Unique pelvic fin in a tetrapod-like fossil fish, and the evolution of limb patterning

Jonathan E. Jeffery[a,1], Glenn W. Storrs[b], Timothy Holland[c], Clifford J. Tabin[d], and Per E. Ahlberg[e]

[a]School of Earth Sciences, University of Bristol, BS8 1TQ Bristol, United Kingdom; [b]Cincinnati Museum Center, Cincinnati, OH 45203; [c]Kronosaurus Korner, Richmond, QLD 4822, Australia; [d]Department of Genetics, Harvard Medical School, Boston, MA 02115; and [e]Subdepartment of Evolution and Development, Department of Organismal Biology, Uppsala University, 752 36 Uppsala, Sweden

All living tetrapods have a one-to-two branching pattern in the embryonic proximal limb skeleton, with a single element at the base of the limb (the humerus or femur) that articulates distally with two parallel radials (the ulna and radius or the tibia and fibula). This pattern is also seen in the fossilized remains of stem-tetrapods, including the fishlike members of the group, in which despite the absence of digits, the proximal parts of the fin skeleton clearly resemble those of later tetrapods. However, little is known about the developmental mechanisms that establish and canalize this highly conserved pattern. We describe the well-preserved pelvic fin skeleton of *Rhizodus hibberti*, a Carboniferous sarcopterygian (lobe-finned) fish, and member of the tetrapod stem group. In this specimen, three parallel radials, each robust with a distinct morphology, articulate with the femur. We review this unexpected morphology in a phylogenetic and developmental context. It implies that the developmental patterning mechanisms seen in living tetrapods, now highly constrained, evolved from mechanisms flexible enough to accommodate variation in the zeugopod (even between pectoral and pelvic fins), while also allowing each element to have a unique morphology.

zeugopod | pelvis | limb patterning | tetrapodomorph | rhizodontid

The evolution and developmental patterning of the tetrapod limb has been the subject of intense research in recent decades (1–9). Limbs arose as a modification of the paired fins of sarcopterygian fishes, and the skeletal morphology is well known in several of the fish-like members of the tetrapod stem group, including such Paleozoic genera as *Gogonasus* (10, 11), *Eusthenopteron* (12), *Panderichthys* (3, 5), and *Tiktaalik* (4, 9). Developmental data are available from a living sister taxon of the tetrapods, the Australian lungfish *Neoceratodus* (13).

Research into the evolution of skeletal patterning of limbs has focused principally on the origin of the autopod (the ankle/wrist and digits) (1, 3, 5, 14–19). In contrast, the pattern in the proximal part of the skeleton has been seen as substantially conserved across the fish-tetrapod transition (4, 20), comprising a single basal element (the humerus or femur) articulating distally with paired elements (the radius and ulna or tibia and fibula).

Pelvic material of stem-tetrapods is rare (compared with pectoral material), and few examples have been described to date (9, 20). Specimen MCZ 11916 from the Museum of Comparative Zoology, Harvard University is a large oil shale nodule from the Asbian Wardie Shales (Viséan, Early Carboniferous, 339.4–336 Mya) of Wardie Beach near Edinburgh, United Kingdom (21) (Fig. 1) containing a near-complete skeleton of the rhizodontid stem-tetrapod *Rhizodus hibberti* (22, 23) (*SI Appendix*, Fig. S1). *Rhizodus* is the largest known sarcopterygian fish (24, 25) and MCZ 11916 was a medium-sized individual, ~3.5 m long. Both pelvic fins are articulated and are preserved in natural association with the spine, and the dorsal and anal fins (Fig. 2 and *SI Appendix*, Fig. S1B). This exceptional preservation offers a unique insight into the morphology of the pelvic region at an early stage of tetrapod evolution.

Results

Pelvic Girdle. The pelvic girdle of MCZ 11916 comprises a single, long bone on each side, and would have been ~120 mm long in life. The shaft of the right pelvis is incomplete, but the distal ends of both left and right bones are well preserved and associated with their respective fin skeletons. Each pelvis has a robust pubic ramus with a posterior-facing acetabulum, flanked by lateral ("iliac"; ref. 12) and mesial flanges (Fig. 2B and *SI Appendix*, Fig. S2), similar to those described for other fishlike stem-tetrapods (Fig. 3A) (9, 12, 24). The pubic ramus is fairly straight and lenticular in cross-section for much of its length. Anteriorly it terminates in jagged, unfinished bone, suggesting that the shaft continued as cartilaginous tissue. The outer (lateral) surface of the shaft is smooth except for a process near the base of the mesial flange (more pronounced on the right pelvis). The inner (mesial) surface bears a shallow longitudinal ridge anteriorly. Posteriorly, the shaft thickens to a mesial buttress, triangular in cross-section, encompassing the acetabulum. The acetabulum itself not well preserved (it was likely cartilaginous and not finished bone), and its shape cannot be determined with any certainty. The mesial flange is a robust triangular area of bone. The iliac process is broken off at its base on the left side, but on the right side it is a large, flat flange with a rounded tip.

