A newly recognized fossil coelacanth highlights the early morphological diversification of the clade

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Previously considered an actinopterygian or an osteichthyan *incertae sedis*, the Devonian (Givetian–Frasnian) *Holopterygius nudus* is reinterpreted as a coelacanth. This genus is among the oldest coelacanths known from articulated remains, but its eel-like morphology marks a considerable departure from the conventional coelacanth body plan. A cladistic analysis places *Holopterygius* as the sister taxon of the Carboniferous (Serpukhovian) genus *Allenkypterus*. Despite the specialized morphology of these genera, they occupy a surprisingly basal position in coelacanth phylogeny; only *Diplocercides* and *Miguashaia* are further removed from the crown. A morphometric analysis reveals that coelacanths were anatomically disparate early in their history. Conflicts between this result and those of previous studies challenge the adequacy of systematic character sets for describing historical patterns of morphological variety. Coelacanths have long had an iconic place in the study of vertebrate evolution for their apparent anatomical conservatism over geological time, but *Holopterygius* provides clear evidence for rapid morphological evolution early in the history of this clade.

Keywords: Actinistia; Devonian; disparity; geometric morphometrics; Palaeozoic; Sarcopterygii

1. INTRODUCTION

The affinities of *Holopterygius nudus* Jessen, from the latest Givetian–earliest Frasnian Upper Plattenkalk of Bergisch-Gladbach, Germany, have been enigmatic since its description. While a long, diphyccercal caudal fin and eel-like body distinguish *Holopterygius* from its contemporaries, these features have frustrated efforts to assign it to a higher-level taxon. Jessen (1973), followed by Lund & Melton (1982), speculated on a relationship between this genus and Carboniferous tarrasiid actinopterygians (Moy-Thomas 1934), but offered no characters in support of this arrangement beyond similar body shapes. More recent studies have regarded the position of *Holopterygius* among osteichthyans as uncertain (Taverne 1996; Lund & Poplin 2002). Re-examination of the only known specimen of *Holopterygius* reveals numerous derived characters linking this genus with coelacanths, including a gracile pectoral girdle, an extracleithrum and a mandible with a greatly expanded posterior coronoid. This new interpretation reveals that early coelacanths were more anatomically diverse than previously realized, and challenges the widely held view of this clade as morphologically stagnant.

2. MATERIAL AND METHODS

(a) Systematic methodology

To investigate the systematic placement of *Holopterygius* within coelacanths, we have included this taxon in an updated version of the matrix assembled by Forey (1998). This matrix

was subjected to parsimony analysis using the branch-and-bound algorithm in PAUP* v. 4.0b (Swofford 2002). Initial results were poorly resolved, so characters were re-weighted by their re-scaled consistency indices and the analysis run again. For the complete character matrix and additional details of the cladistic analyses, consult electronic supplementary material B.

(b) Morphometric methodology

We have used relative warps analysis (Bookstein 1991) to summarize variation in coelacanth body form, unlike previous studies, which have examined discrete character data (Schaeffer 1952; Cloutier 1991b; Smith 1994; Forey 1998). Eleven landmarks were digitized from published reconstructions or specimen photographs of 22 genera using the program tpsDig v. 1.40 (Rohlf 2004a). Relative warps analysis was conducted in tpsRelw v. 1.39 (Rohlf 2004b). As this study concerns large- and small-scale morphological variation, the parameter α (which determines the weight of different principal warps) was set to zero. Uniform components of shape change were estimated (Bookstein 1996) and appended to the matrix of principal warps. A principal components analysis of this matrix gives the relative warps and relative warp scores. Coordinate data and the relative warps matrix are given in electronic supplementary material C. Only those axes accounting for over 5% of total variance were examined. Disparity was calculated using four frequently used metrics: sum of variances, product of variances, sum of ranges and geometric mean of ranges (VanValen 1974; Foote 1992).

3. SYSTEMATIC PALAEONTOLOGY

Osteichthyes Huxley (1880). Sarcopterygii Romer (1955). Actinistia Cope (1871). *Holopterygius nudus* Jessen (1973).

