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# Species delimitation and coexistence in an ancient, depauperate vertebrate clade

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## Abstract

**Background:** A major challenge to understanding how biodiversity has changed over time comes from depauperons, which are long-lived lineages with presently low species diversity. The most famous of these are the coelacanths. This clade of lobe-finned fishes occupies a pivotal position on the vertebrate tree between other fishes and tetrapods. Yet only two extant species and fewer than 100 extinct forms are known from the coelacanth fossil record, which spans over 400 million years of time. Although there is evidence for the existence of additional genetically isolated extant populations, a poor understanding of morphological disparity in this clade has made quantifying coelacanth species richness difficult.

**Results:** Here, we quantify variation in a sample of skulls and skeletons of the Triassic eastern North American coelacanth †*Diplurus* that represents the largest assemblage of coelacanth individuals known. Based on the results of these quantitative comparisons, we identify a diminutive new species and show that multiple lacustrine ecosystems in the Triassic rift lakes of the Atlantic coastline harbored at least three species of coelacanths spanning two orders of magnitude in size.

**Conclusions:** Conceptions about the distribution of species diversity on the tree of life may be fundamentally misguided when extant diversity is used to gauge signals of extinct diversity.

Our results demonstrate how specimen-based assessments can be used to illuminate hidden biodiversity and show the utility of the fossil record for answering questions about the hidden richness of currently species-poor lineages.

**Keywords:** Coelacanths, Diversity, Speciation, Paleontology, Triassic

## Introduction

Major changes to biodiversity over the history of life on Earth have shaped extant species richness [1, 68, 78]. Although one end of the spectrum of biodiversity-radiations are a historically well-studied evolutionary phenomenon [1, 31, 33, 75], the origins of species-poor lineages that have persisted for millions or tens of millions of years are gaining attention (e.g., [22, 23, 57]). Phylogenomic studies now recognize depauperons across of different portions of the Tree of Life (e.g., [2, 10, 40, 42,

66, 89]), demonstrating that depauperacy is a consistent evolutionary pattern.

Nonetheless, the fossil records of many currently species-poor clades show how a view of the evolutionary history of these clades based solely on extant forms is often biased. Among vertebrates, clades now represented by one or a handful of species are represented by numerous species with varying morphologies in the fossil record [35–38, 57, 77]. This discrepancy between extant and extinct species richness and disparity in depauperons means that rigorous species delimitation using quantitative methods is particularly important for properly detecting their diversity and understanding their evolutionary history.

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Coelacanths (Actinistia) are one of the most famous species-depauperate lineages. This clade diverged from other jawed vertebrates during the Silurian [3, 29, 30, 43] and represents the living sister clade to all other sarcopterygians, or lobe-finned fishes [3, 8, 55]. Despite their historical notoriety as a species-poor, morphologically conservative lineage, the fossil record of coelacanths has shown that this clade diversified into a wide variety of morphologies in the ancient past [17, 29, 49]. Fossil coelacanths show bursts of species diversity during the Devonian and Triassic [83] and achieved a high degree of body size variation ranging from diminutive species less than 5 cm long to 6+ m giants representing some of the largest freshwater fishes [18].

Only two species of coelacanths confined to deep ocean waters survive today: *Latimeria chalumnae* and *L. menadoensis* [39, 79]. These species diverged from other coelacanths during the Cretaceous [17, 83] and last share common ancestry over 35 million years ago [41]. There is also evidence for additional, deep splits among populations in the two recognized *Latimeria* species [44]. However, the secluded habitats and small population sizes of extant coelacanths mean that there is a dearth of specimens available for assessing morphological variance in these populations. This precludes our ability to understand current coelacanth species diversity and morphological disparity, which might otherwise inform species delimitation in the fossil record.

The eastern margin of North America is known for its extensive fossil record from Triassic-Jurassic rift lakes that formed during the breakup of Pangaea (e.g., [65]). Several formations representing these ecosystems preserve the most extensive collection of coelacanths known, extant or extinct (e.g., [9, 70–72, 76]). Yet, just how many species of coelacanths lived in this region during the Triassic has remained contentious for over a century [9, 70–72, 76].

In this paper, we quantify phenotypic disparity and species richness in a sample of over 500 individual coelacanths from a single locality with a combined approach using tools from geometric morphometrics, meristics, and phylogenetics. This allows us to critically assess coelacanth diversity in the Triassic eastern North American rift, which leads us to recognize one new species and provides a basis for reanalyzing actinistian diversity in deep time. Our study reinforces the necessity of quantitative methods for species delimitation among depauperate fossil lineages and shows how assumptions about the species richness of a lineage might cause underestimation of their ancient diversity.

## Methods

### Sampling

In order to estimate the species richness of Triassic coelacanths in eastern North America, we examined over 500 specimens of coelacanths collected during the 1940s Firestone Library excavation in Princeton, New Jersey [70, 72]. Of these,  $n = 55$  specimens possessed skulls with exceptional preservation allowing us to perform a variety of linear and geometric morphometric comparisons. We selected a subset of  $n = 19$  individuals represented by articulated skulls and skeletons showing details of suspensorium, opercular series, and postcranial anatomy for Bayesian- and parsimony-based phylogenetic analyses. We also sampled an additional five specimens from the Old Granton Quarry in Bergen, New Jersey and examined a skull and partial skeleton of a large coelacanth collected in 1975 from the Solite Quarry site in North Carolina. Measurements made on this dataset using digital calipers were combined with measurement data from [29, 70, 72, 76]. Together, this dataset represents the largest known collection of coelacanth material from a single region and time (Carnian-Norian, e.g., [45]).

### Phylogenetic analysis

We conducted several rounds of phylogenetic analysis on the morphological dataset of Toriño et al. [83] with wildcard genera excluded, which consists of 48 taxa scored for 110 characters. To assess how different phylogenetic methodologies affected relationships among coelacanths, we conducted both Bayesian and parsimony analyses.

We conducted an analysis under parsimony using the program TNT v. 1.5 [34]. Initially, we performed a Wagner search with space for 1000 trees and default parameters for ratchet, tree fuse, drift, and sectorial search. This was followed by a round of traditional bisection-reconnection (TBR) branch swapping with space for 100,000 trees to explore additional topologies. The resulting MPTs were summarized in a strict consensus topology. We also resampled the dataset over 100 replicates to obtain bootstrap support values for branches. Parsimony analysis was conducted using both the dataset including YPM VPPU 14555 and without this specimen, which we resolved as a wildcard in the initial run. A list of apomorphies for each run is in the Additional file 2, and the inputted morphological matrix and output trees are included in the Additional file 3.

We conducted Bayesian analysis of the modified morphological dataset of Toriño et al. [83] and age dates for fossil occurrences taken from that study and additional sources for the new coelacanth material [45, 48] using the program BEAST 2.6.6 [6] with the fossilized birth–death (FBD) model as the tree prior [32]. A single uncorrelated lognormal clock was used with mean and

standard deviation values of 1.0 and 0.33, respectively. We conducted three independent runs over  $1 \times 10^7$  million generations with a  $1 \times 10^6$  pre-burnin. We used Tracer v. 1.7.2 [67] to check for convergence of posteriors. The posterior set of trees generated from this analysis were summarized into a maximum clade credibility (MCC) topology using TreeAnnotator 2.6.4 [6] with a 25% burnin. The input xml file and resulting tree, state, and log files from the Bayesian analysis are included in the Additional file 3.

### Linear morphometric analyses

In order to assess simple dimensional differences among the sample of coelacanths examined in this contribution, we collected measurement data for the following dimensions: anteroposterior skull length from the tip of the premaxilla to the posterior end of the opercle, dorsoventral skull height from the base of the angular to the mid-length of the parietal, maximum orbit height and length, the number of ridges observed on the visible opercle of each specimen, and the number of angular foramina visible. The latter two counts were taken using light microscopy. We compared measurements for  $n=55$  of the best-preserved skulls from the Granton Quarry and Firestone sites, and then among these and an additional  $n=7$  specimens from these sites and other localities of the Newark Supergroup. Plotting was conducted in the R package ggplot2 [88].

### Species-site diversity and per-site size disparity

Based on the results of our phylogenetic, linear meristic and morphometric, and geometric morphometric analyses, we assembled catalogues of coelacanth species presence-absence data at several sites in eastern North America (Schainin 1943; Schaeffer [71, 72]; this study). Plotting was conducted in the R package ggplot2 [88]. As a metric of per-site size disparity, we calculated the difference in total length between the largest and smallest coelacanths reported from each of the localities we investigated. In several cases (i.e., Granton Quarry, Firestone Library), it was necessary to estimate the sizes of the largest reported individuals of the species †*Diplurus longicaudatus* based on complete specimens of the same species reported from elsewhere (i.e., YPM VP 630; Schaeffer [71]). Plotting was conducted in the R package ggplot2 [88].