Pelvic Fins. Both pelvic fins show a well-preserved femur, ~45 mm long (Figs. 2 and 4). It is a wide bone with distinct preaxial and postaxial edges, similar in proportion to that of *Eusthenopteron*, the only other fishlike stem-tetrapod for which a detailed

---

Significance

The fossil fish *Rhizodus hibberti*, a member of the tetrapod stem group, shows a unique skeletal pattern in the pelvic fin. Rather than the highly conserved one-to-two pattern of a femur, tibia, and fibula (seen in all known tetrapods, including the extinct, fishlike members of the group), the fin of *Rhizodus* comprises a femur articulating distally with three bones, each with a distinct morphology. This reveals an early stage in the evolution of limb development, in which the processes patterning the proximal parts of the embryonic fin/limb (the stylopod and zeugopod) were not constrained in the way seen in living tetrapods and could produce more varied skeletal patterns in the adult.

EVOLUTION

Fig. 1. Map of Wardie Beach, Edinburgh, United Kingdom (55.98N, 3.21W). Although the original collection notes are vague (22), all more recent discoveries of *Rhizodus* material at Wardie have been made in the large exposure of bed 2 (21). Data from ref. 21.

description is available (Fig. 3*B*) (12, 26). The ventral face bears two muscle attachment processes and a longitudinal fossa (Fig. 4 *B–D*, *F*, and *G*). A similar fossa is seen in *Eusthenopteron* (Fig. 3*B*) (12, 26), and there is also a longitudinal ridge in the same position as one of the processes seen in *Rhizodus* (26). The femur terminates distally in an expanded region of unfinished bone, divided into three facets, each of which articulates with a robust endoskeletal fin radial. These three radials have distinct individual morphologies, which match perfectly between the left and right fins. The most external (anatomically anterior) radial tapers slightly distally and does not appear to have articulated with more distal radials. The middle radial has a waisted shaft, and the internal (anatomically posterior) radial bears a thick postaxial flange. Both the middle and internal radials have expanded distal ends, and on the right fin they both articulate with a single distal radial of similar size; on the left fin, the three radials contact the edge of the nodule, and nothing more distal is preserved. All these radials are essentially cylindrical "long" bones (*sensu* refs. 7, 17, 18, and 20), with a complete periosteum along their shafts.
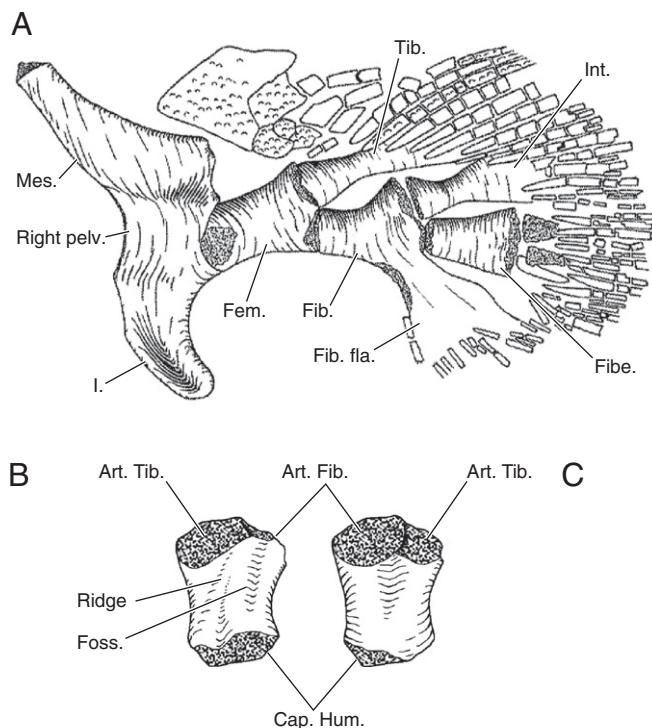

Fig. 3. *Eusthenopteron foordi*, pelvic fin and girdle. (*A*) Right pelvic fin and girdle in dorsal view. Note that the long pubic ramus is not shown. Reproduced by permission of The Royal Society of Edinburgh from ref. 12. (*B*) Reconstruction of the left femur in posteroventral view. (*C*) Reconstruction of the left femur in dorsolateral view. Reproduced with permission from ref. 26. I., illiac flange of pelvis; Mes., mesial flange of pelvis; Art. Fib., articulation for the fibula; Art. Tib., articulation for the tibia; Cap. Hum., caput humeri; Fib. fla., postaxial flange on the fibula; Fibe., fibulare; Int., intermedium.