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Figure 1. *Holopterygius nudus* Jessen (P 7789), latest Givetian–earliest Frasnian, Bergisch-Gladbach, Germany. (a) Photograph of P 7789a; (b) composite drawing based on P7789a–c; and (c) reconstruction. Bones outlined in grey in (c) were reconstructed based on *Allenkypterus*. Scale bar represents 10 mm. Abbreviations: ano, anocleithrum; bp, basal plate of the second dorsal fin; chy, ceratohyal; cla, calvic; cle, cleithrum; cop, principal coronoid; ex, extracleithrum; has, haemal arch and spine; gs, indeterminate components of the gill skeleton; nas, neural arch and spine; op, opercle; ot, otolith; pal, palate; pap, parapophyses; pmx, premaxilla; psph, parasphenoid; rd, radials of the dorsal lobe of the caudal fin; rv, radials of the ventral lobe of the caudal fin; sr, skull roof; sym, symplectic; vs, ventral keel scales.

(a) *Revised diagnosis*

The following combination of characters distinguishes *H. nudus* from all other coelacanth:

- (i) well-developed premaxillary dentition;
- (ii) keel scales along ventral margin of body;
- (iii) anguilliform profile;
- (iv) strongly asymmetrical caudal lobes; and
- (v) well-developed ventral lobe of caudal fin.

(b) *Holotype*

Naturhistoriska Riksmuseet P 7789 a–c, incomplete fish in part and counterpart.

(c) *Locality and horizon*

The type and only specimen of *Holopterygius* is from the Oberer Plattenkalk in the Heiligenstock quarry, east of Bergisch-Gladbach near Cologne, Germany (Ørvig 1960; Jessen 1973). The depositional environment has been interpreted as lagoonal (Jessen 1973).

(d) *Age*

The stage-level dating of the Bergisch-Gladbach fish beds is uncertain. The flags below the Oberer Plattenkalk yield the Givetian goniatite *Maenioceras terebratum* (Ørvig 1960; Harland *et al.* 1990). Although the Frasnian goniatite *Manticoceras* first appears in beds that overlie the Oberer Plattenkalk (Ørvig 1960), the Givetian–Frasnian

Figure 2. Phylogenetic and morphological relationships between *Holopterygius* and other coelacanths. (a) Stratocladogram based on a cladistic solution with characters re-weighted by their rescaled consistency indices ($N=2$; $L=90.83143$; $CI=0.6339$; $RI=0.8714$; $RCI=0.5966$). Equally weighted solution places *Holopterygius* and *Allenopterus* as sister taxa, but cannot resolve the relationships between this clade and other Carboniferous coelacanths from Bear Gulch ($N=58$; $L=245$; $CI=0.4587$; $RI=0.7029$; $RCI=0.3271$). Arrow leads to more crownward coelacanths. Grey cladogram in background is that of Forey (1998). (b) Landmarks used in morphometric analysis. 1, tip of snout; 2, posterior margin of postparietals; 3, anterior insertion of first dorsal fin; 4, posterior insertion of second dorsal fin; 5, posterior insertion of second dorsal fin; 6, anterior insertion of epichordal lobe; 7, posterior tip of accessory lobe; 8, anterior insertion of hypochordal lobe; 9, posterior insertion of anal fin; 10, base of pelvic fin; 11, quadrate/articular joint. (c) Plots of scores on RW1 versus RW2, with coelacanths divided into Devonian/Carboniferous (lower plot) and post-Carboniferous forms (upper plot). RW1 describes caudal fin geometry, while RW2 reflects body depth. Coelacanth profiles (clockwise from bottom left): *Allenopterus*, *Libys*, *Ticnephomis*, *Miguashaia*, *Holopterygius*. Multiple metrics indicate that early coelacanths are more disparate than stratigraphically younger forms (sum of variances: 0.0392 versus 0.00900; product of variances: 1.11×10^{-9} versus 1.75×10^{-11} ; sum of ranges: 1.03 versus 0.505; geometric mean of ranges: 0.227 versus 0.138).

boundary probably precedes its first appearance (Harland *et al.* 1990). Therefore, the age of the fish beds is probably latest Givetian–earliest Frasnian (*ca* 385 Ma; all dates in this article are from Gradstein *et al.* 2004).