## Results

### Geological and environment setting

The massive coelacanth collection presented here was found in the Firestone locality of Princeton, New Jersey during the excavation of the Firestone Library in 1946. This site is centered on the Newark basin, the largest of

the exposed rift basins formed during the breakup of Pangea between the Late Triassic and Early Jurassic [53, 80]. Infilling of the basin occurred over approximately 30 million years in the Triassic and produced three main units in descending chronological order: the Stockton, Lockatong, and Passaic Formations [51, 53]. The Stockton Formation consists largely of red and purple clastic conglomerate rocks, red to yellow-grey well-sorted arkose, and red to brown siltstone and mudstone [19, 54]. Much of the great lateral extent of the geology in this formation has been interpreted as alluvial fans resulting from fluvial and lacustrine processes [80]. Conformably overlying the Stockton Formation is the Lockatong Formation. The Lockatong Formation covers an area of 7000 km<sup>2</sup> and has a maximum thickness of approximately 1100 m [19]. The Lockatong Formation beneath the Firestone locality is around 450 m thick and dips 10 degrees north [19]. Sedimentary infilling of the Lockatong Formation reflects cyclical periods of the rise and fall of lakes, referred to as Van Houten cycles [61, 62, 85]. Van Houten cycles have a periodicity of approximately 20,000 years and are roughly divided into three sections chiefly containing large grey to red clastics to dolomites, laminated red to green organic-rich siltstone and claystone, and largely desiccated calcareous clastic units [19, 60]. These three sections are thought to correspond to periods of lake level rise, lake level stasis, and lake level fall, respectively, driven by orbital climate dynamics [51, 80]. Lacustrine ecosystem changes composed of Van Houten cycles ranging from ~90 kyr to ~2000 kyr have also been observed in the Lockatong Formation [51, 53, 60].

The Firestone locality lies approximately 70 m above the contact between the Stockton and Lockatong Formations [74]. The collection of coelacanths examined for this study were all preserved within a restricted, <20 cm layer of argillite. A number of specimens are preserved in regions where fractionation occurred along bedding planes, resulting in bands of argillite-derived soft limonitic clay [74]. Fossils preserved in these regions are far more visible and better preserved than those found in the unchanged argillite. Other fishes found in surrounding regions of the Lockatong Formation include the actinopterygians †*Turseodus*, †*Cionichthys*, and †*Synorichthys* and the shark †*Carinacanthus* [59, 63].

Coelacanth fossils have also been found in surrounding regions of the Lockatong and Stockton Formations. Shainin [76] described a collection of †*Diplurus* from the Granton quarry in North Bergen, New Jersey. The Stockton Formation at this locality is approximately 700 m thick; †*Diplurus* is found in the upper section, approximately 640 m above the base [74]. The lithology of this section consists of alternating layers of sandy to

silty sandstone and dark sandy to argillaceous shales [76]. Small coelacanths are found here in the dark shale layers [76]. Similar assemblages have been found embedded in dark shale in the upper half of the Lockatong Formation in Montgomery County, Pennsylvania.

Boonton, New Jersey is the site of one of specimens shown as part of the collection here. The Boonton Formation consists of large red siltstone and sandstone sections alternating with grey siltstone, as well as red, brown and grey clastics, and evaporite layers [61, 62]. The unit is part of the Passaic Group (formerly the Brunswick Formation) and is among the youngest sedimentary units in the Newark Basin [61, 62]. Myriad other fish fossils, including †*Semionotus*, †*Redfieldius*, †*Dictyopyge*, and †*Ptycholepis*, have been found in the uppermost section, which is composed of a grey siltstone laminite [61, 62, 73]. Single specimens have also been found in the Lockatong and Passaic formations in the Danville area and Fauquier County, Virginia.

Various remains of †*Diplurus longicaudatus* have also been identified in the Connecticut Valley. While small coelacanth specimens assigned to †*Diplurus* are the vast majority of coelacanths present in the New York-New Jersey areas, such as the Firestone Library site, †*D. longicaudatus* is the only species to have been found in the Connecticut Valley [74]. The lithology of the Shuttle Meadow Formation, which bears †*Diplurus* in this region, consists largely of arkose, sandstone, small amounts of shale, and siltstone [74].

Other samples analyzed in this paper were collected from the Solite Quarry in North Carolina-Virginia, USA. This section rests in the Dan River-Danville basin, a half-graben along the Chatham fault zone of the Mesozoic rift system [5, 64]. This region consists largely of lacustrine shales, sandstones, and mudstones that were layered cyclically and are fossiliferous [28, 64]. Over 30 cyclical layers are present in this area, which are thought to reflect Milankovitch Cycles (orbital dynamic-driven cycles in lake-depth similar to Van Houten Cycles) and contain some of the most productive Triassic fossil assemblages in the world [5, 28].

### Phylogenetic analyses

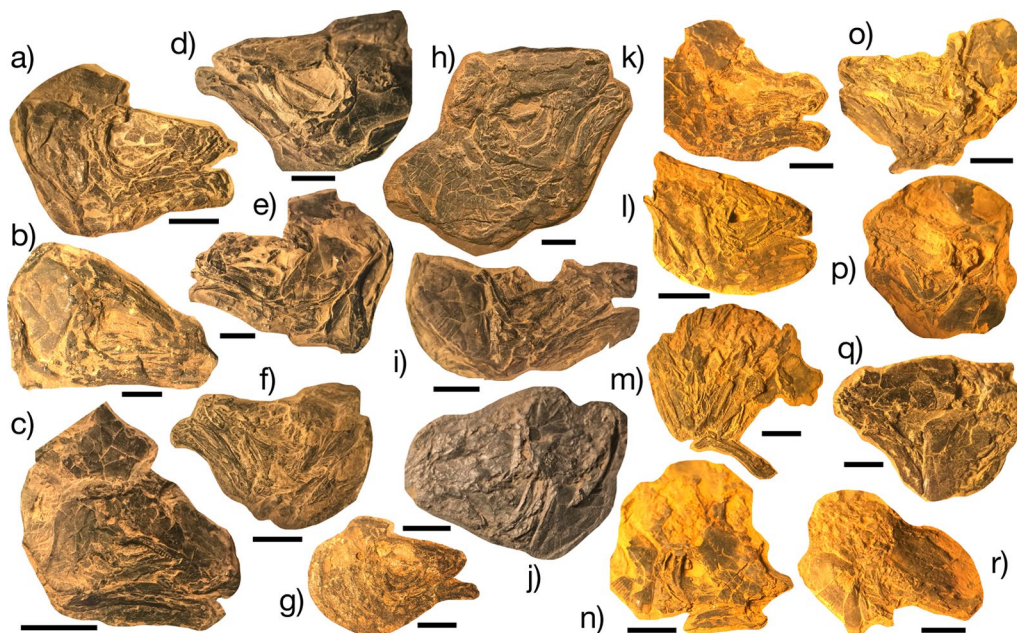
Phylogenetic analysis of the specimen-level dataset (modified from [83]) under Bayesian and parsimony frameworks produced similar positions for the sampled coelacanth specimens (Figs. 2, 3).

Parsimony analysis of the dataset (Fig. 2; Additional file 1: Fig. S1) finds largely unresolved relationships among actinistians and places the Firestone Library and Old Granton Quarry coelacanths in a polytomy at the base of this lineage in the strict consensus topology of 36 most parsimonious trees (MPTs) found with moderate

support (bootstrap value=0.5). MPTs produced from this analysis (length=348; consistency index=0.356, retention index=0.732) position the eastern North American coelacanth clade (bootstrap support=5) sister to Latimeriidae (bootstrap support=6) and resolve distinct subgroups within the eastern North American lineage delimited by the ornamentation of the opercle (Fig. 2). The uncertainty in the phylogenetic relationships among the eastern North American coelacanth clade, which drives the production of the polytomy in the consensus tree, is likely attributable to the lack of material known for YPM VPPU 14,555, a Firestone Library specimen referred to †*Diplurus longicaudatus*. Exclusion of this partial skull resulted in the resolution of a monophyletic eastern North American coelacanth group positioned as the sister to the Latimeriidae in all 18 MPTs (length=347, consistency index=0.355, retention index=0.731) found, as well as in the strict consensus topology (Fig. 1a). 12 MPTs show the formation of a clade of eastern North American Triassic coelacanths sharing a striated opercle (Fig. 2b). The monophyly of Triassic eastern North American coelacanths is supported by a low bootstrap value of 34 (Additional file 1: Fig. S1d), and a value of 0 supported the position of Triassic eastern North American coelacanths in the Latimeriidae.

In the Bayesian time-calibrated tree (Fig. 3), all eastern North American species are resolved as a monophyletic lineage within †Mawsoniidae, a cosmopolitan Mesozoic coelacanth clade [4, 14–16, 25, 26, 50, 81, 83], as the sister lineage to all Jurassic-Cretaceous mawsoniids included in the dataset. The monophyly of eastern North American Triassic coelacanths is supported by a moderate posterior value of 0.58. The inclusion of these eastern North American coelacanths in †Mawsoniidae (excluding †*Hepstanema* and †*Yunnancoelacanthus*) is supported by a higher posterior value of 0.76. The eastern North American clade is estimated to diverge from other mawsoniids 253.22 million years ago (95% CI: 234.10–258.81 Ma), approximately the age of the Permian mass extinction.