The unfinished bone at the proximal and distal ends of the femur and radials is similar in its preservation to the bones of a pectoral fin of *Rhizodus* from the same locality (NMS G 1972.27.434c) (25). The bone degrades and merges with the matrix, so it is often difficult to demark the end of the bone with
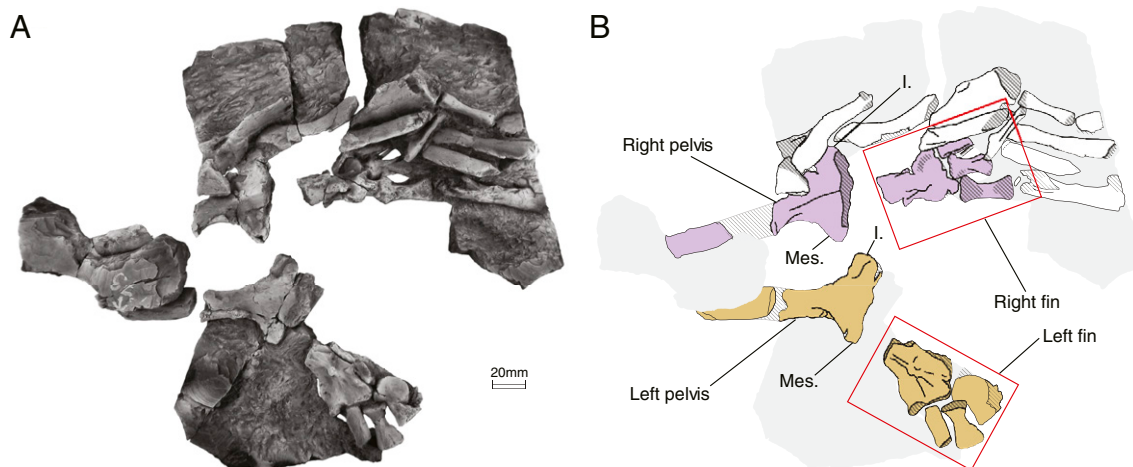
Fig. 2. *R. hibberti* MCZ 11916 pelvic region. (*A*) Overview of the pelvic region in dorsal view; anterior is to the left. (*B*) Interpretative sketch, highlighting the right pelvic skeleton (purple) and left pelvic skeleton (brown). Uncolored bones belong to the spine and first dorsal fin. Red boxes indicate the areas seen in Fig. 4 and *SI Appendix*, Fig. S3. I., illiac flange of pelvis; Mes., mesial flange of pelvis. The specimen was dusted with ammonium chloride to improve contrast. In the interpretative sketch, thick outlines indicate natural margins, narrow lines indicate damaged margins, and diagonal hatching indicates damaged surfaces or reconstructed outlines.
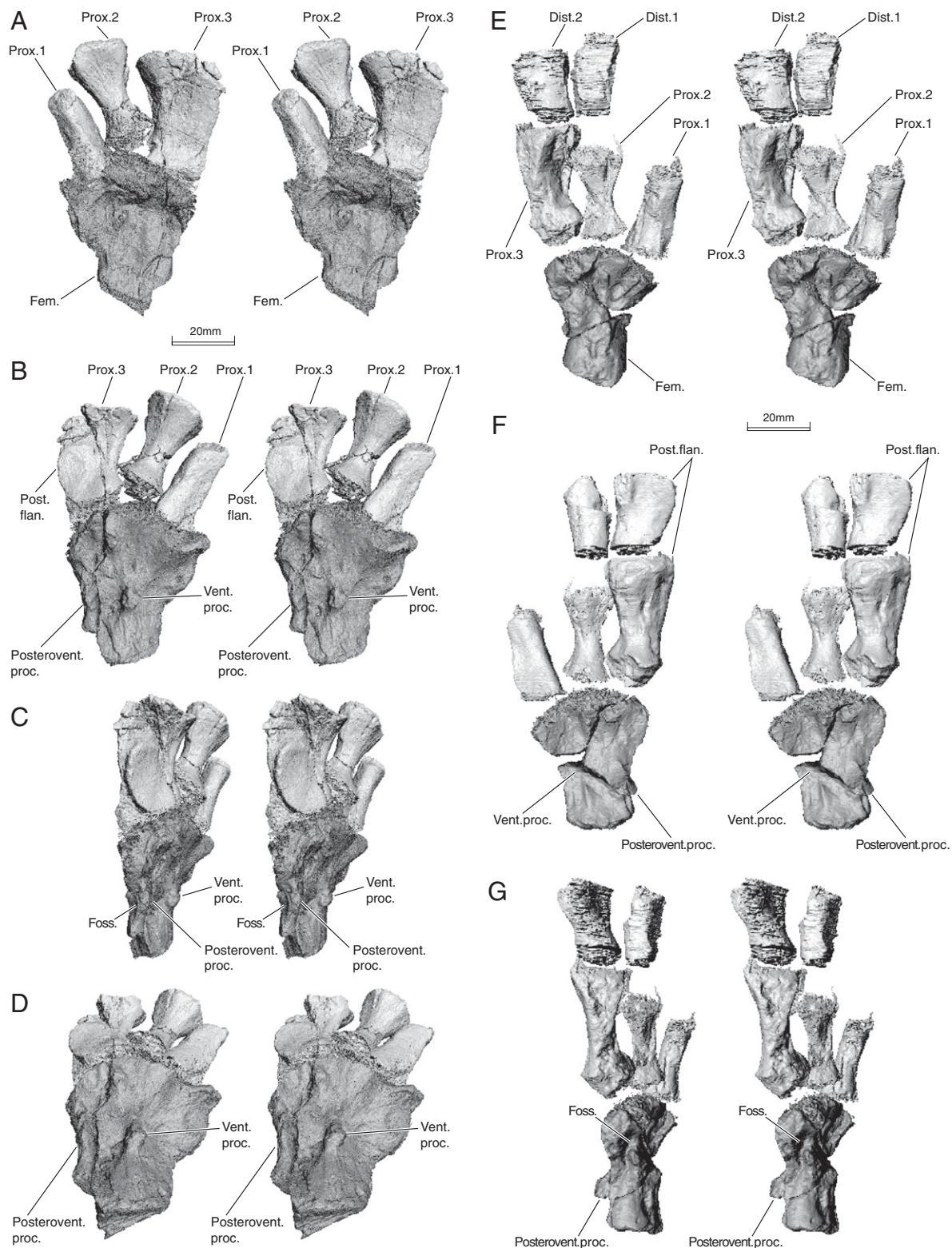
Fig. 4. *R. hibberti* MCZ 11916, 3D computer models of the pelvic fins based on CT scans. (*A*) Left pelvic fin, stereo pair in dorsal view. (*B*) Left pelvic fin, stereo pair in ventral view. (*C*) Left pelvic fin, stereo pair in posteroventral view. (*D*) Left pelvic fin, stereo pair in proximoventral view. (*E*) Right pelvic fin, stereo pair in dorsal view. (*F*) Right pelvic fin, stereo pair in ventral view. (*G*) Right pelvic fin, stereo pair in posteroventral view. Dist., distal endoskeletal radials (1, anterior; 2, posterior); Fem., femur; Foss., longitudinal fossa on ventral face of femur; Post.flan., postaxial flange on distal endoskeletal radial 3; Posterovent. proc., posteroventral process of femur; Prox., proximal endoskeletal radials (1, anterior; 2, middle; 3, posterior); Vent.proc., ventral process of femur.

