Terrestrial-style feeding in a very early aquatic tetrapod is supported by evidence from experimental analysis of suture morphology

Molly J. Markey[*][†] **and Charles R. Marshall**[*][‡]

[*]Department of Earth and Planetary Sciences and [‡]Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, MA 02138

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There is no consensus on when in the fish-tetrapod transition suction feeding, the primary method of prey capture in the aquatic realm, evolved into the direct biting on prey typical of terrestrial animals. Here, we show that differences in the morphology of selected cranial sutures between species that span the fish–tetrapod transition (the Devonian osteolepiform fish *Eusthenopteron*, the aquatic Devonian tetrapod *Acanthostega*, and the Permian terrestrial tetrapod *Phonerpeton*) can be used to infer when terrestrial feeding first appeared. Our approach consists of defining a sutural morphospace, assigning functional fields to that morphospace based on our previous measurements of suture function made during feeding in the living fish *Polypterus*, inferring the functions of the fossil sutures based on where they fall in the morphospace, and then using the correlation between feeding mode and the patterns of inferred suture function across the skull roof in taxa where feeding mode is unambiguous to infer the feeding mode practiced by *Acanthostega*. Using this procedure, we find that the suture morphologies of *Acanthostega* are inconsistent with the hypothesis that it captured prey primarily by means of suction, which suggests that it may have bitten directly on prey at or near the water's edge. Thus, our data strongly support the hypothesis that the terrestrial mode of feeding first emerged in aquatic taxa.

Acanthostega | fish–tetrapod transition | suction feeding | *Eusthenopteron*

The origin of tetrapods and their invasion of terrestrial environments are major events in vertebrate evolution. Comparing early tetrapod taxa such as the Devonian tetrapods *Acanthostega* (1) and *Ventastega* (2) with the closely related osteolepiform fishes *Eusthenopteron* (3), *Panderichthys* (4), and *Tiktaalik* (5, 6) shows that the fish–tetrapod transition was defined by a suite of anatomical changes linked to changes in locomotion, respiration, reproduction, the sensory apparatus, and feeding (7–9).

Feeding in water presents organisms with different challenges than those experienced when feeding on land because water is 900 times as dense, and 80 times as viscous, as air (10). Because of these differences, suction feeding, the most widespread method of prey capture used by aquatic vertebrates, is impossible in air (10), so animals that capture prey in terrestrial settings use different techniques, such as overtaking prey items with the jaws and biting on them (11). Therefore, we assume that fish preceding the transition, such as *Eusthenopteron*, captured prey using suction, whereas later, fully terrestrial tetrapods captured prey items by biting on them (see also ref. 12). Transitional forms such as *Acanthostega* are thought to have captured prey in the water (12–14), but the exact type of prey capture (i.e., suction versus biting) used by *Acanthostega* and other early tetrapods is difficult to determine.

Stepwise morphological changes in the lower jaw, dentition, degree of ossification of the operculum, and relative size of the gill chamber in taxa that span the fish–tetrapod transition provide clues as to whether early tetrapods, including *Acanthostega*, captured prey using suction or biting (15). Specifically, the fishes *Eusthenopteron*, *Panderichthys*, and *Tiktaalik*, and the early tetrapod *Ventastega*, all possess large coronoid fangs, whereas these teeth are absent in the more derived *Acanthostega*. In addition, *Eusthenopteron* and *Panderichthys* both exhibit an ossified operculum, whereas the bony gill cover is lost in *Tiktaalik*, *Ventastega*, and *Acanthostega*. Finally, the glenoid fossa of the articular faces posteriordorsally in the fish taxa discussed here (*Eusthenopteron*, *Panderichthys*, and *Tiktaalik*) whereas, in the tetrapods *Ventastega* and *Acanthostega*, this fossa points dorsally, indicating that the lower jaw changed the nature of its articulation to the skull across the fish–tetrapod transition. (See ref. 15 for a discussion of these changes in all taxa save *Tiktaalik*; for *Tiktaalik*, see refs. 5 and 6.) These changes, along with the reduction of the gill chamber, are hypothesized to indicate a reduced reliance on suction feeding in early tetrapods compared with osteolepiform fishes (15).

