Feeding biomechanics in *Acanthostega* and across the fish–tetrapod transition

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*Acanthostega* is one of the earliest and most primitive limbed vertebrates. Its numerous fish-like features indicate a primarily aquatic lifestyle, yet cranial suture morphology suggests that its skull is more similar to those of terrestrial taxa. Here, we apply geometric morphometrics and two-dimensional finite-element analysis to the lower jaws of *Acanthostega* and 22 other tetrapodomorph taxa in order to quantify morphological and functional changes across the fish–tetrapod transition. The jaw of *Acanthostega* is similar to that of certain tetrapodomorph fish and transitional Devonian taxa both morphologically (as indicated by its proximity to those taxa in morphospace) and functionally (as indicated by the distribution of stress values and relative magnitude of bite force). Our results suggest a slow tempo of morphological and biomechanical changes in the transition from Devonian tetrapod jaws to aquatic/semi-aquatic Carboniferous tetrapod jaws. We conclude that *Acanthostega* retained a primitively aquatic lifestyle and did not possess cranial adaptations for terrestrial feeding.

1. Introduction

Biomechanical aspects of the origin of limbed vertebrates (tetrapods) add significantly to our knowledge of key structural, functional and ecological changes underpinning a major animal radiation [1,2]. In particular, the analysis of feeding mechanisms at the fish–tetrapod transition permits in-depth exploration of adaptive shifts during the assembly of the first terrestrial food webs and the colonization of new terrestrial habitats. In this paper, we analyse the lower jaw biomechanics of *Acanthostega gunnari* from the Devonian of Greenland [3], one of the most informative early limbed vertebrates, and a range of tetrapodomorph taxa spanning the fish–tetrapod transition.

*Acanthostega* plays a central role in debates about terrestrialization [4]. Morphological and palaeoecological data suggest that this tetrapod had a primarily (if not exclusively) aquatic lifestyle. Its branchial skeleton, lateral line system, elbow and wrist joint constructions (indicative of a paddling rather than a weight-bearing function), weakly developed vertebral zygapophyses and extensive tail fin are all consistent with this interpretation [5,6]. In addition, its broad snout suggests that this tetrapod relied on suction as a feeding mechanism [7–10]. Finally, lithological and sedimentological data indicate that *Acanthostega* inhabited an ephemeral, shallow and weakly channelized fluvial system subjected to periodic intense flooding [11–15].

In contrast, certain structural traits of *Acanthostega* appear to be in conflict with its interpretation as an aquatic animal. In particular, a recent study has shown that its complex and interdigitated cranial sutures [16] closely resemble those of terrestrial taxa and are not consistent with an aquatic feeding mode [17]. The cross-sectional shape of cranial sutures is a useful tool for identifying different types of stress and strain in the vertebrate skull. For example, miniature pugs [18,19], goats [20] and fish [21] display complex interdigitating cranial sutures to withstand tension, simple abutting sutures to counteract tension and overlapping sutures to work simultaneously against tension and compression. Comparisons of the cranial sutures of *Acanthostega* to those of...
the extant actinopterygian Polypterus, the Devonian tristichopterid sarcopetorygian Eusthenopteron and presumably terrestrial Permain temnospondyl Phonerpeton have led some researchers to conclude that Acanthostega may have favoured direct biting in a sub-aerial environment as a means of prey capture [17]. In this context, it is therefore logical to ask whether other morphological traits of this tetrapod support this conclusion. Here, we examine the argument in support of a terrestrial feeding mode in Acanthostega by analysing its lower jaw from both morphological and functional standpoints. Furthermore, we compare the biomechanical performance of its jaw with those of various other early tetrapods and near-tetrapod taxa that span the fish–tetrapod transition.

We focus on the lower jaws because they are both easily constrained from a functional perspective (that is, they are predominantly feeding structures) and preserved very well in numerous taxa. For these reasons, they are amenable to combined biomechanical and morphometric analyses. We apply two-dimensional finite-element analysis (FEA) and geometric morphometrics to the lower jaws of 23 taxa. These include: (i) a sample of rhizodontids, megalichthyids and tristichopterid tetrapodomorphs, representing the fish-like portion of the tetrapod stem; (ii) the best-known Devonian digit-bearing tetrapods, including Acanthostega; (iii) a number of Carboniferous aquatic/semi-aquatic stem tetrapods and (iv) some anthracosaurs and temnospondyls, as putative members of the amniote and amphibian stem groups, respectively (figure 1a; electronic supplementary material, table S1). Stem- and crown-group attributions differ in recent analyses of early tetrapod interrelationships. Here, we broadly follow the scheme of relationships in [22], with amendments and additions from [23–26]. Jaw orientation and descriptive terminology conform to [23, 27].