Jeffery et al.

www.manaraa.com
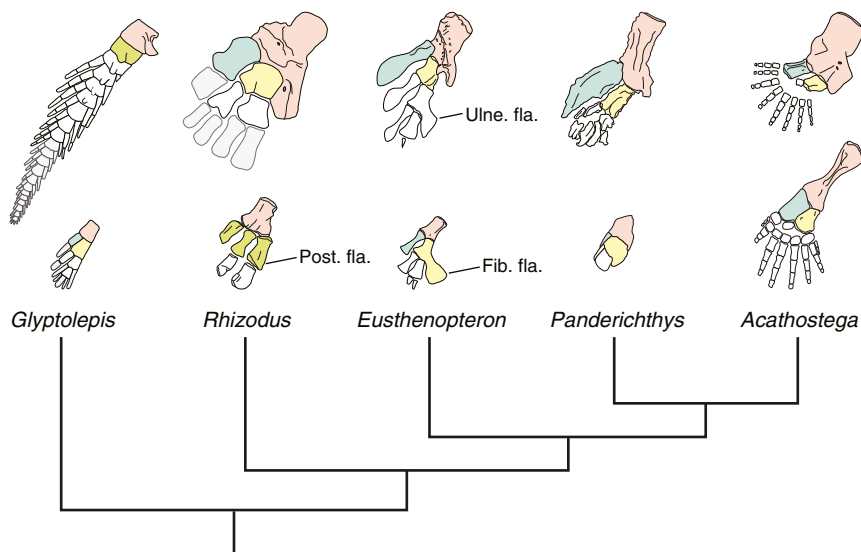
Fig. 5. Pectoral (*Top*) and pelvic (*Bottom*) skeletons of representative fossil taxa, with a cladogram to show their interrelationships: *Glyptolepis*, a stem-lungfish (35), *Rhizodus*, a rhizodontid (24, 25), *Eusthenopteron*, an "osteolepiform" (12), *Panderichthys*, an elpistostegid (3, 5) and *Acanthostega*, an early tetrapod (2). For each taxon, the pelvic and pectoral skeletons are shown to the same scale, highlighting their relative sizes. Bones formed in the stylopod are colored pink (humerus and femur), and bones formed in the zeugopod are colored yellow (ulna and fibula), blue (radius and tibia), or green (fused or uncertain). More distal bones are white, and reconstructed elements are shaded gray. In the pelvic fin of *Panderichthys*, it is uncertain whether the most distal element comprises a single, broad bone or several smaller bones like the distal end of the pectoral fin. Data from ref. 37. Fib. fla., postaxial flange on the fibula; Post. fla., postaxial flange on the posterior radial; Ulne. fla., postaxial flange on the ulnare.

any precision. This is most readily interpreted as the decayed remains of cartilaginous joint surfaces.