However, it is unclear how definitive the morphological changes described above are in helping us understand when in the fish–tetrapod transition taxa were no longer dependent on suction feeding. For example, extant fish that capture prey by means of suction exhibit an incredible variety of tooth arrangements and jaw shapes (see ref. 16). In addition, the loss of the operculum observed in *Acanthostega* is reminiscent of the condition seen in the extant lungfish *Neoceratodus* (17), which nonetheless employs suction to capture prey (18). Therefore, whereas the changes noted above certainly indicate major changes in the details of the feeding mechanisms between taxa such as *Eusthenopteron* and *Acanthostega*, and may indicate a reduced ability of *Acanthostega* to develop a pressure drop within the buccal cavity compared with *Eusthenopteron*, these morphological changes do not enable us to determine how reliant *Acanthostega* might have been on suction feeding, *per se*.

Thus, motivated by these uncertainties, we here provide an approach for evaluating whether transitional tetrapods, specifically *Acanthostega*, captured prey primarily using suction, or by biting directly on prey items. This work follows the suggestion that the shift from suction to biting prey capture should be reflected in the morphology of the cranial sutures of taxa that span the fish–tetrapod transition and the tetrapod invasion of land (13, 14, 19).

In vivo experiments demonstrate that cranial sutures are important indicators of skull function (20–23). However, no

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Abbreviations: IF, interfrontal suture; IP, interparietal suture; IPP, interpostparietal suture; FP, frontoparietal suture; NF, nasofrontal suture; SMNH, Swedish Museum of Natural History; MCZ, Harvard Museum of Comparative Zoology; CT, computed tomography.

[†]To whom correspondence should be addressed. E-mail: markey@fas.harvard.edu.

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previous studies have documented quantitative changes in sutural morphology across the fish–tetrapod transition or linked specific sutural morphologies to specific feeding modes (e.g., suction feeding). Here, we assess where in the transition feeding changes occurred by (*i*) quantifying the three-dimensional morphology of selected sutures in taxa that span the fish–tetrapod transition and the tetrapod invasion of land; (*ii*) inferring the function of these sutures using correlations between suture morphology and deformation during feeding in the extant fish *Polypterus* (23); and (*iii*) associating specific fossil suture morphologies with aquatic (suction) feeding or terrestrial feeding (biting on prey).

Here, the fish–tetrapod transition is represented by the osteolepiform fish *Eusthenopteron* (3) and the Devonian tetrapod *Acanthostega*, the best-known early tetrapod (14). Although *Panderichthys* and *Elpistostege* are more closely related to tetrapods than *Eusthenopteron* is (8), we did not have access to any panderichthyid specimens so those taxa were not included. We selected the Permian terrestrial tetrapod *Phonerpeton* (Dissorophoidea) (24) to represent the invasion of terrestrial environments by tetrapods because of its terrestrial lifestyle (24), the fact that its small skull size falls within the range exhibited by *Eusthenopteron* and *Acanthostega* (24), and the excellent three-dimensional preservation exhibited by several specimens in the Museum of Comparative Zoology, Harvard University.

