into the origin of Tetrapoda (defined here provisionally as 'vertebrates with limbs', thus including the crown group and top end of the stem of the total group Tetrapodomorpha^{3,12}) focused on the osteolepiforms as potential ancestors^{14–17}. Particular emphasis was placed on *Eusthenopteron*, the first osteolepiform to be described in exhaustive anatomical detail^{14,16}. *Eusthenopteron* was frequently used as a starting point for explaining the origin of tetrapod characters^{14,16,17}. However, the first thorough cladistic review of sarcopterygian interrelationships¹⁸ dismissed the osteolepiforms as an ill-defined assemblage of primitive lobe-fins, remote from tetrapods. Further work reinstated the osteolepiforms in the tetrapod stem group^{10,19,20}, but has generally avoided the issue of osteolepiform

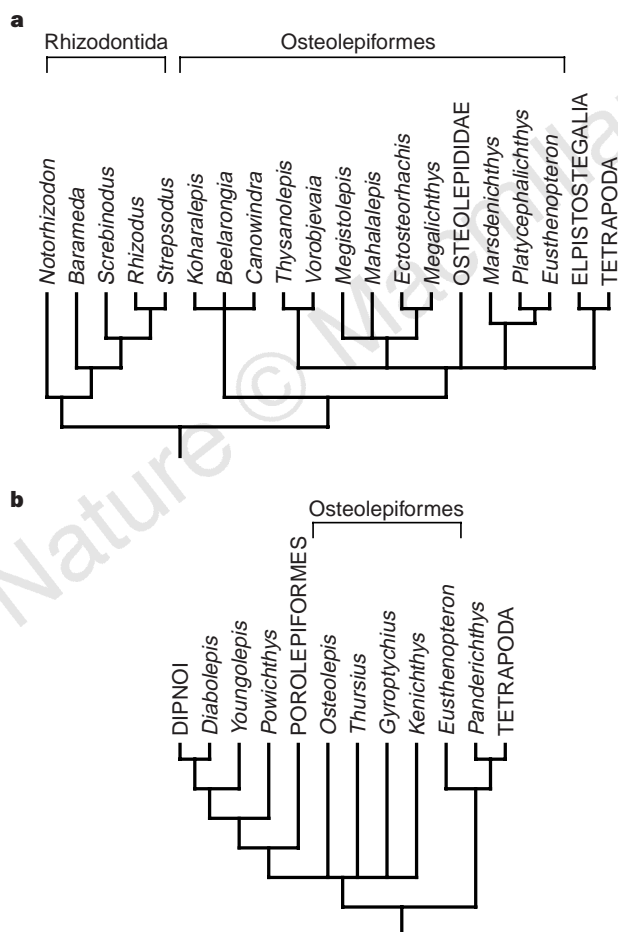


Figure 1 Previous osteolepiform phylogenies. **a**, Young *et al.*'s analysis²¹. **b**, Chang and Yu's analysis²². The elpistostegid–tetrapod sistergroup relationship is the only point of agreement. Both cladograms contain large unresolved polytomies. Young *et al.*'s analysis (produced 'by hand') is based on 38 characters, of which 20 match characters in our matrix, 9 are inapplicable to our analysis, and 9 were rejected by us. Chang and Yu's analysis (produced by PAUP3.1.1) is based on 90 characters, of which 48 match ours, 21 are inapplicable, and 21 were rejected. Judgements of character states for certain taxa differ from ours in both cases.