2. Material and methods

(a) Phylogeny

The tree in figure 1a (for alternative schemes of early tetrapod interrelationships, see [28]) was time-calibrated with methods available at: http://www.graemetlloyd.com/methdpf.html. Tree branch lengths were scaled based on first appearance data for all taxa. Branches with identical first appearances are allowed to share a proportion of the time elapsed between their first appearance and that of an earlier branch. As a result, no branches have zero-length duration [29, 30]. Branch scaling allowed us to measure ‘phylogenetic distances’ between all pairs of taxa in millions of years. These distances were used in correlations with biomechanical and morphological distances (see below). This approach allowed us to assess the degree of intertaxon separation (both functional and morphological) based on time elapsed since the time of divergence of any pair of taxa.

(b) Jaw reconstructions

The use of published jaw reconstructions (figure 1b; electronic supplementary material, table S1) maximizes the amount of information rarely observed in individual specimens owing to incompleteness or deformation [30]. Taxon selection was determined in part by the reliability of the jaw reconstructions, assessed through either first-hand observations of material or comparisons with accompanying photographs in relevant publications. Different jaw reconstructions are available for Ichthyostega, Crassigyrinus, Megalocephalus and Gephyrostegus, so these reconstructions were all included in our analyses to assess their impact on our results.

(c) Two-dimensional finite-element analysis

We could not apply three-dimensional FEA owing to a lack of computed tomography (CT) data and the laterally crushed or fragmented nature of most specimens. Two-dimensional models allow us to sample a broader range of taxa but treat the mandible as a thin plate and thus assume that stresses and strains act only in the sagittal plane. Therefore, a limitation of the methodology used in our study is that some details of constructional differences among different jaws could not be taken into account. These differences include, among other features, sutural patterns of dermal bones, proportions and degree of ossification of the Meckelian element and size of coronoid fangs [31–33]. We acknowledge that such constructional differences may have had a substantial effect on the overall jaw biomechanics. However, two-dimensional FEA permits a comparative analysis of the performance of jaw shape without having to estimate precise values of material properties, muscle forces, muscle fibre distributions or yield/failure stresses, all of which have been shown by recent validation studies to be difficult to estimate even in extant taxa [34]. Furthermore, we assume that the taxa in our study were capable of performing simple orthal jaw movements, although the jaw musculature itself may have undergone some degree or reorganization at the fish–tetrapod transition (this is borne out by the observation that the adductor fossa changes in shape and proportions at the fish–tetrapod transition [23]). Orthal movements imply that dorsoventral bending is chiefly responsible for the primary stress and strain occurring during jaw closure and prey capture. Using
this approach, we assume that both mediolateral and torsional loads exerted a negligible effect on the jaw.

It may be argued that the simplifications and assumptions of our models may be unwarranted or biologically unrealistic. However, our analysis of the distribution of forces along the sagittal plane (as stated above) is a first pass towards a more detailed treatment of jaw biomechanics that also accounts for details of constructional differences (research in progress by Laura Porro, E.J.R. and J.A.C.). Crucially, our protocols are not conceptually different from those adopted in other studies [30], where certain traits of a morphofunctional complex (e.g. input and output moment arms of lower jaws treated as ‘levers’ in [30]) are considered as specific variables in isolation from constructional details of those complexes.