4. DESCRIPTION

The skull roof of *Holopterygius* (figure 1b, sr) is preserved primarily as an impression of its visceral surface, but intact areas are perforated by large, irregular pores for the supraorbital sensory canal. The premaxilla (figure 1b, pmx) is squat and bears four large, irregularly shaped teeth. The dorsal surface of the splint-like parasphenoid (figure 1b, psph) is exposed, and is marked by a well-developed hypophysial fossa. Much of the palate is visible (figure 1b, pal), and it has the triangular shape

characteristic of coelacanths (Forey 1998). The quadrate is preserved as a thickened region at the posteroventral corner of the palate, while a series of teeth along its ventral margin represent the remains of the ectopterygoid. A large, subspherical structure in the otic region is interpreted as an otolith (figure 1b, ot; cf. Clack 1996). No dermal bones of the cheek can be identified. The opercle (figure 1b, op) is a large rectangular bone with a long vertical axis, and resembles that of *Allenopterus* (Lund & Lund 1985; Forey 1998).

The lower jaw of *Holopterygius* bears a long anterior ramus, a well-developed dorsal process at mid length, and another ramus posteriorly. The anterior arm of the lower jaw resembles the slender dentary of many early coelacanths (Lund & Lund 1985; Forey *et al.* 2000). Although the dentary of the intact jaw is preserved only as an

impression, a long tooth-bearing fragment on the opposite side of the skull probably represents a portion of the dentary from the other mandible. The deep dorsal process of the jaw is composed of an expanded posterior coronoid (figure 1*b*, cop), which is a coelacanth synapomorphy (Forey 1998). Small teeth anterior to the principal coronoid may be the remains of additional members of the series. The posterior ramus of the jaw corresponds to the retroarticular process of other coelacanth, and is overlain by a stocky cylindrical bone that is identified as the symplectic (figure 1*b*, sym), a major component of the coelacanth tandem jaw joint. The ceratohyals (figure 1*b*, chy) are flared distally and proximally. Narrow endoskeletal rods represent remains of the gill skeleton (figure 1*b*, gs).

The cleithrum and clavicles (figure 1*b*, cle, cla) are well-preserved and exhibit the slender proportions characteristic of coelacanth crownward of *Miguashaia* (Cloutier 1996; Forey 1998). *Holopterygius* also possesses an extracleithrum (figure 1*b*, ex), an additional dermal ossification that is a coelacanth synapomorphy (Forey 1998). Although Jessen (1973) noted the similarities between the pectoral girdles of *Holopterygius* and coelacanth, he did not consider this resemblance sufficient to justify placement within the group. Fragments of the anocleithrum (figure 1*b*, ano) are located dorsal to the tip of the cleithrum, and suggest this bone was of the simple unbranched morphology primitive for actinistians.

The distinctive postcranium of *Holopterygius* is leaf-shaped, with a greatly elongated caudal region. Despite the unusual body shape of this genus, the components of its postcranial skeleton conform to the general coelacanth pattern. There are approximately 80 postcranial segments, just over 20 of which are abdominal. Vertebral centra are unossified, but small ossifications located below the abdominal neural arches may represent parapophyses (figure 1*b*, pap). There are no ossified ribs. Neural arches and spines (figure 1*b*, nas) and haemal arches and spines (figure 1*b*, has) are co-ossified.