The eastern North American clade itself is divided into four distinct groups. The first to diverge consists of the large-bodied specimen YPM VP 7516 from the Carnian of North Carolina preliminarily referred to †*Diplurus longicaudatus* in the Yale Peabody Museum collections (Fig. 3). This result seems to be primarily driven by the age of YPM VP 7516. Next, two clades consisting of coelacanths from the Lockatong Formation diverge from each other separated by the presence of extensive opercle ornamentation. Two subclades of note are present in the clade consisting of species with extensively ornamented opercles. One of these subclades consists of the large Firestone coelacanth specimen YPM VPPU 14555 (cf. †*Diplurus longicaudatus*) and the small skull YPM VPPU



**Fig. 1** Examples of exceptionally preserved †*Diplurus* from the Firestone Library Excavation and Granton Quarry sites. **a** YPM VPPU 14,944 †*D. newarki*, **b** YPM VPPU uncatalogued †*D. newarki*, **c** YPM VPPU 14918a †*D. newarki*, **d** YPM VPPU 14,558 †*D. newarki*, **e** YPM VPPU uncatalogued †*D. newarki*, **f** YPM VPPU 14,924 †*D. enigmaticus*, **g** YPM VPPU uncatalogued †*D. newarki*, **h** YPM VPPU 14,920 †*D. newarki*, **i** YPM VPPU uncatalogued †*D. newarki*, **j** YPM VPPU 14,929 †*D. newarki*, **k** YPM VPPU 29,366 †*D. newarki*, **l** YPM VPPU 14,933 †*D. newarki*, **m** YPM VPPU 14,935 †*D. newarki*, **n** YPM VPPU 14,949 †*D. enigmaticus*, **o** YPM VPPU 14,932 †*D. newarki*, **p** YPM VPPU 14,940 †*D. newarki*, **q** YPM VPPU 14,921 †*D. newarki*, and **r** YPM VPPU 14,939 †*D. enigmaticus*

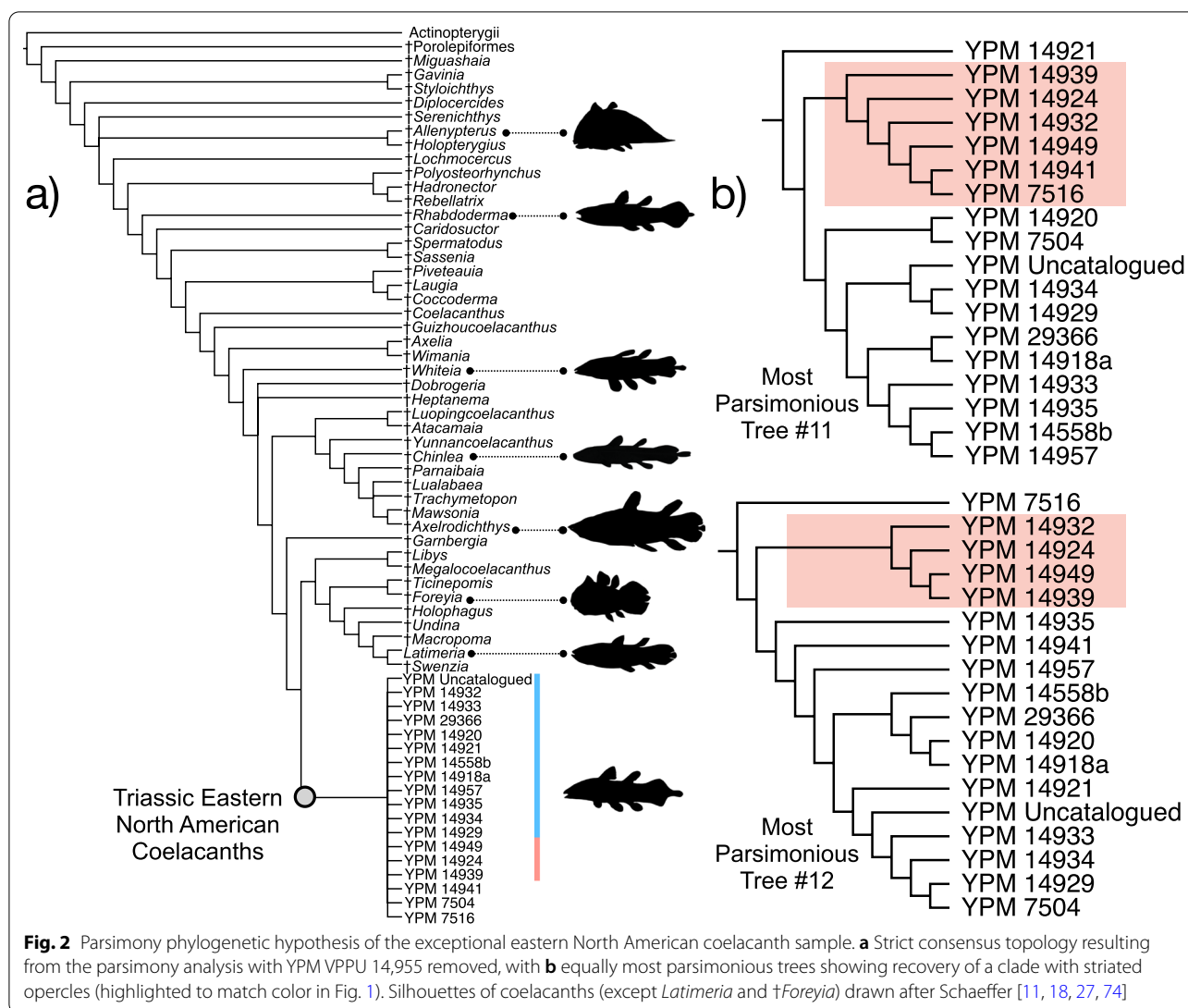
14941 (Fig. 3). The other subclade consists of all small-bodied coelacanth specimens from the Firestone Library excavation with heavily striated opercles (Fig. 3). The striated opercle lineage and that containing YPM VPPU 14555 and YPM VPPU 14941 form the sister clade to all coelacanth with minimal opercle ornamentation from Firestone and Old Granton Quarry (Fig. 3).

### Morphometric analyses

To investigate the morphological variation in the eastern North American coelacanth sample that might underlie our phylogenetic results, we performed both linear and 2D geometric morphometric analyses on the sample of coelacanths from the Firestone Library locality (with the exceptionally preserved Old Granton Quarry specimen YPM VPPU 14558a also included) to assess the level of variation in skull proportions, ornamentation, and neurovasculature in this sympatric population or set of populations (Figs. 4, 5). Two groups consistently distinguished by the frequency of radiating striations on the opercle (0–6 vs. 20+) and foramina on the angular (5+ vs. 4) were found to exist in the Firestone sample of small-bodied coelacanths (Fig. 4a, b). These different groups differed little in size and showed similar skull and orbital sizes (Fig. 4c, e) and proportions (Fig. 5). Higher

opercle striation and angular foramina counts are not associated with longer skull or deeper skulls in the Firestone Library and Granton Quarry sample (Fig. 5), suggesting these traits are independent of head and body dimensions.

We expanded our linear morphometric dataset to include records of coelacanths from several other localities across eastern North America, including further samples from the Old Granton Quarry site, the giant North Carolina specimen YPM VP 7516, several specimens of †*Diplurus longicaudatus*, skulls assigned by Schainin (1943) to the species †*Osteopleurus milleri*, and an opercle referred by [76] to †*O. milleri grantonensis*. We found that cranial material assigned to †*O. milleri* falls within the range of variation seen in the crania of †*D. newarki*, suggesting these are synonymous [74]. Skulls assigned to †*D. longicaudatus* (including YPM VP 7516) were much larger than all other specimens and possessed the numerous opercle ornamentations characteristic of that species [74]. Finally, the opercle from Granton Quarry tentatively referred to †*O. milleri grantonensis* by Schainin (1943) shows a similar degree of ornamentation as the ornamented-opercle group from Firestone Library and belonged to a small-bodied coelacanth of similar size.



(See figure on next page.)

**Fig. 3** Bayesian phylogenetic hypothesis of the exceptional eastern North American coelacanth sample. **a** Bayesian time-calibrated maximum clade credibility tree of coelacanth relationships, including specimen-level analysis of Lockatong specimens. The clade identifiable as †*Diplurus newarki* is highlighted in blue and the new species of †*Diplurus*, †*D. enigmaticus*, highlighted in red. **b** Exemplar skulls of three major lineages within †*Diplurus*, color-coded to match the phylogeny (see **b**)

### Systematics

Actinistia Cope 1871.

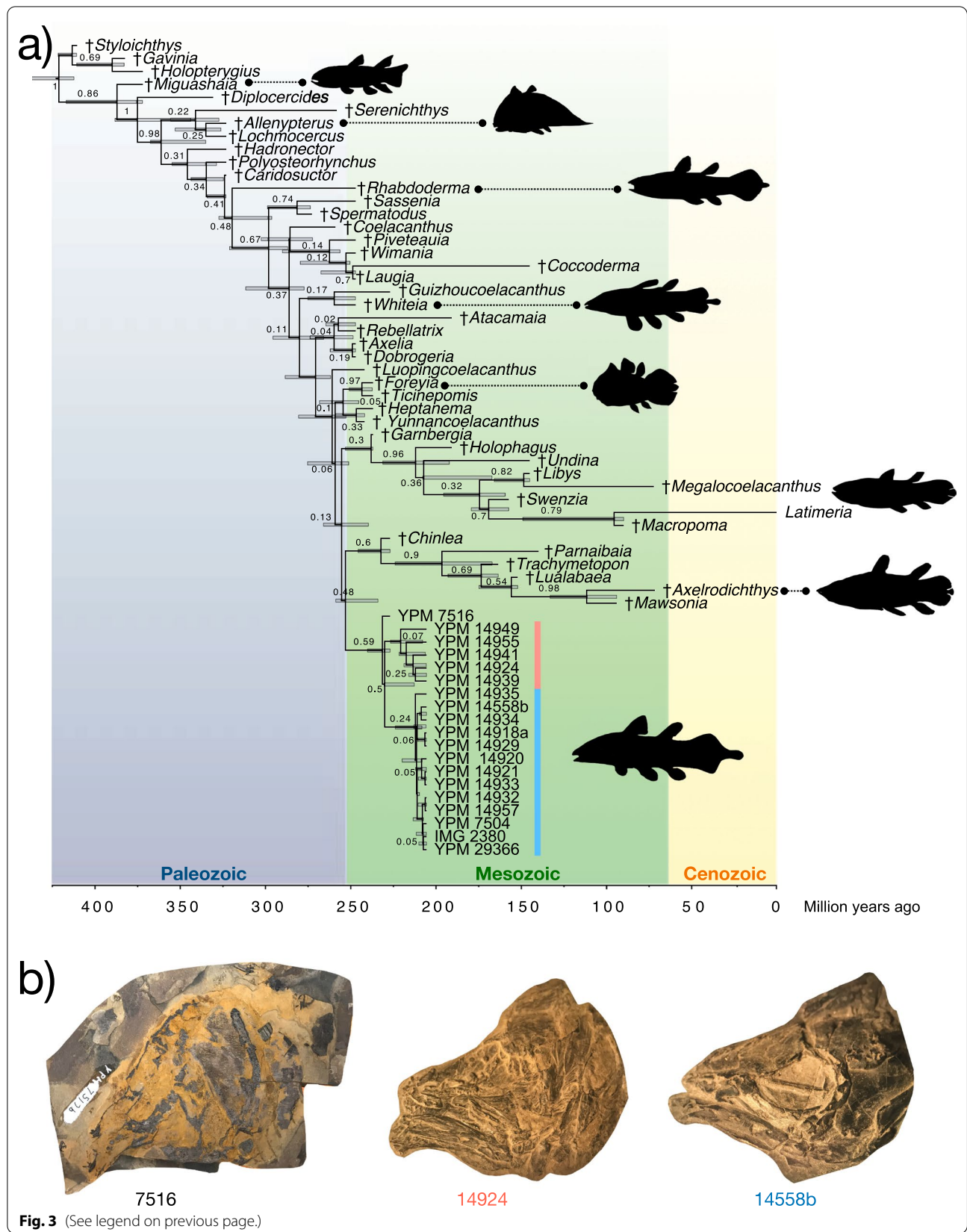
Latimerioidei Schultze, 1993.