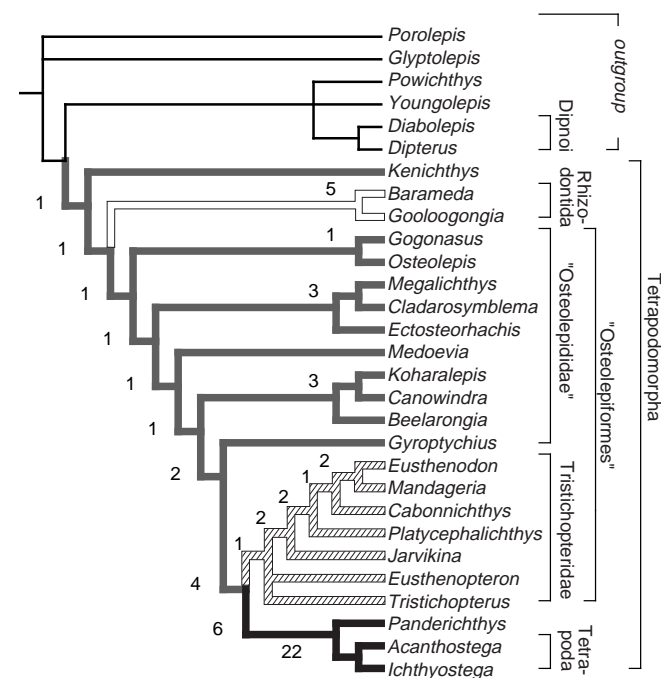


Figure 2 New phylogeny of the tetrapodomorph stem group (consensus of 9 trees, based on 99 characters scored for 29 taxa). Bremer support values are shown at nodes. Tree length, 196 steps; consistency index, 0.571; homoplasy index, 0.429; retention index, 0.772; rescaled consistency index, 0.441. Thin black lines represent outgroups; grey lines indicate 'osteolepids' (including the problematic genus *Kenichthys*³⁰); empty outline indicates rhizodonts; positive slope hatching indicates tristichopterids; thick black lines indicate elpistostegids+tetrapods. 'Tetrapoda' indicates the clade 'vertebrates with limbs' which contains, but is more inclusive than, the tetrapodomorph crown group.

monophyly by using *Eusthenopteron*, explicitly or implicitly, as the principal representative.

Two analyses have attempted to resolve osteolepiform interrelationships cladistically, with incompatible results (Fig. 1)^{21,22}. Both were based on relatively small data sets of 760 and 1,260 data points, respectively, as compared with 2,871 for our analysis. More important, one analysis²¹ included the 'rhizodont' *Notorhizodon*, which appears to be a mixture of at least two unrelated fishes (P.E.A. and Z.J., manuscript in preparation), whereas the other²² included published data on *Thursius*²³, which contain some inaccuracies because of preparation damage (P.E.A., personal observation). Our analysis is also the first to incorporate the perfectly preserved three-dimensional osteolepiforms *Medoevia*²⁴ and *Gogonasus*²⁵, and the articulated rhizodont *Gooloogongia*¹³, which add greatly to the quality of the data.

Our analysis (Fig. 2) shows the Osteolepiformes to be paraphyletic. Of the two traditionally accepted osteolepiform subgroups, the Tristichopteridae (=Eustenopteridae) are closer to tetrapods than are the Osteolepididae, and the latter are themselves paraphyletic. Bremer support values for the nodes are generally low (Fig. 2). However, specifying a monophyletic Osteolepiformes increases the tree length by six steps. Reversing the positions of osteolepids and tristichopterids relative to tetrapods, by specifying an osteolepid–elpistostegid–tetrapod clade, likewise requires six steps. In contrast, a monophyletic Osteolepididae can be achieved with only two extra steps. We conclude that osteolepiform paraphyly relative to Tetra-

poda+Elpistostegalia, and the position of Tristichopteridae crownward to Osteolepididae, is well supported, but that the support for osteolepidid paraphyly is weak. Osteolepiformes should no longer be used as a formal taxonomic group.

The implications of this are profound. If the 'osteolepiforms' are paraphyletic, their numerous shared characteristics are attributes of the stem lineage, and thus 'ancestral characters' for the Tetrapoda+Elpistostegalia. The characters include *inter alia* (Fig. 3) a hinged braincase where the hinge ran through the profundus nerve foramen, a unique pattern of dermal bones, a small tripodal scapulocoracoid (endoskeletal shoulder girdle), anal and posterior dorsal fin supports comprising a basal plate and three unjointed radials, and a pectoral fin skeleton comprising four axial elements (humerus, ulna, ulnare, IV), preaxial unjointed radials and a postaxial flange on the ulnare^{14–17}.

This information allows more precise statements to be made about the evolution of tetrapod morphologies, and will thus allow more rigorous framing of hypotheses in tetrapod phylogenetics, biomechanics and evolutionary developmental genetics. The paraphyletic condition of the 'Osteolepiformes' relative to Tetrapoda and the comparatively crownward position of *Eusthenopteron* both agree surprisingly well with precladistic perceptions of this group^{14–16}.

Derived characters which originate within the 'osteolepiform' part of the Tetrapodomorpha include loss of cosmine, loss of extratemporal bones, narrowing of the otic part of the skull, and lengthening of the snout, orbitotemporal region and corresponding parts of the lower jaw. Most of these characters appear at the ((Tetrapoda+Elpistostegalia) Tristichopteridae) node (Fig. 2). The last character complex may be functionally associated with the reduction in intracranial joint mobility and the adoption of a snapping mode of prey capture.