The dorsal and ventral lobes of the diphyccercal caudal fin are each supported by a single row of endoskeletal radials (figure 1*b*, rd, rv). There is a one-to-one ratio between radials and neural or haemal spines and a greater than one-to-one relationship between fin rays and radials. Jessen (1973) reconstructed *Holopterygius* with multiple radials per body segment, but this seems to have been informed by reference to conditions in tarrasiid actinopterygians (Lund & Melton 1982; Taverne 1996). Direct comparison with *Tarrasius problematicus* (Natural History Museum, London, P.1167, P.18064, P.18065, P.18061) confirms the difference in spine to radial ratios. It is not possible to determine whether the fin rays were segmented in *Holopterygius* as in most coelacanth, or unsegmented as in *Allenkypterus* (Lund & Lund 1985). The dorsal and ventral lobes of the caudal fin are strongly asymmetrical, with the dorsal lobe extending much further anteriorly, as in *Allenkypterus* (Lund & Lund 1985; Forey 1998). No components of the first dorsal, pectoral, anal or pelvic fins are preserved. An irregularly shaped ossification located dorsal to the neural spines immediately anterior to the first radial of the caudal fin probably represents the basal plate of the second dorsal fin (figure 1*b*, bp).

No squamation is preserved on the flanks of *Holopterygius*, but a series of keel scales run along the

ventral margin of the body from just behind the skull to approximately the midpoint of the abdominal region (figure 1*b*, vs). It is possible that the absence of scales covering the body of *Holopterygius* is size-related, as scales are often not preserved in small fossil coelacanth (Lund & Lund 1985). There is no indication of the ossified swim bladder characteristic of derived coelacanth.

5. DISCUSSION

Widely cited studies place coelacanth as the most basal extant sarcopterygian radiation (Cloutier & Ahlberg 1996; Forey 1998), but little is known about their early history. While the first crown-group sarcopterygians are known from Lower Devonian (Lochkovian; 411–416 Ma) deposits (Cloutier & Ahlberg 1996), the oldest unequivocal coelacanth are of Givetian age (385–392 Ma; Forey 1998; Long 1999; Forey *et al.* 2000). Previously described Devonian coelacanth fall into two morphological categories: primitive forms (*Gavinia*, *Miguashaia*) with postcrania resembling those of other plesiomorphic sarcopterygians, and more crownward taxa (*Chagrinia*, *Diplocercides*) whose postcranial anatomy is similar to that of stratigraphically younger and phylogenetically more derived coelacanth, including the Recent *Latimeria*.

Holopterygius marks a considerable anatomical departure from other Devonian forms, and a cladistic analysis places it as the sister taxon of *Allenkypterus*, another early coelacanth with unusual postcranial morphology (analysis and results are described in figure 2*a*). Two unequivocal synapomorphies link these genera: a series of ventral keel scales and an asymmetrical caudal fin in which the dorsal lobe extends far beyond the anterior extremity of the ventral lobe. Both of these fishes have unstable taxonomic histories resulting from their unconventional body profiles; like *Holopterygius*, *Allenkypterus* was identified as an actinopterygian (Melton 1969) before being recognized as a coelacanth (Lund & Lund 1984).

Although *Holopterygius* and *Allenkypterus* are unusual among coelacanth in having greatly elongated caudal regions, they are easily distinguished. While the deep body of *Allenkypterus* is strongly arched dorsally and comparatively straight ventrally, the postcranium of *Holopterygius* is shallower with more symmetrical dorsal and ventral margins. Small specimens of *Allenkypterus* have a less exaggerated dorsal hump than larger individuals (Lund & Lund 1985; Field Museum, Chicago, PF10942, PF10943a,b), but they retain greatly elongated neural spines above the abdominal region, unlike the short structures in *Holopterygius*. Both genera share asymmetrical lobes of the caudal fin, but the ventral lobe is more extensive in *Holopterygius* than in *Allenkypterus*, where it is reduced to a minor series of shortened fin rays near the tip of the tail. Additional dissimilarities are present in the skulls. The premaxillae and mandibles of *Allenkypterus* are edentulous (Lund & Lund 1985; Forey 1998) but bear well-developed teeth in *Holopterygius*. Additionally, lower jaw proportions of *Holopterygius* are unlike those of *Allenkypterus*, but are similar to those of other early coelacanth (Lund & Lund 1985; Forey *et al.* 2000), suggesting that it had a more conventional skull shape than *Allenkypterus*, in which the cranial region is drastically foreshortened.