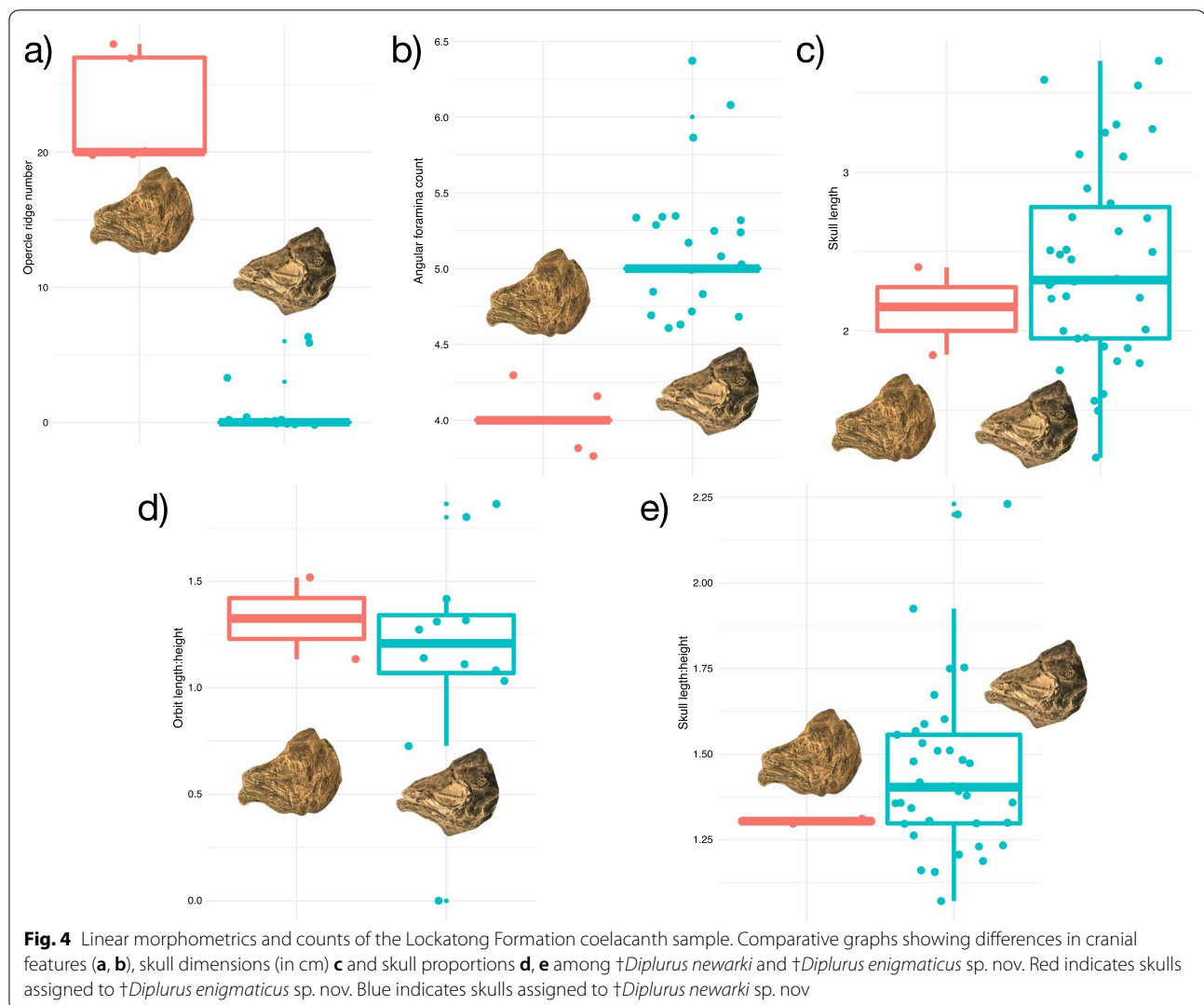
†*Diplurus* Newberry 1878.

†*Diplurus enigmaticus* sp. nov.

**Material.** YPM VPPU 14924 (holotype), skull and mandibles (Firestone Library). YPM VPPU 14949, 14939, 14943, 14558b; skulls with mandibles (Firestone Library). AMNH 15222, opercle (Granton Quarry).

**Diagnosis.** †*Diplurus enigmaticus* is distinguished by the following combination of features: maximum standard length of approximately 150 mm (shared with †*Diplurus newarki*; 690 + mm in †*D. longicaudatus*), numerous (>20) well-delimited radiating ridges on opercle (maximum of seven observed in †*D. newarki*; irregular lineations and tubercles present in †*Diplurus longicaudatus*; Figs. 4, 5); four angular foramina (zero to two in †*D. longicaudatus*; five or more in †*D. newarki*; Figs. 4, 5);



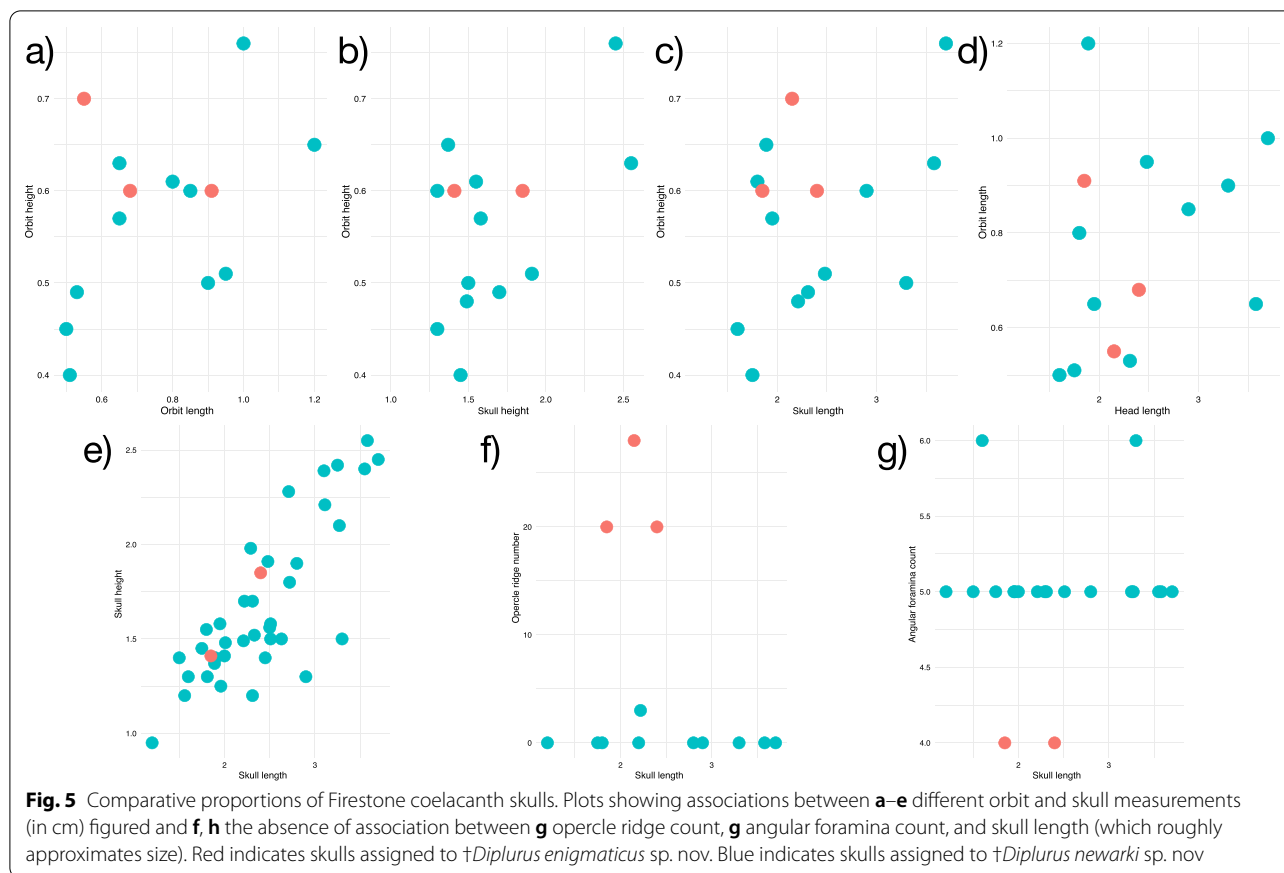


premaxilla with reduced number (8) of enlarged, conical teeth (11 in each element in †*D. newarki*; [74]).