The 'osteolepiform' part of the stem lineage probably consisted

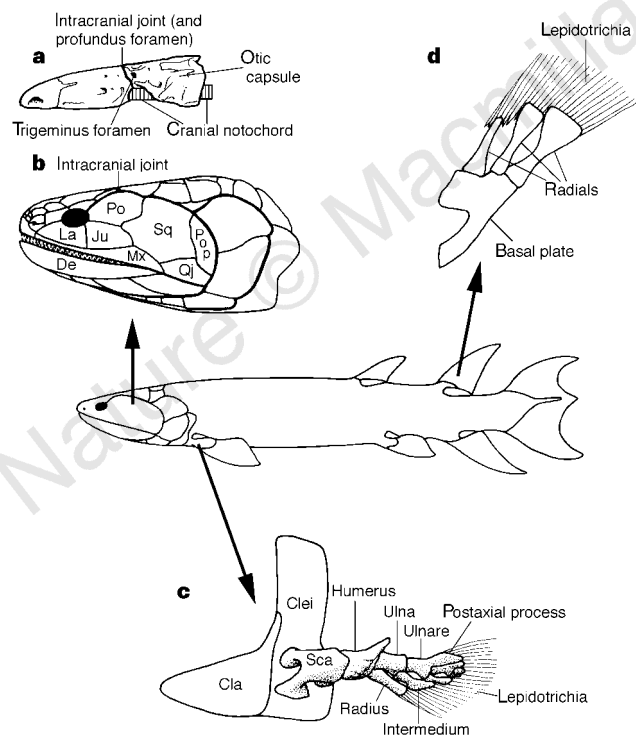


Figure 3 Ancestral characters for clade Elpistostegalia+Tetrapoda. These precise morphologies, illustrated by *Eusthenopteron* (modified from ref. 16), characterize the tetrapod stem lineage between the *Osteolepis*+*Gogonasus* node and the Tristichopteridae node. **a**, Braincase (known in many genera, including *Osteolepis*, *Gogonasus*, *Ectosteorachis* and *Medoevia*). **b**, Dermal skull bones (known in most genera). La, lacrimal; Ju, jugal; Po, postorbital; Sq, squamosal; Qj, quadratojugal; Pop, preopercular; De, dentary; Mx, maxilla. **c**, Pectoral girdle and fin, mesial view (pectoral fin skeleton known in *Megalichthys*, *Sterropterygion* and tristichopterids; girdle known in many genera). Cla, clavicle; clei, cleithrum; Sca, scapulocoracoid. **d**, Posterior dorsal fin support (known in *Megalichthys*, *Rhizodopsis* and tristichopterids). (Redrawn by permission of the Royal Society of Edinburgh from ref. 14.)

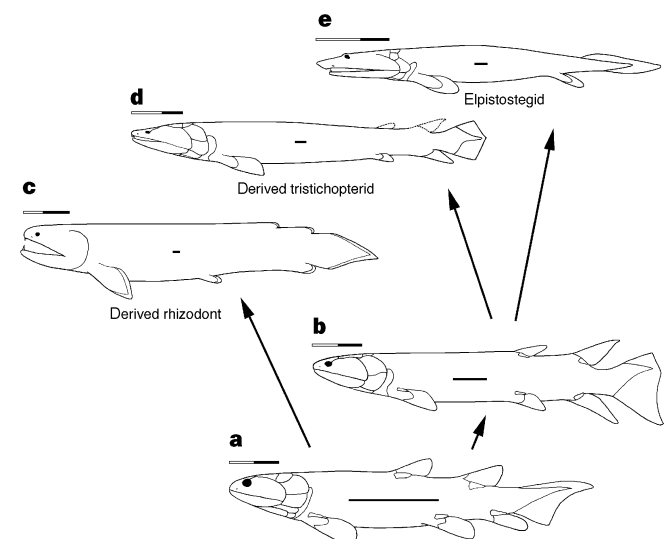


Figure 4 Parallel evolution in the tetrapod stem group, inferred from the phylogeny in Fig. 2. **a**, The 'osteolepidid' *Osteolepis* (modified from ref. 16), approximating to the stem-lineage condition between the *Kenichthys* and *Gyropterygion* nodes. **b**, The tristichopterid *Tristichopterus* (from ref. 27) approximating to the common ancestor of the clade (Tristichopteridae (Elpistostegalia+Tetrapoda)). **c**, The rhizodont ?*Strepsodus* (modified from ref. 26). **d**, The tristichopterid *Mandageria* (from ref. 27). **e**, The elpistostegid *Panderichthys* (modified from ref. 28). Scale bars within fishes, 5 cm; bars above heads show the length of the postparietal bones (black) as a proportion of the total head length. The intracranial joint lies at the anterior margin of postparietals. Rhizodont skull proportions are based on *Barameda* (ref. 11). (Redrawn by permission of the Royal Society of Edinburgh from ref. 29.)