Previous studies have placed *Allenkypterus* crownward of one or more of its contemporaries from Bear Gulch (Cloutier 1991a,b; Forey 1991; Forey 1998), but our preferred solution (figure 2a) reconstructs the clade containing it and *Holopterygius* as basal to all other coelacanths in the analysis with the exception of *Miguashaia* and *Diplocercides*. This result implies that the lineages leading to *Allenkypterus* and to *Hadronector* plus all more crownward taxa diverged by the Middle Devonian. Previous minimum age estimates for these lineage-splitting events were centred on the Lower Carboniferous (Cloutier 1991a; Forey 1998). Consequently, our findings extend taxon ranges by between 27 and 44 million years, and indicate that much of early coelacanth diversity remains unsampled.

Perhaps the most surprising result of this study is the discovery of an unusual coelacanth so early in the history of the clade, particularly since this group is often presented as an exemplar of morphological conservatism (Simpson 1944, 1953; Stanley 1998). In contrast to this standard view, several authors have inferred high evolutionary rates early in coelacanth history followed by a near monotonic decrease. However, the magnitude of this shift is disputed, with some studies finding a rapid exponential decay (Schaeffer 1952; Cloutier 1991b) while others report a more gradual decline (Forey 1998). Nevertheless, the repeated recovery of an early peak in evolutionary rate reflects a clear biological signal: the early accumulation of characters uniting coelacanths to the exclusion of other sarcopterygians. Interestingly, existing estimates of coelacanth morphological disparity are not positively correlated with evolutionary rates, but instead show an increase throughout the Palaeozoic and much of the Mesozoic (Smith 1994; Forey 1998), peaking during an interval of low rates of anatomical change.

The postcranial morphologies of *Allenkypterus* and *Holopterygius*—and presumably their ecologies—differ radically from those of ‘typical’ coelacanths, but this is not reflected in previous measures of disparity. This appears to result from methods used previously to calculate morphological diversity. The pairwise comparisons made by Smith (1994) and Forey (1998) were based upon data matrices that avoided phylogenetically uninformative characters. Prior to our reinterpretation of *Holopterygius*, most of the unusual features of *Allenkypterus* were unique to that genus and, therefore, not brought to bear on disparity estimates. This presents a major problem: while autapomorphies are uninformative for parsimony-based methods of phylogenetic inference, they are essential for calculations of dissimilarity. Consequently, previous measurements of disparity in coelacanths are incomplete because they omit these critical data.

Here, rather than manipulating matrices designed to resolve phylogeny or revising such data to include autapomorphies, we have adopted a morphometric approach in order to describe anatomical variety in coelacanths. The results of this analysis are summarized in figure 2c. The apparent conservatism of coelacanth postcrania has contributed profoundly to notions of this clade as a bradytelic lineage (Schaeffer 1952), and, once again, our results show that most taxa cluster together in morphospace, suggesting that this impression of coelacanths is not entirely unwarranted. Similar regions are

occupied by both Devonian/Carboniferous and post-Carboniferous samples, but there are notable outliers early in coelacanth history (figure 2c). *Miguashaia*, which is the plesiomorphic sister taxon of all other coelacanths (Cloutier 1991a,b, 1996; Forey 1998; Forey *et al.* 2000), lies far from the major cluster. This reflects the unusual postcranium of this genus, which is probably closer to that of a generalized, and perhaps primitive, sarcopterygian than a typical coelacanth. Likewise, *Holopterygius* and *Allenkypterus* are distantly removed from the cluster of ‘conventional’ coelacanths, but these two genera are also placed far from one another. As this separation reflects differences in body depth and caudal fin morphology, it is not an artefact of uncertainties surrounding the positions of the anal and dorsal fins of *Holopterygius*. These results clearly contradict those of previous studies (Smith 1994; Forey 1998) that found low levels of morphological disparity early in coelacanth history.