**Remarks.** Schaeffer [7, 70, 71] provided comprehensive descriptions of the Lockatong, Stockton, and Boonton Formation †*Diplurus* material, including several specimens examined for this study. We refer the reader to these illustrated osteologies for details about the anatomy of the genus. The differential diagnosis given by Schaeffer [74] for †*Diplurus* (†*D. longicaudatus* + †*D. newarki*) includes the following features: (1) incomplete braincase ossification; (2) three posterior flanges on the anterior ethmoid; (3) large ovoid antotic flanges on the basisphenoid; (4) ossified otooccipital region; (5) basisphenoid not fused to parasphenoid; (6) ungrouped parasphenoid teeth; (7) largely unornamented skull dermal bones; (8) numerous small rostral bones; (9) small tooth-bearing premaxilla; (10) three subequal frontal-ethmoid shield bones; (11) anterior

frontals meet at midline (variable; (12) rectangular supratemporals do not reach posterior to intertemporals; (13) large dermosphenotic medially borders intertemporal; (14) extrascapulars reduced in size; (15) absence of distinct antorbital; (16) no sclerotic ring; (17) large sensory canal pores line postorbital and squamosal; (18) absence of subopercle; (19) short lower jaw; (20) dentary and splenial elongated; (21) lower jaw concave. Of these, 1, 2, 3, 4, 5, 6, 8, 9, 10, 11, 12, 13, 14, 15, 16, 18, 19, and 21 are found together in other Triassic or post-Devonian coelacanths described subsequently (i.e., *Foreyia* and *Ticinepomis*; [17, 69, 74]). Specimens of †*Diplurus enigmaticus* show features 7, 8, 9, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, and 21 and have previously been assigned to this genus [74]. Apart from the features noted in the diagnosis section, †*Diplurus enigmaticus* individuals fall within the range of variation observed in †*Diplurus newarki* and †*Diplurus*





*longicaudatus*. Accordingly, our comparisons below focus on the three features that we argue are apomorphies of †*Diplurus enigmaticus*.

Schainin (1943) considered the presence of discrete striations on the opercle to be a diagnostic apomorphy of †*Osteopleurus*, whereas Schaeffer [74] suggested this feature was not diagnostic based on the variation in opercle ornamentation he observed in the Firestone Library excavation coelacanth assemblage. Our quantification of key skull characteristics in coelacanths from both Firestone Library and Granton Quarry shows that small-bodied coelacanths with heavily striated opercles also consistently possess four angular foramina, whereas †*Diplurus newarki* consistently possesses fewer than 10 opercle striations and five angular foramina. There is no continuous variation in either of these features. The opercle ornamentation of †*D. enigmaticus* also distinguishes this species from the much larger †*D. longicaudatus*. The ornamentation on the opercle of †*D. longicaudatus* consists of numerous weak ridges that span the antero-posterior axis of the opercle and run posteroventrally (Fig. 8). In †*D. enigmaticus*, these ridges are straightened and radiate from a center located midway along the dorso-ventral axis of the bone (Figs. 6, 7, Fig. 8). Further, there

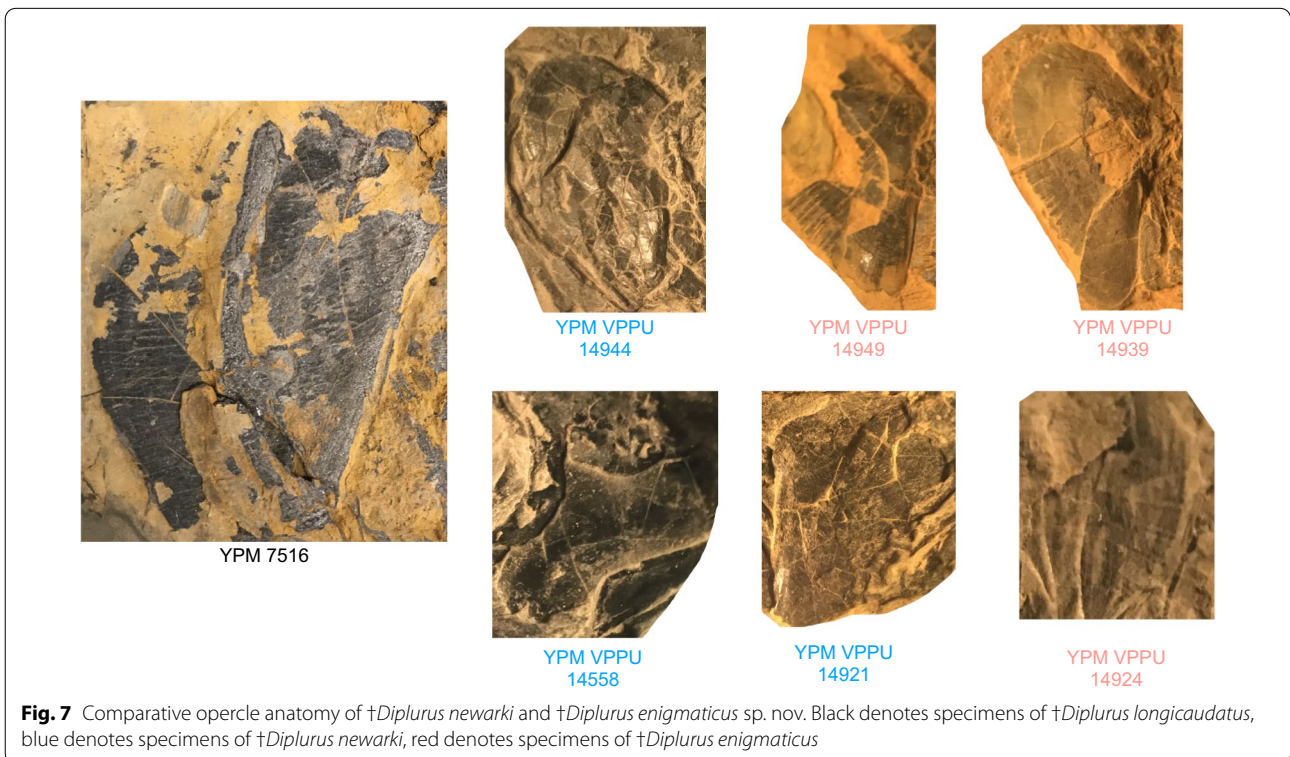
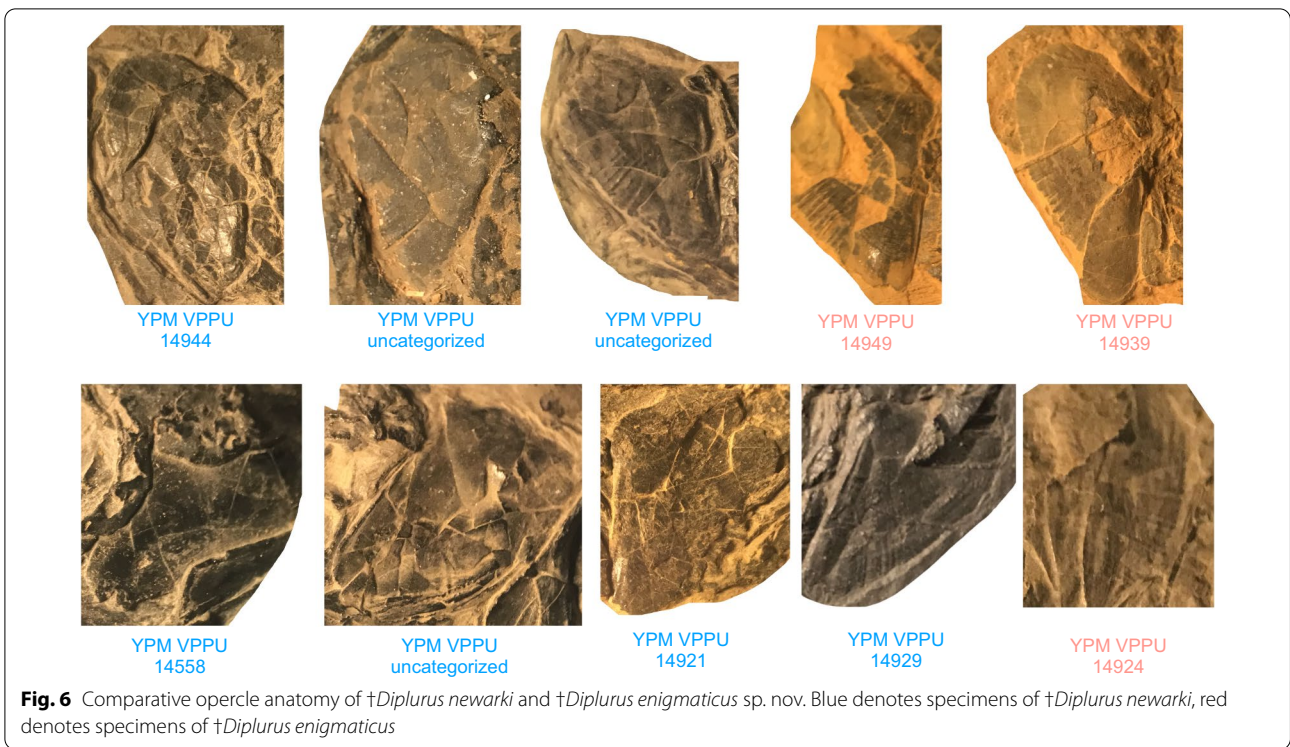
is no evidence for more than one or two distinct angular foramina in any specimen of †*D. longicaudatus* [71, 72] in contrast to the four foramina found in †*D. enigmaticus*. †*D. enigmaticus* almost certainly does not represent a juvenile form of †*D. longicaudatus*, as the skull and skeleton are strongly ossified and are not drastically proportionally different [71] as in the skulls of small juveniles and adults of the extant coelacanth *Latimeria* [24].