Numerous scales and lepidotrichia were preserved in association with the fin endoskeletons. The basal segments of the lepidotrichia are very long and overlap the whole endoskeleton distal to the femur. This is similar to the condition observed in rhizodontid pectoral fins (25, 27–29). Most of the lepidotrichia were removed during preparation (to expose the endoskeleton), although one was left in situ to demonstrate the high degree of overlap with the endoskeleton (*SI Appendix*, Fig. S3 *G* and *H*).

Discussion

Phylogenetic Context. Within the sarcopterygian crown group (including tetrapods), a single basal bone articulating with two radials appears to be the primitive morphology for both the pectoral fin/limb (the humerus, ulna, and radius) (30) and the pelvic fin/limb (the femur, tibia, and fibula). This pattern can be identified in the only living groups of sarcopterygian fishes, the coelacanths (31) and lungfishes (13), although in lungfishes the two developing radials fuse together late in ontogeny (13, 32, 33).

In fossil crown group sarcopterygian fishes, there are numerous well-preserved examples of the (adult) morphology of the pectoral fin endoskeleton, but in contrast, only a handful of fossil sarcopterygian fishes have well-preserved pelvic fin endoskeletons (9, 12, 34, 35). Nevertheless, all cases, there is a single basal bone articulating with two radials.

In the very few species in which the endoskeleton of both the pectoral and pelvic fins are known, there are clear differences between endoskeletal patterns distal to the two radials (20). For example, in the porolepiform *Glyptolepis* (Fig. 5), a stem-lungfish (35), the pelvic fin endoskeleton is short and asymmetrical, whereas the pectoral fin is long and symmetrical, similar to the pectoral fin of the living lungfish *Neoceratodus* (13).

In *Rhizodus*, in addition to the pelvic girdle and fin of MCZ 11916 described above, the pectoral girdle and fin endoskeleton is known from several specimens (24, 25). It shows the general tetrapod pattern of a humerus articulating with a radius and ulna, with the ulna articulating distally with an ulnare and

intermedium. All the bones are robust, and the fin is much larger overall than the pelvic fin: parts of the pectoral fin are preserved on MCZ 11916, allowing cross-scaling with more complete pectoral specimens (cf. ref. 9).

The endoskeleton of the pectoral fin (but not the pelvic fin) is known is several other rhizodontid genera, including *Screbinodus* (25), *Strepsodus* (25, 27), *Barameda* (29), and *Sauripterus* (16, 28). In all cases, it is very similar to that of *Rhizodus*. Finally, while the pelvic fin endoskeleton of the basal rhizodontid *Gooloogongia* has been reconstructed with paired radials (36) the actual morphology is unknown (37).

It should be noted that trichotomous articulations are seen in the pectoral and/or pelvic fins of numerous fossil sarcopterygian fin skeletons, including *Tiktaalik* (4) and several rhizodontids (24, 25, 28), as well as in *Neoceratodus* and the living coelacanth. However, these trichotomies only ever occur in the distal endoskeleton (i.e., distal to the two radials).

Developmental Context. The proximal bones of the tetrapod limb form from an initially continuous bifurcating chondrogenic condensation that forms in a proximal-to-distal progression. Individual skeletal elements are generated through segmentation, yielding three distinct limb segments: the stylopod, zeugopod, and autopod. The condensation in the stylopod ultimately forms the humerus in the forelimb or the femur in the hindlimb, while those in the zeugopod ultimately form the ulna and radius in the forelimb or the tibia and fibula in the hindlimb. The condensations in the autopod give rise to the more distal skeletal elements.