In this study, we are not concerned with the exact homologies between the skull roof bones of these taxa. Instead, we wish to compare bones that are similar in size, proportion (compared with the rest of the skull), and location in the skull, on the grounds that these bones experienced similar functional regimes. Traditionally, the large paired bones in the skull roof located between the orbits have been called "frontals." (This terminology is still used in the fish literature; for example, see ref. 25.) However, these paired bones in tetrapods and in fishes are not homologous. Instead, fish do not possess true frontals; the large paired elements in *Eusthenopteron* and *Polypterus* are homologous to the parietals of tetrapods (see refs. 14 and 26, respectively). Similarly, the "parietals" of *Eusthenopteron* and *Polypterus* are not homologous to the parietals of *Acanthostega* and *Phonerpeton*. However, because we wish to evaluate the functional similarity of these bones, we refer to the largest midline skull roof bones of *Eusthenopteron* and *Polypterus* as frontals, and compare them with the true frontals of *Acanthostega* and *Phonerpeton*. In addition, we consider the bones the lie immediately posterior to these large bones (the parietals) of *Eusthenopteron* and *Polypterus* to be functionally comparable with the parietals of *Acanthostega* and *Phonerpeton*, given their similar shapes and positions in the skull.

Results

Quantifying Sutural Morphology. Five metrics (27) were used to quantify the surface traces and cross-sectional morphologies of the interfrontal (IF), interparietal (IP), frontoparietal (FP), and nasofrontal (NF) sutures in *Eusthenopteron*, *Acanthostega*, and *Phonerpeton*: (*i*) interdigitation index: the length of the suture in cross-section divided by the distance between its ends (21); (*ii*) amount of overlap (= beveling) in cross-section (19); (*iii*) size of the largest interdigitation in the suture's cross-section; (*iv*) bone thickness at the suture; and (*v*) the index of sinuousity: length of the suture on the surface of the skull divided by the distance between its ends (equals the index of interdigitation in ref. 28). Metrics *i*–*iv* were measured at several locations across each suture analyzed (see Figs. 1–3 for locations and representative suture morphologies). All measurements of metrics *i*–*v* [see supporting information (SI) Table 1] were made by using ImageJ 1.32j (NIH, Bethesda, MD), and statistical analysis was conducted by using SPSS 12.0 (Chicago, IL). The mean values of the metrics used to quantify suture morphology in *Eusthenopteron*, *Acanthostega*, and *Phonerpeton* are provided in SI Table 1.

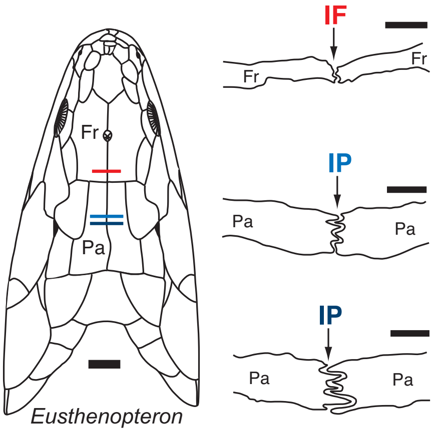

Fig. 1. Cross-sections through the IF and IP sutures of the osteolepiform fish *Eusthenopteron* and their approximate positions through the skull roof (see Introduction for discussion of the terminology used for these bones). The cross-section drawings are modified after the original drawings in the literature (29). The color of the sutural label indicates the location of the slice through the skull. The dorsal reconstruction is modified from the literature (30) and was largely based on SMNH P222, the specimen used to generate the grinding series and cross-sectional drawings. [Scale bars: 1 mm (sutures) and 1 cm (skull).] Fr, frontal; Pa, parietal.

Surface Versus Cross-Sectional Sutural Shape. Interestingly, our data show that the two major aspects of sutural shape [cross-sectional morphology and ectocranial (surface) trace] are not significantly correlated in the taxa examined here (Pearson correlation: $r^2 = 0.045$; $P = 0.464$), a result anticipated by Clack (13) in her analysis of the skull roof sutures of *Acanthostega*. The fact that the cross-sectional complexity of a suture is not predictably reflected by its ectocranial trace, and that sutures with identical ectocranial traces can exhibit different cross-sectional shapes and perform different functions (23), means that the cross-sectional morphology of a suture is a better indicator of suture function than its surface appearance. Therefore, our efforts to quantify sutural morphologies across the fish–tetrapod transition and associate these morphologies with specific feeding styles focus on cross-sectional sutural morphology.