More remarkable than the degree of morphological separation between *Holopterygius*, *Miguashaia* and other early coelacanths is the short interval over which this variety was generated. With a probable origin of actinistians during the Early Devonian or Late Silurian, each of these distinctive morphologies was established by the close of the Middle Devonian. In contrast, post-Carboniferous forms show no evidence of the radical morphological shifts that characterize the initial phases of the coelacanth radiation, despite higher levels of taxonomic diversity (Forey 1998) and a longer interval over which to develop anatomical novelties. The most extreme departure during this later interval is the Jurassic *Libys*, which, although deep-bodied, conforms to the stereotypical coelacanth body plan. Such rapid accumulation of morphological variety early in clade histories is a recurrent theme in studies of disparity in the fossil record (Foote 1997), but the causes underlying this pattern remain uncertain (Foote 1996). What is clear, however, is that *Holopterygius* and its disparate contemporaries provide evidence for early anatomical experimentation in coelacanths that is strongly at odds with the textbook portrayal of the clade as morphologically invariant over geological time.

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REFERENCES

- Bookstein, F. L. 1991 *Morphometric tools for landmark data: geometry and biology*. Cambridge, UK: Cambridge University Press.
- Bookstein, F. L. 1996 Standard formula for the uniform shape component in morphometric data. In *Advances in morphometrics* (ed. L. F. Marcus, M. Corti, A. Loy, G. Nalor & D. E. Slice), pp. 153–168. New York: Plenum Press.
- Clack, J. A. 1996 Otoliths in fossil coelacanths. *J. Vert. Paleontol.* **16**, 168–171.
- Cloutier, R. 1991a Interrelationships of Palaeozoic actinistians: patterns and trends. In *Early vertebrates and related problems of evolutionary biology* (ed. M.-M. Chang, Y.-L. Liu & G.-N. Zhang), pp. 379–428. Beijing: Science Press.