of rather generalized, small (20–70 cm in length) fishes, with dentitions lacking anterior fangs, a morphological category represented in the analysis by *Kenichthys*, *Gogoniasus*, *Osteolepis* (Fig. 4a), *Medoivia*, the canowindrids and *Tristichopterus* (Fig. 4b). Rhizodonts²⁶, derived tristichopterids²⁷ and elpistostegids+tetrapods^{5,16,28}, in contrast, show parallel trends towards a quite different morphology: they increased dramatically in size, reduced or lost their median fins, acquired diphyccercal tails with a low aspect ratio, and developed a pair of fangs at the lower jaw symphysis (Fig. 4c–e). Rhizodonts and derived tristichopterids also acquired premaxillary fangs^{27,29}. Rhizodonts seem to have retained a primitive, short-snouted skull morphology (J. Jeffery, personal communication). However, tristichopterids and elpistostegids+tetrapods, having a moderately lengthened snout as a synapomorphy (Fig. 4b), independently developed this character further in parallel (Fig. 4d, e). Derived tristichopterids such as *Mandageria*²⁹ (Fig. 4d) have very elpistostegid-like head proportions.

These changes seem to have occurred during the Middle/Late Devonian period in all three groups. Elpistostegids originated in the latest Givetian⁶; the earliest known derived tristichopterid is the Frasnian *Platycephalichthys*^{23,27}; and the earliest known large rhizodont is the Famennian *Sauripterus*¹⁵.

Our analysis indicates that much of the lower part of the tetrapodomorph stem lineage consisted of 'osteolepiform' fishes. The character attributes of this part of the stem lineage can be reconstructed with precision. Parallel evolution towards the morphology of a large predator, with reduced median fins and elaborate anterior dentition, occurred at about the same time in rhizodonts, tristichopterids, and elpistostegids+tetrapods (Fig. 4). The evolution of two latter clades, having extra synapomorphies, also paralleled each other more closely. The Tetrapoda thus arose out of one of several similar evolutionary 'experiments' with a large aquatic predator role. Closer study of these parallel radiations should cast much new light on the ecological background to the origin of tetrapods. □

Methods

Phylogenetic analysis. The analysis was performed using the software package PAUP3.1 with a data matrix of 29 taxa scored for 99 morphological characters (Supplementary information). Characters were scored from specimens or good photographs, not reconstruction drawings. Most parsimonious trees were identified using the heuristic search algorithm, stepwise addition, with 500 random iterations. All characters were weighted equally. Characters 15, 20, 23, 25, 32, 70 and 80 were ordered.

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Supplementary information is available on Nature's World-Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial office of Nature.

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Weak trophic interactions and the balance of nature

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Ecological models show that complexity usually destabilizes food webs^{1,2}, predicting that food webs should not amass the large numbers of interacting species that are in fact found in nature^{3–5}. Here, using nonlinear models, we study the influence of interaction strength (likelihood of consumption of one species by another) on food-web dynamics away from equilibrium. Consistent with previous suggestions^{1,6}, our results show that weak to intermediate strength links are important in promoting community persistence and stability. Weak links act to dampen oscillations between consumers and resources. This tends to maintain population densities further away from zero, decreasing the statistical chance that a population will become extinct (lower population densities are more prone to such chances). Data on interaction strengths in natural food webs^{7–11} indicate that food-web interaction strengths are indeed characterized by many weak interactions and a few strong interactions.

Here we combine formally the influence of interaction strength with modern food-web data and models, uniting verbal arguments^{12–16} with the rigorous formulations of May¹². Our analysis differs from May's contributions in five important ways. First, we use a measure of interaction strength that is based upon empirical estimates of per capita interaction strength; second, we assume that communities can display nonequilibrium dynamics; third, we construct complexity as simple food webs (after ref. 17) in a manner consistent with patterns found in nature^{14–16}; fourth, we use biomass as the model currency; and fifth, we use consumption rates that become saturated as resource density increases (that is, we use type II functional responses). We describe our model and define terms in Box 1.