Digitized jaw outlines were used to build FE models and these were constructed and analysed in Comsol M v. 2.0 (Dessault Systems, MA, USA). Jaws were scaled to their correct size using published measurements. Adductor muscle loads were then added and scaled. We assigned a hypothetical adductor muscle force of 10 N to Acanthostega, herein referred to as the Acanthostega unit force. We then scaled this load for each jaw according to its surface area, following the protocol suggested and employed in recent comparative FE studies, where validation or data on input parameters are either unknown or difficult to obtain, for example in fossil taxa [35]. Applying a constant unit force per surface area has the advantage of removing the effect of size, so that only the effect of shape on jaw performance is quantified. This method makes the assumption that muscle cross-sectional area (and hence isometric force output) scales to jaw surface area. It is important to note that this technique does not provide a measure of the ecological performance of specimens; however, it does provide a comparative analysis of shape mechanical performance. Therefore, the resulting von Mises (VM) stress values should not be interpreted as the actual stresses experienced by the jaws, but instead represent comparative performance values. If we assume that all specimens operate to a common safety factor (the ratio between everyday load and load at failure), then tetrapods in which the jaws experience low stress (as recorded in our analysis) could, in theory, be capable of biting harder than predicted by exerting a stronger adductor muscle force. Conversely, jaws that experience high stress (as recorded in our analysis) could, in theory, be capable of generating smaller input forces in life and hence generate lower bite forces than predicted. We have chosen this approach, rather than applying an incremental load until a nominal safety factor is reached, because it allows us to determine which taxa deviate from a simple relationship between surface area and jaw muscle force. Furthermore, it is not clear whether skulls and jaws of different taxa operate at similar safety factors. Recent in vivo strain data from mammals, lizards and crocodilians show marked variation in peak cranial strains between taxa, suggesting that these animals operate at very different cranial safety factors [36–38]. Additionally, it can be problematic to record performance metrics from peak stresses in FE models, as these stresses may be localized peaks at constraint points and may not reflect accurately the mechanical behaviour of the structure. The alternative approach of estimating a realistic adductor muscle force for each taxon is problematic, as a number of specimens do not possess adequately preserved cranial material to assess muscle size and orientation. Muscle loads were applied at an angle of 60° to a horizontal axis between the tip of jaw and articular surface. This angle was selected following sensitivity analyses that considered varying muscle vector orientations (see the electronic supplementary material, methods and figure S1). Material properties were then applied to the model. However, as no material property data for fish or amphibian skulls are available, we selected the Young’s modulus of the pelvic metapterygium of the actinopterygian fish Polypterus (17.6 GPa [7]) and applied an average Poisson’s ratio of 0.35. The jaws were constrained at the condyle in three translational degrees of freedom.

Furthermore, the anteriormost end of the tooth row was constrained in the Y-axis (five nodes) to simulate a bite. We then derived values for VM stress, which was measured at five evenly spaced points along a dorsoventrally transect situated at the middle of the tooth row (electronic supplementary material, figure S1; [39]). VM stress is a function of the three principal stress directions along the X-, Y- and Z-axes and effectively predicts failure in a structure [40]. In addition, we recorded reaction forces from five restrained nodes at the anteriormost end of the tooth row in order to provide an estimate of ‘bite force’ for each model, which we name a ‘relative’ bite force as our input muscle forces are scaled to the surface area. As our models have muscle loads scaled in proportion to the jaw surface area, relative bite forces allow us to use reaction force as a proxy for jaw performance (figure 2). For taxa with more than one model (i.e. Ichthyostega, Crassigyrinus, Megaloselachus and Gephyrostegus), relative bite forces were measured for each model individually to derive a mean value. We then calculated relative bite force as a proportion of Acanthostega bite force. Finally, we compared bite ‘efficiency’ by calculating the ratio of relative bite force to the scaled muscle input force. This provides a size-independent measure of how effectively jaw shape converts applied muscle load to output bite force [41]. In addition, to ensure our models contained enough elements to provide reliable results, a convergence test was performed on the jaw of Acanthostega (electronic supplementary material, figure S2).

(d) Geometric morphometrics
We applied landmark-based geometric morphometric methods to explore shape variation in our taxon sample. Twelve landmarks on the lateral surface of each jaw were digitized in 21 taxa using Image [42] (electronic supplementary material, table S3; inset, figure 3). Two taxa were excluded from the morphometric analyses, namely Tiktaalik, in which certain landmark positions could not be discerned, and Dendrerpeton, in which the splenial and postspenial have little or no exposure on the lateral aspect of the jaw. Landmarks conform to Bookstein’s [43] types 1 and 3 (electronic supplementary material, table S3; type 1: landmarks identifying homologous points, for example triple joints among bones; type 3: landmarks placed at ‘extremes’ of a structure, for example most anterior end of a given distance). Morphometric analyses were performed in PAST [44].

(e) Comparisons among distance matrices
We further carried out traditional and modified Mantel tests [44,45] to establish the degree of correlation among intertaxon distance matrices generated from the functional analyses, morphometric analyses and consensus phylogeny (see the electronic supplementary material, methods). Note that the morphological distances are the Procrustes distances derived from the morphometric analysis, whereas the phylogenetic distances are the temporal distances that separate any two taxa along the time-calibrated branch lengths of the preferred phylogeny. The traditional Mantel tests simply considered pairwise correlations between any two of the three distance matrices. The modified Mantel test was conducted on morphological and functional distances while taking phylogeny into account, using codes supplied in [45].