Of the living sarcopterygian fishes, only the Australian lungfish *Neoceratodus* lends itself to developmental analysis, and only the pectoral fin has been studied in detail (13). Here the pattern of condensation is somewhat different from that of tetrapods. Nevertheless, the fin has a clear anatomic stylopod and zeugopod (13, 32, 38, 39; see also ref. 40 for comparisons with fossil material), which lends support to the view, based on the adult skeletal patterns discussed above, that there are direct one-to-one
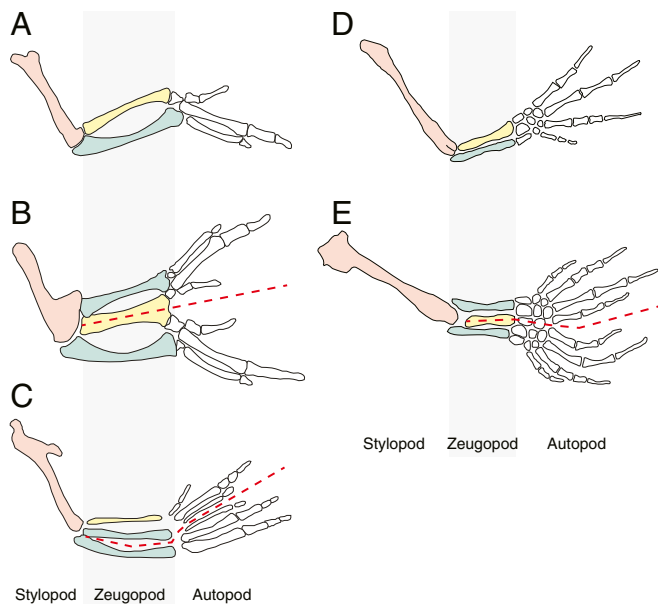
Fig. 6. Examples of three skeletal elements developing in the zeugopod following a ZPA graft at early stages of limb development. (*A*) A normal chick wing. (*B*) A mirror-image duplication of the chick zeugopod and autopod following a ZPA graft to the anterior margin. Republished with permission of Company of Biologists, from ref. 44; permission conveyed through Copyright Clearance Center, Inc. (*C*) A more complex duplication following a ZPA graft to the apex of a chick limb bud. Republished with permission of Company of Biologists, from ref. 46; permission conveyed through Copyright Clearance Center, Inc. (*D*) A normal axolotl forelimb. (*E*) A mirror image duplication of the axolotl zeugopod and autopod following a ZPA graft. Republished with permission of Company of Biologists, from ref. 48; permission conveyed through Copyright Clearance Center, Inc. In all cases, the humerus is colored pink, the ulna is yellow, the radius is blue, and more distal bones are white. Dashed red lines show the approximate axis of symmetry for the mirror-image duplications. In *C*–*E*, the orientation of the humerus has been adjusted slightly to aid comparisons.

homologies between the bones that develop in these regions in sarcopterygian fins and tetrapod limbs.

While it is impossible to establish such one-to-one homologies between the three radials in the pelvic fin skeleton of *Rhizodus* and the tibia and fibula seen in other sarcopterygian fishes and tetrapods, it does seem likely that the femur and the adjacent three radials represent the products of a stylopod and zeugopod, respectively. The only concern with this interpretation stems from the fact that a trichotomous articulation has formed in the putative zeugopod, something entirely unknown in any sarcopterygian fish or tetrapod.

Some insights can be gained from experimental embryology, where it is has proven possible to generate limbs with three radials in the zeugopod. This is most clearly seen when Shh-producing ZPA tissue is taken from the posterior of a donor limb bud and grafted to an anterior location along the distal margin of a host limb bud. Shh plays key roles both in patterning the anterior-posterior axis of the limb (41, 42) and in driving expansion of the limb bud tissue (43). In various species, including chicks and axolotls, grafts of ZPA tissue (or the implantation of a bead carrying Shh protein) causes mirror-image duplications of the autopod elements of the host limb, but can

also result in a broader zeugopod containing three radials if done at a sufficiently early developmental stage (Fig. 6). Significantly, the space between each of the three radials is similar to the space between the two radials in a normal zeugopod, implying that the zeugopod skeleton is established through a reiterative mechanism, and that the wider the primordial field, the more radials that will form.

The major difference between these experimental cases and the pelvic fin of *Rhizodus* is that the former involves mirror-image duplications—either ulna-radius-ulna, with an axis of symmetry through the radius, or radius-ulna-ulna, with an axis of symmetry between the two ulnas (Fig. 6) (44–48)—while the latter contains three unique and distinct radials. This suggests that in all likelihood, the broadening of the zeugopod primordium in *Rhizodus* necessary for producing the increased number of radials seen in the adult was not caused simply by an ectopic anterior expression of Shh in the pelvic finbud.

Finally, in some experimental ZPA grafts, the distal end of the humerus expands to become a triangular flange (Fig. 6*B*), similar to the expanded distal femur of *Rhizodus*, indicating that even without additional regulatory changes, it is possible for the shape of the developing stylopod cartilage to alter to accommodate the need to articulate with additional distal radials.

Conclusion

The pelvic fin endoskeleton of *R. hibberti*, with a trichotomous articulation distal to the femur, is unique and unexpected. It is in stark contrast to the more general form of the endoskeleton of its pectoral fin. The patterning mechanisms that gave rise to the trichotomous articulation remain unclear; a change in Shh expression may have been involved but is unlikely to have been sufficient on its own to generate the observed morphology.