- Cloutier, R. 1991*b* Patterns, trends and rates of evolution within the Actinistia. *Environ. Biol. Fishes* **32**, 23–58. (doi:10.1007/BF00007444)
- Cloutier, R. 1996 The primitive actinistian *Miguashaia bureaui* Schultze (Sarcopterygii). In *Devonian Fishes and Plants of Miguasha, Quebec, Canada* (ed. H.-P. Schultze & R. Cloutier), pp. 227–247. München: Verlag Dr. Friedrich Pfeil.
- Cloutier, R. & Ahlberg, P. E. 1996 Morphology, characters, and the interrelationships of basal sarcopterygians. In *Interrelationships of fishes* (ed. M. L. J. Stiassny, L. R. Parenti & G. D. Johnson), pp. 445–479. San Diego, CA: Academic Press.
- Cope, E. D. 1871 Contribution to the ichthyology of the Lesser Antilles. *Trans. Am. Philos. Soc.* **14**, 445–483.
- Foote, M. 1992 Rarefaction analysis of morphological and taxonomic diversity. *Paleobiology* **18**, 1–16.
- Foote, M. 1996 Models of morphological diversification. In *Evolutionary paleobiology* (ed. D. Jablonski, D. H. Erwin & J. H. Lipps), pp. 62–86. Chicago, IL: University of Chicago Press.
- Foote, M. 1997 The evolution of morphological diversity. *Annu. Rev. Ecol. Syst.* **28**, 29–52. (doi:10.1146/annurev.ecolsys.28.1.129)
- Forey, P. L. 1991 *Latimeria chalumnae* and its pedigree. *Environ. Biol. Fishes* **32**, 75–97. (doi:10.1007/BF00007446)
- Forey, P. L. 1998 *History of the coelacanth fishes*. London: Chapman & Hall.
- Forey, P. L., Ahlberg, P. E., Lukševičs, E. & Zupinš, I. 2000 A new coelacanth from the Middle Devonian of Latvia. *J. Vert. Paleo.* **20**, 243–252.
- Gradstein, F. M., Ogg, J. G. & Smith, A. G. 2004 *A geologic time scale 2004*. Cambridge, UK: Cambridge University Press.
- Harland, W. B., Armstrong, R. L., Cox, A. V., Craig, L. E., Smith, A. G. & Smith, D. G. 1990 *A geologic time scale 1989*. Cambridge, UK: Cambridge University Press.
- Huxley, T. H. 1880 On the applications of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proc. Zool. Soc.* **1880**, 649–662.
- Jessen, H. 1973 Weitere fischreste aus dem Oberen Plattenkalk der Bergisch-Gladbach—Paffrather mulde (Oberdevon, Rheinisches Schiefergebirge). *Palaeontogr. Abt. A. Palaeozool.-stratigr.* **143**, 159–187.
- Long, J. A. 1999 A new genus of fossil coelacanth (Osteichthyes: Coelacanthiformes) from the Middle Devonian of southeastern Australia. *Rec. West. Aust. Mus. Suppl.* **57**, 37–53.
- Lund, R. & Lund, W. L. 1984 New genera and species of coelacanth from the Bear Gulch Limestone (lower Carboniferous) of Montana (USA). *Geobios* **17**, 237–244.
- Lund, R. & Lund, W. L. 1985 Coelacanth from the Bear Gulch Limestone (Namurian) of Montana and the evolution of the Coelacanthiformes. *Bull. Carnegie Mus. Nat. Hist.* **25**, 1–74.
- Lund, R. & Melton Jr, W. G. 1982 A new actinopterygian from the Mississippian Bear Gulch Limestone of Montana. *Palaeontology* **25**, 485–489.
- Lund, R. & Poplin, C. 2002 Cladistic analysis of the relationships of the tarrasiids (Lower Carboniferous actinopterygians). *J. Vert. Paleo.* **22**, 480–486.
- Melton Jr, W. G. 1969 A new dorypterid fish from central Montana. *Northwest Sci.* **43**, 196–206.
- Moy-Thomas, J. A. 1934 The structure and affinities of *Tarrasius problematicus* Traquair. *Proc. Zool. Soc.* **1934**, 367–376.
- Ørvig, T. 1960 New finds of acanthodians, arthrodiros, crossopterygians, ganoids and dipnoans in the upper Middle Devonian calcareous flags (Oberer Plattenkalk) of the Bergisch Gladbach—Paffrath Trough (Part 1). *Paläont. Z.* **34**, 295–335.
- Rohlf, F. J. 2004*a* *tpsDig, version 1.40*. Department of Ecology and Evolution: Stony Brook, New York.
- Rohlf, F. J. 2004*b* *tpsRelw, version 1.39*. Stony Brook, New York: Department of Ecology and Evolution.
- Romer, A. S. 1955 Herpetichthyes, Amphibioidei, Choanichthyes or Sarcopterygii? *Nature* **176**, 126.
- Schaeffer, B. 1952 Rates of evolution in the coelacanth and dipnoan fishes. *Evolution* **6**, 101–111.
- Simpson, G. G. 1944 *Tempo and mode in evolution*. New York: Columbia University Press.
- Simpson, G. G. 1953 *The major features of evolution*. New York: Columbia University Press.
- Smith, A. B. 1994 *Systematics and the fossil record*. Oxford, UK: Blackwell Scientific Publications.
- Stanley, S. M. 1998 *Macroevolution: pattern and process*. Baltimore: Johns Hopkins University Press.
- Swofford, D. L. 2002 *PAUP*. Phylogenetic analysis using parsimony (*and other methods), version 4*. Sunderland, MA: Sinauer Associates.
- Taverne, L. 1996 Ostéologie et position systématique des Tarrasiiformes, actinopterygians (Pisces) du Carbonifère de l'Écosse de des États-Unis. *Biol. Jb. Dodonaea* **64**, 138–159.
- VanValen, L. 1974 Multivariate structural statistics in natural history. *J. Theor. Biol.* **45**, 235–247.