3. Results
(a) von Mises stress
Stress values are reported here based on the overall patterns observed across the jaw and the mean values recorded from the dorsoventrally orientated mid-tooth row transect during a simulated bite. The VM stress values recorded in the
The lowest value was recorded at the base of tetrapodomorph and 75% quartile points up to the jaw mid-point (50%), where 100% points, respectively); values decreased through the 25 and 75% quartile points up to the jaw mid-point (50%), where the lowest value was recorded. At the base of tetrapodomorph sarcopterygians, the rhizodont *Rhizodus* and the megaleichthyid *Megalichthys* experienced the least stress, particularly in the anterior half of the jaw (mean of the stress recorded in the mid-tooth row transect = 0.21 and 0.16 MPa, respectively). Marginally higher stresses were observed in the anterior jaw in the more derived tetrapodomorph, *Eusthenopteron*, which exhibited very similar mean transect stress values to those of most Devonian tetrapods. The highest values among fish occurred in *Tiktaalik* and *Panderichthys* (transect means = 0.69 and 1.18 MPa, respectively) and were similar in magnitude to those of Carboniferous tetrapods.

Among Devonian tetrapods, *Elginerpeton* experienced by far the highest stress value at every point in the jaw (transect mean = 1.71 MPa). All other Devonian tetrapods, including *Acanthostega*, showed much lower values; stresses were more uniformly distributed across the jaw and had less variable transect means (0.38–0.66 MPa). *Acanthostega* has an estimated average value of 0.58 MPa at the mid-tooth row transect, well within the range of two of the *Ichthyostega* models [23], both of which show similarly distributed and comparable values (transect means = 0.50 and 0.63 MPa).

The Carboniferous semi-aquatic/aquatic stem amniotes consistently showed the highest stresses of all tetrapods, and also resembled each other in terms of mean stresses at the transect. The more terrestrial anthracosaurs, particularly *Gephyrostegus*, exhibited low stress (means = 0.16 and 0.23 MPa for the two jaw models). *Proterogyrinus* emerged as an outlier (mean = 1.01 MPa), showing a much higher value than any other anthracosaur and resembling closely Carboniferous stem tetrapods.

Terrestrial temnospondyls generally showed low stresses, with average values being lower than those of the Devonian tetrapods. *Phonerpeton* is an exception, as its mean value (0.48 MPa) was similar to that of the Devonian tetrapods, especially *Ichthyostega*.

![Figure 2](http://rspb.royalsocietypublishing.org/Downloaded from http://rspb.royalsocietypublishing.org/)
had moderately efficient jaws. Acanthostega clustered with other Devonian tetrapods, Metaxygnathus and Denisoniatus, and was mid-range in terms of its efficiency. The Devonian tetrapods Ventastega, Ymeria and Ichthyostega, and the large tetrapodomorph fish Rhizodus and Megalichthys, were the least efficient.

Relative bite force values and mean VM stress values are significantly correlated (Spearman’s $\rho = 0.68182$; $p = 0.00304$; figure 2c; electronic supplementary material, S3). However, Megalocephalus and Rhizodus exhibited lower VM stress than predicted from bite forces.

(c) Morphometric analysis

Principal components (PC) 1 and 2 accounted for 45.13% and 22.95% of the total morphological variance, respectively (figure 3). Each group plotted in a distinct region of morphospace, with the exception of Elginerpeton, which fell within the convex hull delimited by semi-aquatic/aquatic Carboniferous tetrapods. Acanthostega plotted closer to some Devonian tetrapods, but some distance from Icthyostega and Elginerpeton. Devonian and Carboniferous tetrapods are not significantly separate (non-parametric multivariate analysis of variance or NPMANOVA [44]; $F = 4.282$, $p = 0.08$), even if Elginerpeton is removed. Tetrapodomorphs were distributed chiefly along PC2 owing to differences in jaw curvature between rhizodonts and megalichthyids (with straight jaws and tooth rows), at positive PC2 values, and Panderichthys and Eusthenopteron (with more curved jaws and tooth rows), at negative PC2 values. The latter two taxa plotted closer to Icthyostega. Sarcopterygian fish and Devonian tetrapods were significantly separate (NPMANOVA; $F = 4.282$, $p = 0.007$), probably owing to the broad separation of rhizodonts and megalichthyids from other tetrapodomorphs. The anthracosaurs were distributed mostly along PC1 and were well separated from most other groups except rhizodonts, megalichthyids and temnospondyls. The two temnospondyl taxa, however, were not close to each other in morphospace. Although they were almost aligned in a direction parallel to PC2, they plot at nearly opposite ends of PC1 and only show significant separation from the Devonian taxa (NPMANOVA; $F = 4.282$, $p = 0.04$).