Unexpectedly, we observe no overall increase or decrease in cross-sectional sutural complexity (SI Table 1 and SI Fig. 6) across the transition from fish to terrestrial tetrapods, at least for the taxa examined here. Instead, certain sutures in *Phonerpeton* are more interlocking than in *Eusthenopteron* and *Acanthostega*, whereas other sutures are not (SI Fig. 6). In addition, whether a particular suture seems more or less complex across the transition also depends on the metric used to quantify it (SI Fig. 6).

Sutural Morphospace. To fully describe the suture morphologies exhibited by the fossil taxa, we used a sutural morphospace, rather than considering each metric individually. We used three of the four cross-sectional sutural metrics to make the morphospace, omitting bone thickness because prior analysis of suture form and function during feeding in the extant fish *Polypterus* showed that bone thickness does not affect the deformation pattern exhibited by a suture (27). Therefore, we plotted only the index of interdigitation, beveling amount, and largest interdigitation size measured in the fossil sutures together with values from positionally comparable sutures in the extant fish *Polypterus* to create the sutural morphospace (Fig. 4) (27).

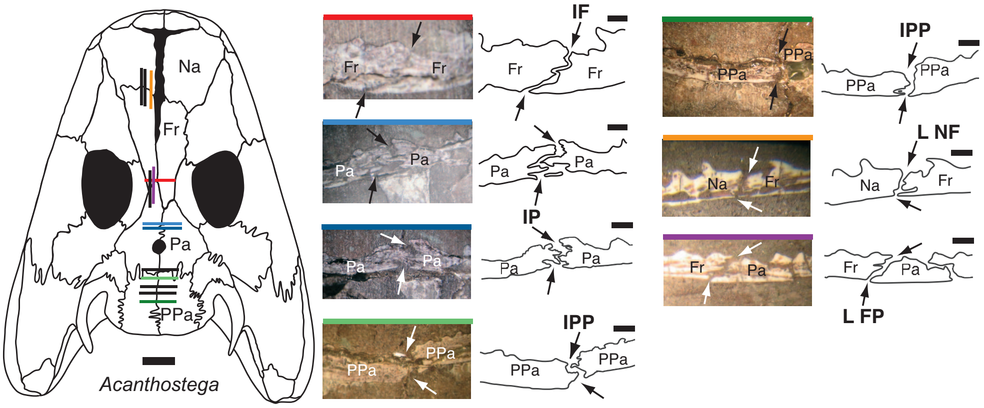

Fig. 2. Photographs and camera lucida drawings of selected midline and coronal sutures in the aquatic Devonian tetrapod *Acanthostega*. The midline IF, IP, and IPP sutures were observed in coronal sections of MGUH f.n. 236. The NF and FP sutures were observed in MGUH f.n. 1305 (sectioned sagittally). The black arrows indicate the endocranial and ectocranial emergence of each suture. The colored bar on the top of each suture photograph indicates the approximate position of that slice through the skull roof of *Acanthostega*. Slices whose positions are shown in black on the dorsal reconstruction of *Acanthostega* were measured in this study but are not figured here. Note the dramatic shape changes within the IP and IPP sutures. [Scale bars: 1 mm (suture) and 1 cm (skull).] The dorsal reconstruction of the skull of *Acanthostega* is modified from the literature (31). Na, nasal; Fr, frontal; Pa, parietal; PPa, postparietal; L NF, left nasofrontal suture; L FP, left frontoparietal suture.

Assigning Functions to the Sutural Morphospace. The fact that we have previously measured the loading conditions experienced by these sutures in *Polypterus* during feeding (23) means that particular regions of the morphospace can be linked to particular strain polarities (i.e., tension or compression). Specifically, we found that the IF suture in *Polypterus* is tensed, whereas the IP suture is compressed during feeding (23). The FP suture of *Polypterus* may experience tension or compression (23), which probably indicates shearing or bending (27).