Rhizodus may offer a glimpse of an early stage of zeugopod evolution, before the bifurcating process seen in living tetrapods became canalized in both pectoral and pelvic limbs. The fact that the pectoral fin skeleton of *Rhizodus* resembles that of more derived tetrapods suggests that the bifurcating mechanism became established in the pectoral fin first and was only later coopted to the pelvic fin. This also could help explain the differing pectoral and pelvic fin endoskeleton patterns seen in other fish-like stem-tetrapod species (Fig. 5).

Materials and Methods

1. Coates MI, Clack JA (1990) Polydactyly in the earliest known tetrapod limbs. *Nature* 347:66–69.
2. Coates MI (1996) The Devonian tetrapod *Acanthostega gunnari* Jarvik: Postcranial anatomy, basal tetrapod interrelationships and patterns of skeletal evolution. *Trans R Soc Edinburgh Earth Sci* 87:363–421.
3. Boisvert CA (2005) The pelvic fin and girdle of *Panderichthys* and the origin of tetrapod locomotion. *Nature* 438:1145–1147.
4. Shubin NH, Daeschler EB, Jenkins FA, Jr (2006) The pectoral fin of *Tiktaalik roseae* and the origin of the tetrapod limb. *Nature* 440:764–771.
5. Boisvert CA, Mark-Kurik E, Ahlberg PE (2008) The pectoral fin of *Panderichthys* and the origin of digits. *Nature* 456:636–638.
6. Coates MI, Ruta M, Friedman M (2008) Ever since Owen: Changing perspectives on the early evolution of tetrapods. *Annu Rev Ecol Evol Syst* 39:571–592.

Jeffery et al.

EVOLUTION

7. Woltering JM, Duboule D (2010) The origin of digits: Expression patterns versus regulatory mechanisms. *Dev Cell* 18:526–532.

8. Zeller R (2010) The temporal dynamics of vertebrate limb development, teratogenesis and evolution. *Curr Opin Genet Dev* 20:384–390.

9. Shubin NH, Daeschler EB, Jenkins FA, Jr (2014) Pelvic girdle and fin of *Tiktaalik roseae*. *Proc Natl Acad Sci USA* 111:893–899.

10. Long JA, Young GC, Holland T, Senden TJ, Fitzgerald EMG (2006) An exceptional Devonian fish from Australia sheds light on tetrapod origins. *Nature* 444:199–202.

11. Holland T (2013) Pectoral girdle and fin anatomy of *Gogonasus andrewsae* Long, 1985: Implications for tetrapodomorph limb evolution. *J Morphol* 274:147–164.

12. Andrews SM, Westoll TS (1970) The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. *Trans R Soc Edinburgh* 68:207–329.

13. Johanson Z, et al. (2007) Fish fingers: Digit homologues in sarcopterygian fish fins. *J Exp Zoolog B Mol Dev Evol* 308:757–768.

14. Clack JA (2006) The emergence of early tetrapods. *Palaeogeogr Palaeoclimatol Palaeoecol* 232:167–189.

15. Zákány J, Fromental-Ramain C, Warot X, Duboule D (1997) Regulation of number and size of digits by posterior *Hox* genes: A dose-dependent mechanism with potential evolutionary implications. *Proc Natl Acad Sci USA* 94:13695–13700.

16. Daeschler EB, Shubin N (1998) Fish with fingers? *Nature* 391:133.

17. Wagner GP, Chiu CH (2001) The tetrapod limb: A hypothesis on its origin. *J Exp Zool* 291:226–240.

18. Metscher BD, et al. (2005) Expression of Hoxa-11 and Hoxa-13 in the pectoral fin of a basal ray-finned fish, *Polyodon spathula*: Implications for the origin of tetrapod limbs. *Evol Dev* 7:186–195.

19. Zákány J, Kmita M, Duboule D (2004) A dual role for *Hox* genes in limb anterior-posterior asymmetry. *Science* 304:1669–1672.

20. Coates MI, Jeffery JE, Ruta M (2002) Fins to limbs: What the fossils say. *Evol Dev* 4:390–401.

21. Wood SP (1975) Recent discoveries of Carboniferous fishes in Edinburgh. *Scott J Geol* 11:251–258.

22. Stock T (1881) On the discovery of a nearly entire *Rhizodus* in the Wardie shales. *Geol Mag* 8:77–78.

23. Dineley DL, Metcalf SJ (1999) *Fossil Fishes of Great Britain* (Joint Nature Conservation Committee, Peterborough, UK).

24. Andrews SM, Westoll TS (1970) The postcranial skeleton of rhipidistian fishes excluding *Eusthenopteron*. *Trans R Soc Edinburgh* 68:391–489.