(d) Shape-function correlation

With traditional Mantel tests [44], the stress-based (functional) distances were not significantly correlated with either morphological (Pearson’s $r = 0.01411$; $p = 0.4136$) or phylogenetic distances (Pearson’s $r = -0.1048$; $p = 0.7262$). However, the correlation between morphological and phylogenetic distances was significant (Pearson’s $r = 0.4066$; $p = 0.0013$). With the modified Mantel test [45], we found that, once again, the stress-based and morphological distances were not significantly correlated (Pearson’s $r = 0.01411$; $p = 0.3882$).

4. Discussion

It is important to reiterate here that our analysis is comparative, and that relative bite forces and stress values are used for this purpose, and do not reflect the absolute magnitude of stress and force experienced or generated by the jaw.

(a) Bite performance

Mechanically, the semi-aquatic/aquatic Carboniferous stem tetrapods (Crassigyrinus, Megalocephalus) exerted by far the strongest relative bites, consistent with their powerful jaws and massive teeth. Anthracosaurs and temnospondyls showed, on average, the weakest relative bites and appear
to have been capable of quick, snapping jaw movements (figure 2a; electronic supplementary material, figure S3b). Generally, relative bite force increases linearly with VM stress, except in \textit{Megalecephalus}, \textit{Rhizodus} and \textit{Megachilichthys}, all of which are outliers (figure 2c; electronic supplementary material, figure S3b) and show relatively low stress for a given relative bite force. Using these results, we can consider which taxa are operating at notably high or low safety factors in our comparative analysis. It might be predicted that in life such taxa could have modified their feeding performance, by either decreasing or increasing muscle force input, respectively, in order to equilibrate the stresses within their jaws. Following this rationale, taxa can be divided into three categories, as described below.

(i) \textit{Low-stress, high relative bite force}. Two outlier taxa exhibited this pattern, the semi-aquatic \textit{Megalecephalus} and the fully aquatic \textit{Rhizodus}. If all taxa are assumed to operate to a similar safety factor, these taxa, in life, may have been able to generate higher adductor input forces than modelled here, thereby generating an increased bite force yet still operate within a margin of safety. Although not closely related, both taxa possess cranial features suited for crushing and/or stabbing relatively large prey [23,46,47].

(ii) \textit{High-stress, high relative bite force}. The most basal tetrapod, \textit{Acanthostega}, also exhibits the most divergent jaw morphology of the group, possibly indicating a different feeding mode [23,31,32]. This conclusion is supported by the mechanical performance of the jaw, which boasts a very high relative bite force and by far the highest comparative stress levels recorded, probably owing to its narrow and elongate morphology. Again, assuming similar safety factors, this taxon in life may have generated a reduced adductor muscle force, thereby lowering the elevated stresses in the jaw. This slender jaw shows thickened and tightly sutured dermal bones and a reduced Meckelian space [23,31,32]. The overall construction is consistent with quick, forceful movements through the water column, possibly when the animal chased small, fast prey. Similar functional considerations apply to the seemingly secondarily aquatic Carboniferous tetrapod, \textit{Crassigyrinus} [48,49]. Morphological evidence indicates that this animal was an extremely agile aquatic predator. Its size, morphology, high bite force and high efficiency are consistent with hunting large prey and seizing it with a powerful bite.

(iii) \textit{Low-stress, low bite force}. Some predominantly terrestrial taxa show exceptionally low comparative jaw performance. Examples include \textit{Gephyrostegus} and \textit{Balancerpeton}. Our results indicate intrinsically different mechanical demands on skull function, presumably owing to their postulated terrestrial lifestyle. Increasing adductor muscle force could have generated an increased bite force within these taxa and maintained skull stress within acceptable levels of safety. The majority of Devonian taxa (including \textit{Acanthostega}) and the fish \textit{Eusthenopteron} plot fairly close to these terrestrial forms, but with slightly higher average stresses and relative bite forces, intermediate between those of terrestrial forms and those of sarcopterygian fish and Carboniferous aquatic tetrapods.