Based on these correlations between suture form and function, we assume the following: that fossil sutures that plot in the morphospace volume defined by the *Polypterus* IF suture measurements (pink) experienced tension; that sutures that lie in the *Polypterus* IP volume (blue) experienced compression; and that fossil suture morphologies that fall in the *Polyperus* FP volume (green) of the morphospace experienced more complex loading conditions that would have been manifested as a combination of tension and compression (Fig. 4). For example, we infer that the IF suture of *Eusthenopteron* was loaded in tension, whereas this suture was compressed in *Phonerpeton* (Fig. 4). In contrast, the IF suture in *Acanthostega* plots outside all three volumes of known deformation; therefore, it probably did not experience any of the specific loading conditions we observed in *Polypterus* (Fig. 4). The inferred deformation types (where they could be made) for the IF, IP, interpostparietal (IPP), NF, and FP sutures in all three fossil taxa, as well as the known sutural deformation patterns in *Polypterus*, are shown in Fig. 5.

Discussion

Linking Patterns of Sutural Morphology to Feeding Modes. At the outset of this work, we hypothesized that taxa that practice aquatic feeding should exhibit similar sutural morphologies, and that at least some of these sutures would be quantitatively different from those found in terrestrial taxa. Our measurements support these hypotheses. *Eusthenopteron* and *Polypterus* are both characterized by tension anteriorly across the IF suture and compression posteriorly at the IP suture (Fig. 5), despite the taxonomic distance between these "fish" (*Eusthenopteron* is a sarcopterygian, whereas *Polypterus* is a basal actinopterygian). One or more common activities among fish (e.g., swimming, gill breathing, and suction feeding) could result in this strain pattern (Fig. 5). However, our previous work shows that, in *Polypterus*, pumping water across the gills and steady swimming do not cause appreciable sutural deformation; instead, the sutures are

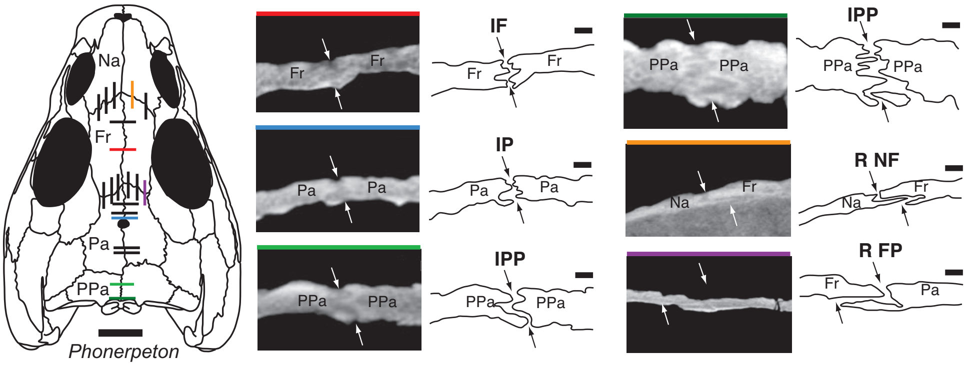

Fig. 3. Cropped CT slices and line drawings of selected midline and coronal sutures in the Permian terrestrial tetrapod *Phonerpeton* and their positions in the skull roof. The white and black arrows indicate the ecto- and endocranial ends of each suture in cross-section. [Scale bars: 1 mm (suture) and 1 cm (skull).] The colored line across the top of each CT image indicates the position of that slice in the skull. Slices whose positions are shown in black on the dorsal reconstruction of *Phonerpeton* were measured in this study but are not figured here. The CT slices were obtained from *Phonerpeton* specimen MCZ 1414. Note the obvious shape change within the IPP suture. The dorsal reconstruction at left has been modified from the literature (24). Fr, frontal; Pa, parietal; PPa, postparietal; Na, nasal; R NF, right nasofrontal; R FP, right frontoparietal.