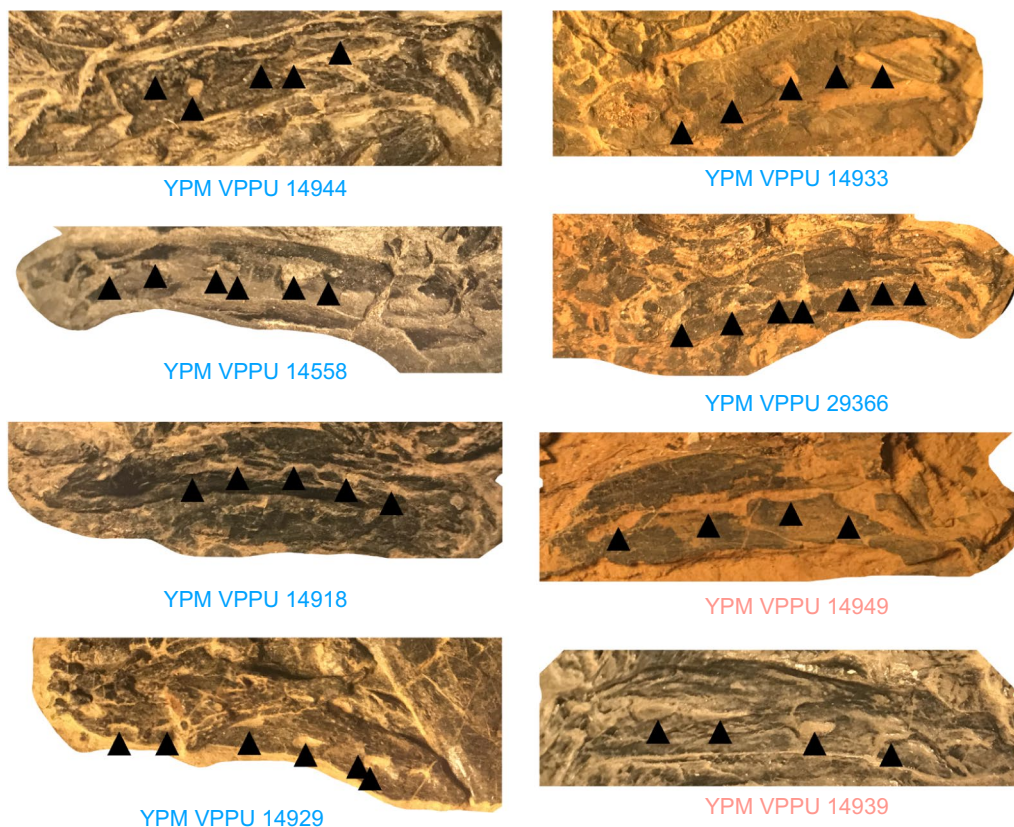
A third osteological feature that distinguishes specimens of †*D. enigmaticus* from †*D. newarki* is the size of the premaxillary dentition (Fig. 9). YPM 14924, the holotype complete skull of †*D. enigmaticus*, includes an enlarged premaxilla with at least 8 conical teeth that appear much larger than in specimens of †*D. newarki*, such as YPM 14558a (see also Fig. 4 in [74]). Specimens of †*D. newarki* also possess a higher premaxillary tooth count of 11 tooth positions in each premaxilla [74].

## Discussion

### Diversity and phylogenetic position of †*Diplurus*

In this study, we have quantified coelacanth diversity at several exceptional assemblages from the Triassic rift lakes of eastern North America. This approach allows us to quantitatively assess the validity of several previously





**Fig. 8** Comparative angular anatomy of †*Diplurus newarki* and †*Diplurus enigmaticus* sp. nov. Blue denotes specimens of †*Diplurus newarki*, red denotes specimens of †*Diplurus enigmaticus*

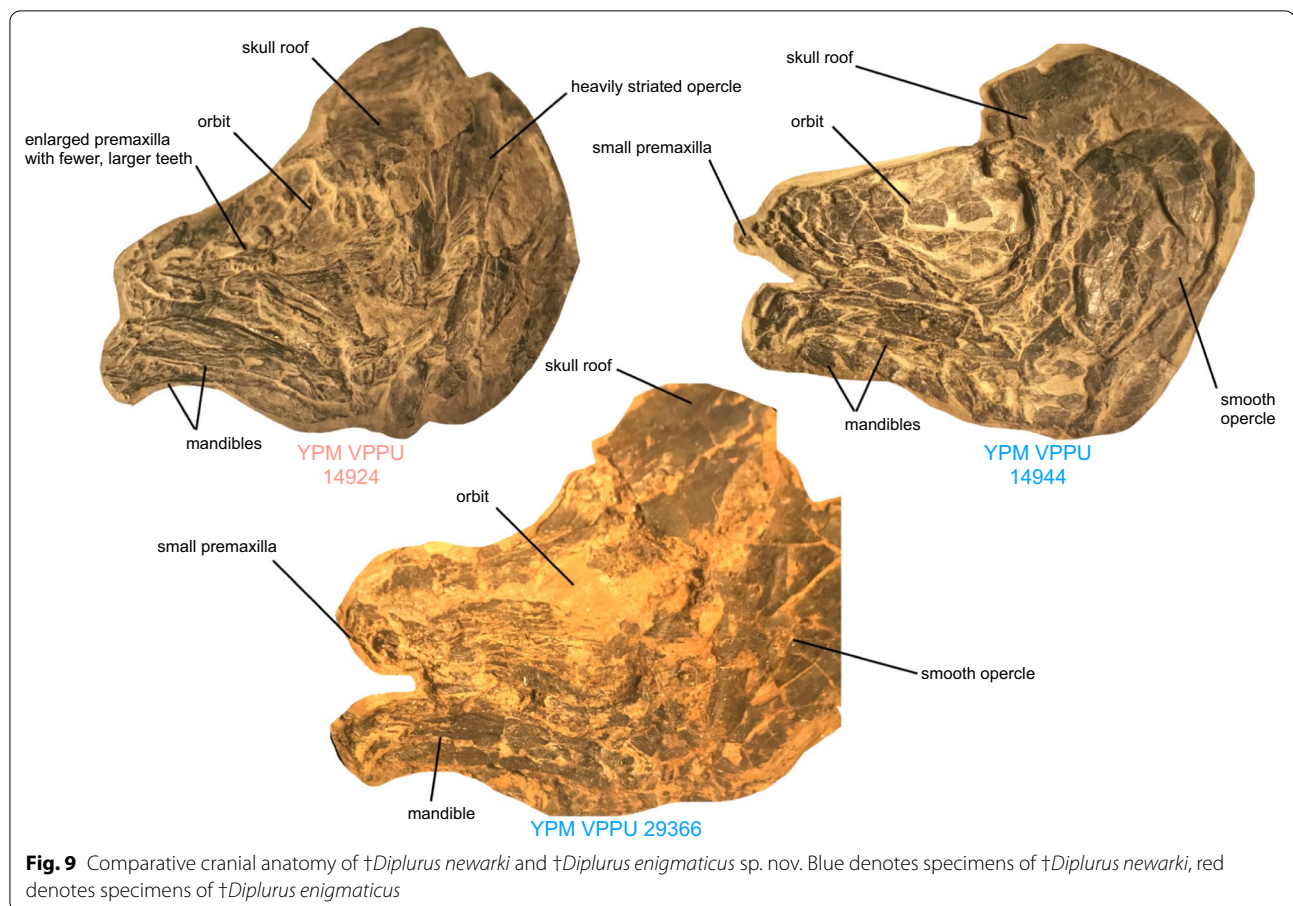
named species from this region [76] and provide strong phylogenetic and morphometric evidence for the existence of the unrecognized, small-bodied form, †*Diplurus enigmaticus*, living in sympatry with the similarly-sized †*Diplurus newarki* and the much larger †*Diplurus longicaudatus* at the Firestone Library excavation and possibly Granton Quarry [70–72]. Our results also support synonymy of †*Osteopleurus milleri* with †*D. newarki* [74] and corroborate the hypothesis that minor size differences among coelacanth specimens from northeastern North America do not warrant the recognition of new species (thereby making †*O. m. grantonensis* a nomen dubium sensu [74]).

Intensive sampling of these Triassic eastern North American coelacanths also provides new information on the evolutionary relationships of these freshwater species. Placing †*Diplurus* among coelacanths has been difficult. Alternative approaches to phylogenetic reconstruction have allied this genus with both the Latimeriidae and the extinct coelacanth clade †Mawsoniidae, which was the dominant lineage during much of the Mesozoic [15, 17, 18, 83]. Although we still found conflicts between the relationships of †*Diplurus newarki*,

†*Diplurus longicaudatus*, and †*D. enigmaticus* to other coelacanths resolved in parsimony and Bayesian frameworks (cf. [83], our intensive sampling suggests (1) that these eastern forms are more likely early-diverging members of †Mawsoniidae than Latimeriidae (Figs. 2, 3,[17]) and (2) the somewhat ambiguous phylogenetic positions of these eastern North American coelacanth species may result from an incomplete understanding of character evolution at a critical junction in the coelacanth tree: the divergence of the Mesozoic mawsoniids from *Latimeria* and its closest relatives in Latimeriidae [13, 15, 17, 83].