(b) \textbf{Jaw shape}

Jaw curvature (changing mostly along PC2) and proportion of tooth row length relative to total jaw length (changing mostly along PC1) define the pattern of taxon distribution in morphospace. Some Devonian tetrapods share similarities in lower jaw morphology with Carboniferous aquatic/semi-aquatic tetrapods and with \textit{Eusthenopteron} and \textit{Panderichthys} and are morphologically distinct from anthracosaurs, temnospondyls, rhizodonts and megalichthyids. Shape changes along PC2 are particularly noteworthy (figure 3), as tooth row curvature affects mechanical performance. The development of a straight tooth row and the presence of a coronoid process (e.g. \textit{Proterogyrinus}, \textit{Eospermopterus}, \textit{Gephyrostegus}) imply that all marginal dentary teeth are brought into contact with prey simultaneously in a vice-like manner. A similar jaw action may have characterized the stem tetrapod \textit{Greererpeton}, and the rhizodonts and megalichthyids. Conversely, a curved jaw with an upturned tip brings the tip in contact with the prey first. This could be interpreted as an adaptation for snapping feeding, and a likely adaptation for dealing with fast prey. Posterior inclination of the anteriormost teeth and fangs in these taxa support the interpretation of a jaw adapted for fast closure and prey seizure.

(c) \textbf{Form, function and phylogeny}

As comparative jaw stress does not appear to be correlated with morphology, jaw shape alone cannot be used to infer its function. Convergent biomechanical performances can be achieved with different morphologies. Notable examples are \textit{Acanthostega} and \textit{Phonerpeton}. These taxa are both phylogenetically separate and morphologically distinct, yet their jaw performances are similar. Functional distances from comparative jaw stress values do not correlate with phylogenetic distances. We interpret this result as evidence of divergent functions in closely related species (e.g. \textit{Elginerpeton} and other Devonian tetrapods; \textit{Crassigyrinus} and \textit{Megalecephalus} and other Carboniferous, aquatic/semi-aquatic tetrapods), though comprehensive analyses of biting performance evolution must await data collection from a larger taxon sample than that used here. By contrast, morphological and phylogenetic distances correlate well, implying that, at least for our sample, morphology is constrained to some degree by taxon position in phylogeny.

(d) \textbf{Feeding in \textit{Acanthostega}}

With the exception of \textit{Elginerpeton}, \textit{Acanthostega} plots out in proximity to other Devonian taxa, which it also resembles mechanically (figures 1b, 2 and 3). In terms of average VM stress, its lower jaw shape resembles that of \textit{Ichthyostega}, has similar relative bite force to \textit{Ventastega} and \textit{Densiglyptus} and similar relative bite efficiency to \textit{Densiglyptus} and \textit{Metaxaglyptus}. Devonian tetrapods share similarities in overall jaw shape with \textit{Panderichthys} and \textit{Eusthenopteron} as well as Carboniferous aquatic/semi-aquatic forms, providing limited evidence for notable morphological change in jaw morphology across the fish–tetrapod transition. There are some functional differences, however; for example, Carboniferous forms, such as \textit{Crassigyrinus} and \textit{Megalecephalus}, generate greater relative bite forces than Devonian taxa, but at the expense of increased jaw stress. As Devonian tetrapods (with the exception of \textit{Elginerpeton}) tend to have low relative bite forces and concomitant lower jaw stress, this places their functional capabilities midway between those of aquatic Carboniferous forms and those of anthracosaurs and temnospondyls. Devonian tetrapod jaws are therefore not functioning in exactly the same manner as aquatic Carboniferous tetrapod jaws, but certainly do not conform functionally to terrestrial tetrapod jaws either. Given
the anatomical evidence supporting a predominantly (if not exclusively) aquatic mode of life in *Acanthostega* and other Devonian tetrapods, we conclude that these tetrapods fed primarily in an aquatic rather than terrestrial environment.

**Acknowledgements.** We thank P. Anderson, M. Bell, J. Bright, T. Fletcher and M. Saka moto for valuable discussions and input. We are also grateful to two anonymous reviewers and to our Associate Editor, Prof. Peter Aerts, whose comments greatly improved the manuscript. This study was completed as part of J.M.N.’s MSC project at the University of Bristol.

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