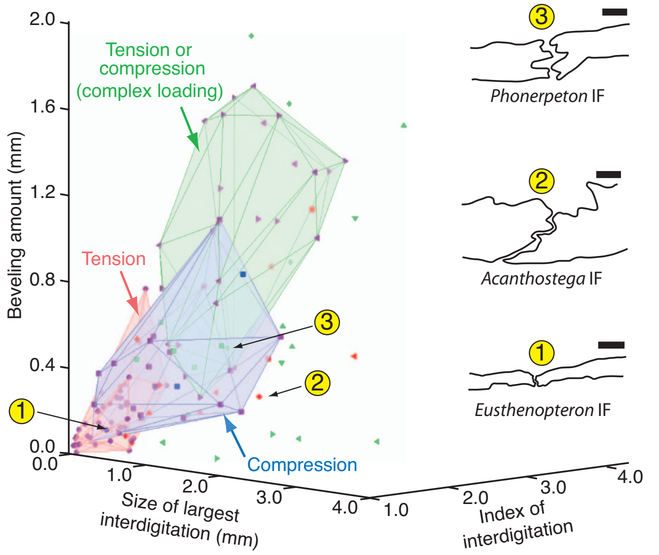

Fig. 4. Sutural morphospace defined by cross-sectional sutural measurements in *Eusthenopteron*, *Acanthostega*, and *Phonerpeton*. The volumes defined by suture morphologies in the extant fish *Polypterus* known to experience tension, compression, or a combination of tension and compression that reflects more complex loading conditions (such as shearing or bending) are shown in pink, blue, and green, respectively. The locations of the fossil data points within these volumes are used to infer the loading conditions experienced by the fossil sutures. Taxa: *Polypterus*, purple; *Eusthenopteron*, blue; *Acanthostega*, red; *Phonerpeton*, green. Sutures: IF, ●; IP, ■; IPP, ♦; left frontoparietal (LFP), ◀; right frontoparietal (RFP), ▶; left nasofrontal (LNF), ▲; right nasofrontal (RNF), ▼. (Scale bars: 1 mm.)

strained by feeding activity, most prominently by sucking a prey item into the mouth (23). Therefore, the "tension anteriorly, compression posteriorly" strain pattern that we observed in *Polypterus*, and have inferred for *Eusthenopteron*, probably results from suction feeding, which is widely used by aquatic vertebrates (10).

In contrast to the "tension anteriorly, compression posteriorly" strain pattern found in the unequivocally aquatic *Polypterus* and *Eusthenopteron*, the terrestrial tetrapod *Phonerpeton* exhibits compression between the frontals and parietals and a possible tension-compression shift denoting complex loading between the postparietals (Fig. 5). No clear evidence of tensile strain in isolation was found at any suture in *Phonerpeton*. Although the specific method *Phonerpeton* used to obtain food cannot be determined here, we can at least be certain that this terrestrial tetrapod did not capture prey by means of suction. Instead, *Phonerpeton* probably captured prey by biting. Therefore, we suggest that the inferred compression of the IF and IP sutures in this terrestrial taxon (Fig. 5) resulted from biting on prey items.