#### Coelacanths as a depauperate vertebrate clade

The existence of depauperate, evolutionarily stagnant lineages has been a matter of great interest since this pattern was first recognized (e.g., [12, 13, 21, 47, 82]). One central point of contention has been whether continuously low species diversity across time scales of tens of millions of years in many of these clades is driven by genuinely low speciation rates or simply the incompleteness of the fossil record (e.g., [12, 13, 18, 57, 77]). In the case of depauperons, rigorous species delimitation is therefore all the more essential, as these clades might show



a lower level of morphological disparity across species boundaries if taxic depauperacy is coupled with reduced evolvability. Extant coelacanths present an example of this phenomenon, despite diverging over 30 million years ago, the two recognized species of *Latimeria* vary little in morphology [39, 41, 79]. The low number of characteristics distinguishing coelacanths with old common ancestors obscures whether deep divergences in this clade are indicative of speciation [44].

The diversity and size disparity of coelacanths found in the Triassic of eastern North America is higher than most previously reported assemblages of actinistians from the Mesozoic. Although multiple coelacanths have been described from the same geological units dating to the early Mesozoic [17], our site-based approach confirms that three species spanning a large range of body sizes were living in the same lakes and waterways. At the same time, the anatomy of all three species at Firestone and Granton Quarry are remarkably similar, these species all show similar fusiform body plans and differ extensively only in the ornamentation of their opercles, number of foramina in their lower jaws, the size and number of their premaxillary teeth,

the form of their scalation, and the form and counts of their fins [71, 72]. The observation of high size disparity coupled with low skeletal differentiation in the Lockatong coelacanth fauna supports the observation that the prevailing pattern in this clade is morphological conservatism [13, 15, 18, 83, 87], but see [17].

The species diversity of †*Diplurus* observed in Lockatong and Boonton Formation assemblages clearly contrasts with the view of coelacanths as a perpetually depauperate lineage (e.g., [13, 18, 52]). Instead, our results underscore the importance of quantitative approaches to species delimitation in the fossil record (e.g., [84]). In the case of coelacanths, our understanding of the evolutionary history of the total clade might be warped by observations of the evolutionary history of the crown group. *Latimeria* is currently represented by two species with an estimated common ancestor living >30 million years ago [41, 46] that may have consistently lived in the marine benthos [20]. Further, *Latimeria chalumnae* and *L. menadoensis* possess slow molecular substitution rates at selectively constrained genes than most vertebrates (e.g., [3, 7, 58, 86]), although other regions of the genome thought

to undergo neutral evolution (i.e., fourfold degenerate sites) show similar rates of change to other chordates [56].

There is genomic evidence for additional deep (> 10 million year) divergences among extant coelacanth populations that may imply unsampled extant coelacanth diversity [44, 58]. However, the deep-marine ecology, restricted distribution, and low populations of extant *Latimeria* greatly restrict our ability to investigate phenotypic disparity in the only extant actinistians [44]. Our analyses, which examine the largest morphological dataset for sympatric coelacanth individuals available, demonstrate how phenotypic variability denoting probable species distinctions might be overlooked even in sympatric populations of similarly-sized species (e.g., †*Diplurus newarki* and †*D. enigmaticus*). Thus, the depauperacy of coelacanths and the extensive temporal ranges of several mawsoniid and latimeriid genera might be artifacts of unrecognized subtle species distinctions in this species-poor clade rather than reflecting the existence of exceptionally long-lived genera [18, 27]. In contrast to what might be expected based on the apparent low morphological disparity and genomic rates of change in the crown group, the species richness of coelacanths and other depauperons may still largely be hidden in the geological past.

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12862-022-02043-4>.

**Additional file 1.** Apomorphies optimized in phylogenetic analyses. Additional Figure Captions.

**Additional file 2.** Measurement data.

**Additional file 3.** Phylogenetic data.

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## Author contributions

CDB and ICB collected and analyzed the data and wrote and edited drafts of the paper. Both authors read and approved the final manuscript.

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## Availability of data and materials

All data is in the manuscript and the supplement. All material examined is in the collections of the Yale Peabody Museum of Natural History, a public repository in New Haven, CT. No living animals were examined.

## Declarations

### Ethics approval and consent to participate

Not applicable.

### Consent for publication

Not applicable.

### Competing interests

The authors declare no competing interests.

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## References

- Alfaro ME, Santini F, Brock C, Alamillo H, Dornburg A, Rabosky DL, Carnevale G, Harmon LJ. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc Natl Acad Sci*. 2009;106(32):13410–4.
- Álvarez-Carretero S, Tamuri AU, Battini M, Nascimento FF, Carlisle E, Asher RJ, Yang Z, Donoghue PC, Dos Reis M. A species-level timeline of mammal evolution integrating phylogenomic data. *Nature*. 2022;602(7896):263–7.
- Amemiya CT, Alföldi J, Lee AP, Fan S, Philippe H, MacCallum I, Braasch I, Manousaki T, Schneider I, Rohner N, Organ C. The African coelacanth genome provides insights into tetrapod evolution. *Nature*. 2013;496(7445):311–6.
- Arratia G, Schultze HP. Mesozoic fishes from Chile. *Mesozoic Fishes*. 1999;2:565–93.
- Bailey CM, Coiner LV. eds. 2014. Elevating Geoscience in the Southeastern United States: New Ideas about Old Terranes: Field Guides for the GSA Southeastern Section Meeting, Blacksburg, Virginia, 2014 (Vol. 35). Geological Society of America.
- Bouckaert R, Vaughan TG, Barido-Sottani J, Duchêne S, Fourment M, Gavryushkina A, Heled J, Jones G, Kühnert D, De Maio N, Matschiner M. BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Comput Biol*. 2019;15(4):e1006650.
- Braasch I, Gehrke AR, Smith JJ, Kawasaki K, Manousaki T, Pasquier J, Amores A, Desvignes T, Batzel P, Catchen J, Berlin AM. The spotted gar genome illuminates vertebrate evolution and facilitates human-teleost comparisons. *Nat Genet*. 2016;48(4):427–37.
- Brinkmann H, Venkatesh B, Brenner S, Meyer A. Nuclear protein-coding genes support lungfish and not the coelacanth as the closest living relatives of land vertebrates. *Proc Natl Acad Sci*. 2004;101(14):4900–5.
- Bryant WL. New fishes from the Triassic of Pennsylvania. *Proc Am Philos Soc*. 1934;73(5):319–26.
- Burbrink FT, Grazziotin FG, Pyron RA, Cundall D, Donnellan S, Irish F, Keogh JS, Kraus F, Murphy RW, Noonan B, Raxworthy CJ. Interrogating genomic-scale data for Squamata (lizards, snakes, and amphisbaenians) shows no support for key traditional morphological relationships. *Syst Biol*. 2020;69(3):502–20.
- Cavin L, Buffetaut E, Dutour Y, Garcia G, Le Loeuff J, Méchin A, Méchin P, Tong H, Tortosa T, Turini E, Valentin X. The last known freshwater coelacanths: New Late Cretaceous mawsoniid remains (Osteichthyes: Actinistia) from southern France. *Plos one*. 2020;15(6):e0234183
- Casane D, Laurenti P. Why coelacanths are not 'living fossils' A review of molecular and morphological data. *BioEssays*. 2013;35(4):332–8.
- Cavin L, Guinot G. Coelacanths as "almost living fossils." *Front Ecol Evol*. 2014;2:49.
- Cavin L. Palaeobiogeography of cretaceous bony fishes (Actinistia, Dipnoi and Actinopterygii). *Geol Soc Lond Special Publ*. 2008;295(1):165–83.