25. Jeffery JE (2001) Pectoral fins of rhizodontids and the evolution of pectoral appendages in the tetrapod stem-group. *Biol J Linn Soc Lond* 74:217–236.

26. Jarvik E (1980) *Basic Structure and Evolution of Vertebrates* (Academic, London).

27. Andrews SM (1985) Rhizodont crossopterygian fish from the Dinatian of Foulden, Berwickshire, Scotland, with a re-evaluation of this group. *Trans R Soc Edinburgh Earth Sci* 76:67–95.

28. Davis MC, Shubin N, Daeschler EB (2004) A new specimen of *Sauripterus taylori* (Sarcopterygii, Osteichthyes) from the Famennian Catskill Formation of North America. *J Vertebr Paleontol* 24:26–40.

29. Garvey JM, Johanson Z, Warren A (2005) Redescription of the pectoral fin and vertebral column of the rhizodontid fish *Barameda decipiens* from the lower carboniferous of Australia. *J Vertebr Paleontol* 25:8–18.

30. Zhu M, Yu X (2009) Stem sarcopterygians have primitive polybasal fin articulation. *Biol Lett* 5:372–375.

31. Forey PL (1998) *History of the Coelacanth Fishes* (NHM/Chapman & Hall, London).

32. Holmgren N (1933) On the origin of the tetrapod limb. *Acta Zool* 14:185–295.

33. Boisvert CA, Joss JMP, Ahlberg PE (2013) Comparative pelvic development of the axolotl (*Ambystoma mexicanum*) and the Australian lungfish (*Neoceratodus forsteri*): Conservation and innovation across the fish-tetrapod transition. *Evodevo* 4:3.

34. Rackoff JS (1980) The origin of the tetrapod limb and the ancestry of tetrapods. *The Terrestrial Environment and the Origin of Land Vertebrates*, ed Panchen AL (Academic, London), pp 255–292.

35. Ahlberg PE (1989) Paired fin skeletons and relationships of the fossil group Porolepiformes (Osteichthyes: Sarcopterygii). *Zool J Linn Soc* 96:119–166.

36. Swartz B (2012) A marine stem-tetrapod from the Devonian of western North America. *PLoS One* 7:e33683.

37. Johanson Z, Ahlberg PE (2001) Devonian rhizodontids (Sarcopterygii; Tetrapodomorpha) from East Gondwana. *Trans R Soc Edinburgh Earth Sci* 92:43–74.

38. Rosen DE, Forey PL, Gardiner BG, Patterson C (1981) Lungfishes, tetrapods, paleontology, and plesiomorphy. *Bull Am Mus Nat Hist* 167:163–275.

39. Hodgkinson VS, Ericsson R, Johanson Z, Joss JMP (2009) The apical ectodermal ridge in the pectoral fin of the Australian lungfish (*Neoceratodus forsteri*): Keeping the fin to limb transition in the fold. *Acta Zool* 90:253–263.

40. Jude E, Johanson Z, Kearsley A, Friedman M (2014) Early evolution of the lungfish pectoral-fin endoskeleton: Evidence from the Middle Devonian (Givetian) *Pentlandia macroptera*. *Front Earth Sci* 2:1–15.

41. Saunders JW, Gasseling M (1968) Ectodermal-mesenchymal interaction in the origin of limb symmetry. *Epithelial-Mesenchymal Interaction*, eds Fleishmayer R, Billingham RE (Williams & Wilkins, Baltimore), pp 78–97.

42. Riddle RD, Johnson RL, Laufer E, Tabin C (1993) *Sonic hedgehog* mediates the polarizing activity of the ZPA. *Cell* 75:1401–1416.

43. Zhu J, et al. (2008) Uncoupling sonic hedgehog control of pattern and expansion of the developing limb bud. *Dev Cell* 14:624–632.

44. Wolpert L, Hornbruch A (1987) Positional signalling and the development of the humerus in the chick limb bud. *Development* 100:333–338.

45. Summerbell D, Tickle C (1977) Pattern of formation along the antero-posterior axis of the chick limb bud. *Vertebrate Limb and Somite Morphogeneis*, eds Ede DA, Hinchliffe JR, Balls M (Cambridge Univ Press, Cambridge, UK), pp 41–53.

46. Robson LG, Kara T, Crawley A, Tickle C (1994) Tissue and cellular patterning of the musculature in chick wings. *Development* 120:1265–1276.

47. Slack JM (1977) Control of anteroposterior pattern in the axolotl forelimb by a smoothly graded signal. *J Embryol Exp Morphol* 39:169–182.

48. Slack JM (1977) Determination of anteroposterior polarity in the axolotl forelimb by an interaction between limb and flank rudiments. *J Embryol Exp Morphol* 39:151–168.