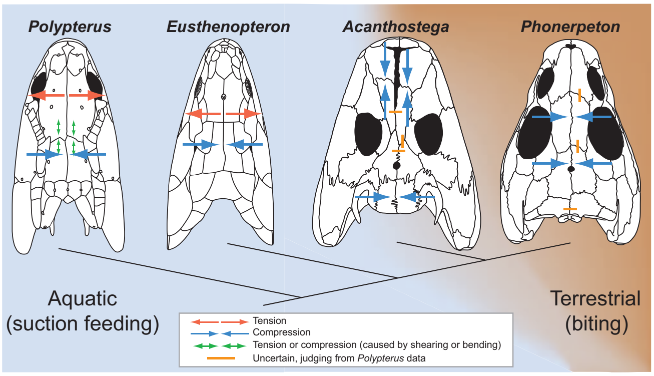

Fig. 5. Inferred strain patterns in the skulls of *Eusthenopteron*, *Acanthostega*, and *Phonerpeton* based on sutural morphology. Strain patterns observed in the extant fish *Polypterus* (23) are included for comparison. The strain pattern inferred for *Acanthostega* suggests that it may have been capable of feeding on land, although *Acanthostega* may also have occasionally captured prey by means of suction in the aquatic realm. Dorsal view reconstructions are modified from published illustrations: *Polypterus* (26), *Eusthenopteron* (30), *Phonerpeton* (24), and *Acanthostega* (31). See Figs. 1–3 for suture morphologies and bone labels.

Feeding in *Acanthostega*. Based on its paddle-like limb morphology, internal gills, and broad tail fin bearing fin rays, *Acanthostega* is inferred to have been a largely aquatic animal (1, 14) that probably fed in the water (13, 14). Therefore, if tension anteriorly and compression posteriorly in the skull is a signature of suction feeding, then this strain pattern would be exhibited by *Acanthostega* if this primarily aquatic tetrapod captured prey by means of suction. However, although the posterior region of the skull of *Acanthostega* was probably loaded in compression (Fig. 5), our measurements of sutural morphology do not support the occurrence of simple tension anteriorly at the midline of the skull (see *Acanthostega* IF suture location in Fig. 4). Therefore, *Acanthostega* probably did not routinely capture prey using suction feeding. In fact, the distant location of the IF suture of *Acanthostega* from the regions of known strain in the sutural morphospace (Fig. 4) suggests that this suture experienced very different loading conditions than the IF of *Eusthenopteron* and *Polypterus*, although the specific conditions cannot be inferred here.

Intriguingly, *Acanthostega* exhibits compression at both the anterior and posterior margins of the skull, a strain pattern more similar to the widespread compression inferred for *Phonerpeton* than to either of the two fish taxa (Fig. 5). Therefore, the feeding mode used by *Acanthostega* was probably more similar to the terrestrial biting prey capture practiced by *Phonerpeton*. Thus, our data suggest that *Acanthostega* bit on prey items in the water or even lurked in shallow water and preyed on terrestrial animals (such as arthropods or possibly other tetrapods whose fossil record is unknown) that approached the water's edge. Therefore, our experimental and morphological data support the hypothesis of Ahlberg and Clack (15) that *Acanthostega* exhibited a reduced reliance on suction feeding to capture prey.

Clack has suggested that the complex morphology of several sutures in *Acanthostega* may be linked to this animal lifting captured prey out of the water during feeding (13); however, our previous work on the extant fish *Polypterus* suggests that prey capture, rather than subsequent prey processing, has a greater influence on sutural morphology in fish (23) (and possibly in tetrapods) that capture prey in the water. Therefore, we favor the hypothesis that the inferred strain pattern in the skull of *Acanthostega* (Fig. 5) may be linked to the initial capture of prey by biting in the water or near the water's edge, rather than lifting prey out of the water during prey processing.

Despite the numerous adaptations to an aquatic lifestyle that *Acanthostega* exhibited (1, 14, 17), our analysis of its cranial suture morphologies coupled with experimental data from living taxa indicates that this early tetrapod most likely used a feeding strategy typical of terrestrial organisms (i.e., biting directly on prey items). Thus, it would seem that the terrestrial mode of feeding, like the tetrapod mode of locomotion, first emerged in an aquatic environment. In this context, it will be interesting to examine sutural morphologies exhibited by taxa that lie phylogenetically between *Eusthenopteron* and *Acanthostega*; the recently discovered tetrapod-like fish *Tiktaalik* (5, 6) would be an ideal candidate. In light of these data, it will also be interesting to revisit the detailed differences in the lower jaw, dentition, and operculum of these taxa (15) in the hope of elucidating the details of the functional changes associated with the shift from suction feeding to biting.

Materials and Methods

Taxa. Although several *Eusthenopteron* specimens housed at the Swedish Museum of Natural History (SMNH), Stockholm, were used as a guide in our analysis of suture morphology in this taxon (specifically SMNH P33, SMNH P236c, SMNH P246a, and SMNH P2609), cross-sectional measurements of the sutures of interest could not be gathered from these fossils. Instead, we measured selected sutures from drawings of the primary specimen (SMNH P222) destructively sampled by Erik Jarvik (using Sollas's grinding method) in his definitive study of *Eusthenopteron* (3). Jarvik abraded away the *Eusthenopteron* specimen at 200-μm increments and photographed the newly revealed cross-sections; therefore, subsequent analyses must rely on the photographs made during the grinding process and on drawings based on the photographs. Our data were collected from the drawings available in the literature (3, 29) (slices 234, 240, and 185) and not the original photographs because they currently cannot be located at the SMNH.

In addition, the morphology of selected sutures was quantified in one specimen of *Phonerpeton* (24) [MCZ 1414; Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts] and in two specimens of *Acanthostega* [Museum Geologicum Universitatis Hafniensis, Copenhagen, Denmark (MGUH) field number 236; MGUH field number 1305] (figured in refs. 13, 14, and 32, respectively). The *Phonerpeton* specimen MCZ 1414 is a small, well preserved, uncrushed skull. The morphology of the sutures in *Phonerpeton* was assessed by using computed tomography (CT) scanning (see *CT Scanning*). In contrast, no CT scan of *Acanthostega* was available for our use. Instead, thick sections of two *Acanthostega* specimens made by J. Clack were used to measure suture morphology in this species. Clack sectioned MGUH f.n. 236 in the coronal plane, whereas MGUH f.n. 1305 was sectioned in the sagittal plane. These *Acanthostega* specimens are currently housed at the University Museum of Zoology, Cambridge, U.K. All data used in this study were collected from M.J.M.'s camera lucida drawings and photographs of specimens MGUH f.n. 1305 and MGUH f.n. 236, not from previous figures (13, 14, 32) of these specimens.

CT Scanning. The skull and cranial sutures of *Phonerpeton* were visualized by using high-resolution x-ray CT scanning. The specimen (MCZ 1414) was scanned by M. Colbert at the University of Texas High-Resolution X-Ray CT Facility (UTCT). The original coronal data set consisted of 583 slices. Each slice is 133 μm thick, 61.0 mm wide by 61.0 mm tall, at an image resolution of 16.8 pixels per mm. To visualize sutures positioned in the coronal plane of the skull, the original CT data set was digitally resliced in the sagittal plane to create a sagittal data set of 942 slices. All digital reslicing was performed at the UTCT facility by using a custom Interactive Data Language (IDL) routine (IDL; Research Systems Inc., Boulder, CO). Each new sagittal slice measures 61.0 mm wide by 61.0 mm tall, and is 52.6 μm thick, at an image resolution of 21.3 pixels per mm. The software program ImageJ 1.32j (NIH, Bethesda, MD) was used to examine all CT slices.

Sutures Included in This Analysis. For ease of comparison between *Eusthenopteron*, *Acanthostega*, and *Phonerpeton*, which possess different skull shapes and proportions, only midline and coronal sutures in approximately equivalent locations were used in this study (see Figs. 1–3). In addition, the relatively small number of slices available for *Acanthostega* and *Eusthenopteron* limited the range of sutures we could measure. Therefore, our analysis of *Eusthenopteron* includes only the IF and IP sutures (Fig. 1) (see introduction for a note on the terminology used for these bones). For *Acanthostega*, we gathered data from the IF and IP, as well as from the IPP, left frontoparietal (L FP), and left nasofrontal (L NF) sutures (Fig. 2). Finally, in *Phonerpeton* we chose to measure the same set of sutures (i.e., IF, IP, IPP, L FP, and L NF) as we measured in *Acanthostega*, plus the right frontoparietal (R FP), and right nasofrontal (R NF) sutures (Fig. 3).

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