15. Cavin L, Cupello C, Yabumoto Y, Fragoso L, Deesri U, Brito PM. Phylogeny and evolutionary history of mawsoniid coelacanths. *Bull Peabody Mus Nat Hist*. 2019;17:3–13.
16. Cavin L, Forey PL, Buffetaut E, Tong H. Latest European coelacanth shows Gondwanan affinities. *Biol Lett*. 2005;1(2):176–7.
17. Cavin L, Mennecart B, Obrist C, Costeur L, Furrer H. Heterochronic evolution explains novel body shape in a Triassic coelacanth from Switzerland. *Sci Rep*. 2017;7(1):1–7.
18. Cavin L, Toriño P, Van Vranken N, Carter B, Polcyn MJ, Winkler D. The first late cretaceous mawsoniid coelacanth (Sarcopterygii: Actinistia) from North America: evidence of a lineage of extinct 'living fossils'. *PLoS ONE*. 2021;16(11):e0259292.
19. Colbert EH, Olsen PE. A new and unusual aquatic reptile from the Lockatong Formation of New Jersey (Late Triassic, Newark Supergroup). *Am Mus Novit*. 2001;2001(3334):1–24.
20. Cupello C, Clément G, Meunier FJ, Herbin M, Yabumoto Y, Brito PM. The long-time adaptation of coelacanths to moderate deep water: reviewing the evidences. *Bull Peabody Mus Nat Hist*. 2019;17:29–35.
21. Darwin C. On the origin of species. London: John Murray; 1859.
22. Donoghue MJ, Sanderson MJ. Confluence, synnovation, and depauperons in plant diversification. *New Phytol*. 2015;207(2):260–74.
23. Dornburg A, Near TJ. The emerging phylogenetic perspective on the evolution of actinopterygian fishes. *Annu Rev Ecol Evol Syst*. 2021;52:427–52.
24. Dutel H, Galland M, Tafforeau P, Long JA, Fagan MJ, Janvier P, Herrel A, Santin MD, Clément G, Herbin M. Neurocranial development of the coelacanth and the evolution of the sarcopterygian head. *Nature*. 2019;569(7757):556–9.
25. Dutel H, Herbin M, Clément G. First occurrence of a mawsoniid coelacanth in the Early Jurassic of Europe. *J Vertebr Paleontol*. 2015;35(3):e929581.
26. Dutel H, Pennetier E, Pennetier G. A giant marine coelacanth from the Jurassic of Normandy France. *J Vertebr Paleontol*. 2014;34(5):1239–42.
27. Forey P. History of the coelacanth fishes. Springer Science & Business Media. 1998
28. Fraser NC, Grimaldi DA, Olsen PE, Axsmith B. A Triassic lagerstätte from eastern North America. *Nature*. 1996;380(6575):615–9.
29. Friedman M, Coates MJ. A newly recognized fossil coelacanth highlights the early morphological diversification of the clade. *Proc R Soc B Biol Sci*. 2006;273(1583):245–50.
30. Friedman M. Styloichthys as the oldest coelacanth: implications for early osteichthyan interrelationships. *J Syst Paleontol*. 2007;5(3):289–343.
31. Gavrillets S, Losos JB. Adaptive radiation: contrasting theory with data. *Science*. 2009;323:732–8.
32. Gavryushkina A, Welch D, Stadler T, Drummond AJ. Bayesian inference of sampled ancestor trees for epidemiology and fossil calibration. *PLoS Comput Biol*. 2014;10(12):e1003919.
33. Gillespie RG, Bennett GM, De Meester L, Feder JL, Fleischer RC, Harmon LJ, Hendry AP, Knape ML, Mallet J, Martin C, Parent CE. Comparing adaptive radiations across space, time, and taxa. *J Hered*. 2020;111(1):1–20.
34. Goloboff PA, Catalano SA. TNT version 15, including a full implementation of phylogenetic morphometrics. *Cladistics*. 2016;32(3):221–38.
35. Grande L. An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of *Holostei*. *Ichthyol Herpetol*. 2010;10(2A):1.
36. Grande L, Bemis WE. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. *Soc Vertebr Paleontol Memoir* 1998;4:i-x, 1–690; supplement to *Journal of Vertebrate Paleontology*.
37. Herrera-Flores JA, Stubbs TL, Benton MJ. Macroevolutionary patterns in Rhynchocephalia: is the tuatara (*Sphenodon punctatus*) a living fossil? *Palaeontology*. 2017;60(3):319–28.
38. Herrera-Flores JA, Stubbs TL, Benton MJ. Ecomorphological diversification of squamates in the Cretaceous. *R Soc Open Sci*. 2021;8(3):201961.
39. Holder MT, Erdmann MV, Wilcox TP, Caldwell RL, Hillis DM. Two living species of coelacanths? *Proc Nat Acad Sci*. 1999;96(22):12616–20.
40. Hughes LC, Ortí G, Huang Y, Sun Y, Baldwin CC, Thompson AW, Arcila D, Betancur-R R, Li C, Becker L, Bellora N. Comprehensive phylogeny of ray-finned fishes (Actinopterygii) based on transcriptomic and genomic data. *Proc Natl Acad Sci*. 2018;115(24):6249–54.
41. Inoue JG, Miya M, Venkatesh B, Nishida M. The mitochondrial genome of Indonesian coelacanth *Latimeria menadoensis* (Sarcopterygii: Coelacanthiformes) and divergence time estimation between the two coelacanths. *Gene*. 2005;11(349):227–35.
42. Jarvis ED, et al. Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science*. 2014;346(6215):1320–31.
43. Johanson Z, Long JA, Talent JA, Janvier P, Warren JW. Oldest coelacanth, from the early Devonian of Australia. *Biol Lett*. 2006;2(3):443–6.
44. Kadarusman SHY, Pouyau L, Hocdé R, Hismayasari IB, et al. A thirteen-million-year divergence between two lineages of Indonesian coelacanths. *Sci Rep*. 2020;10:192.
45. Kent DV, Olsen PE, Muttoni G. Astrochronostratigraphic polarity time scale (APTS) for the Late Triassic and Early Jurassic from continental sediments and correlation with standard marine stages. *Earth Sci Rev*. 2017;1(166):153–80.
46. Lalu XC, Kosen JD, Tjakrawidjaja AH, Kusumah RV, Sadhotomo B, Pouyau L, Slembrong J, Paradis E. Mitochondrial genomic divergence in coelacanths (*Latimeria*): slow rate of evolution or recent speciation? *Marine Boil*. 2010;157(10):2253–62.
47. Lidgard S, Love AC. Rethinking living fossils. *Bioscience*. 2018;68(10):760–70.
48. Liutkus-Pierce CM, Fraser NC, Heckert AB. Stratigraphy, sedimentology, and paleontology of the Upper Triassic Solite Quarry, North Carolina and Virginia. In: *Elevating Geoscience in the Southeastern United States: New Ideas about Old Terranes—Field Guides for the 2014 GSA Southeastern Section Meeting, Blacksburg, Virginia: Boulder, CO, Geological Society of America 2014 Mar 1* (pp. 255–269).
49. Lund R, Lund W. New genera and species of coelacanths from the Bear Gulch Limestone (Lower Carboniferous) of Montana (USA). *Geobios*. 1984;17(2):237–44.
50. Maisey JG. Coelacanths from the Lower Cretaceous of Brazil. *Am Mus Nov*. 1986;2866:1–30.
51. Malenda HF, Simpson EL, Szajna MJ, Fillmore DL, Hartline BW, Heness EA, Kraal ER, Wilk JL. Taphonomy of lacustrine shoreline fish-part conglomerates in the Late Triassic age Lockatong Formation (Collegeville, Pennsylvania, USA): toward the recognition of catastrophic fish kills in the rock record. *Palaeogeogr Palaeoclimatol Palaeoecol*. 2012;313:234–45.
52. Mayden RL. Speciose and depauperate phylads and tests of punctuated and gradual evolution: fact or artifact? *Syst Zool*. 1986;35(4):591–602.
53. Metz R. Ichhnologic study of the Lockatong Formation (Late Triassic), Newark Basin, southeastern Pennsylvania. *Ichnos*. 1995;4(1):43–51.
54. Metz R. Trace fossils in fluvial deposits of the uppermost Stockton Formation (Late Triassic), Newark Basin New Jersey. *Ichnos*. 2020;27(2):142–51.
55. Meyer A. Molecular evidence on the origin of tetrapods and the relationships of the coelacanth. *Trends Ecol Evol*. 1995;10(3):111–6.
56. Naville M, Chalopin D, Casane D, Laurenti P, Volff JN. The coelacanth: Can a "living fossil" have active transposable elements in its genome? Mobile genetic elements. 2015;5(4):55–9.
57. Near TJ, Dornburg A, Tokita M, Suzuki D, Brandley MC, Friedman M. Boom and bust: ancient and recent diversification in bichirs (polypteridae: actinopterygii), a relictual lineage of ray-finned fishes. *Evolution*. 2014;68(4):1014–26.
58. Nikaido M, Sasaki T, Emerson JJ, Aibara M, Mzighani SI, Budeba YL, Ngatunga BP, Iwata M, Abe Y, Li WH, Okada N. Genetically distinct coelacanth population off the northern Tanzanian coast. *Proc Natl Acad Sci*. 2011;108(44):18009–13.
59. Olsen PE, McCune AR, Thomson KS. Correlation of the early Mesozoic Newark Supergroup by vertebrates, principally fishes. *Am J Sci*. 1982;282:1–44.
60. Olsen PE, Kent DV. Milankovitch climate forcing in the tropics of Pangaea during the Late Triassic. *Palaeogeogr Palaeoclimatol Palaeoecol*. 1996;122(1–4):1–26.
61. Olsen PE. Fossil great lakes of the Newark Supergroup in New Jersey. In: *Field studies of New Jersey geology and guide to field trips: New York State Geological Association, 52nd Annual Meeting, Newark, New Jersey, Rutgers University* (pp. 352–398); 1980.
62. Olsen PE. Triassic and Jurassic formations of the Newark Basin. In *Field studies of New Jersey geology and guide to field trips: 52nd annual meeting of the New York State Geological Association, ed. W. Manspeizer* (pp. 2–41); 1980

63. Olsen PE, 1988. Paleontology and paleoecology of the Newark Super-group (early Mesozoic, eastern North America). In: *Developments in Geotectonics* (Vol. 22, pp. 185–230). Elsevier; 1988
64. Olsen PE, Froelich AJ, Daniels DL, Smoot JP, Gore PJ, Horton W, 1991. Rift basins of early Mesozoic age. *Geol Carolinas* 1991:142–170.
65. Olsen PM, Letourneau PE. *The Great Rift Valleys of Pangea in Eastern North America: Sedimentology, stratigraphy, and paleontology* (Vol 2). Columbia: Columbia University Press; 2003.
66. Prum RO, et al. A comprehensive phylogeny of birds (*Aves*) using targeted next-generation DNA sequencing. *Nature*. 2015;526(7574):569–73.
67. Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Syst Biol*. 2018;67(5):901–4.
68. Raup DM, Gould SJ, Schopf TJM, Simberloff DS. Stochastic models of phylogeny and evolution of diversity. *J Geol*. 1973;81:525–42.
69. Rieppel O. A new coelacanth from the Middle Triassic of Monte San Giorgio, Switzerland; 1980.
70. Schaeffer B. A revision of *Coelacanthus newarki* and notes on the evolution of the girdles and basal plates of the median fins in the Coelacanthini. *Am Mus Novit*. 1941;1110:1–18.
71. Schaeffer B. A study of *Diplurus longicaudatus* with notes on the body form and locomotion of the Coelacanthini. *Am Mus Novit*. 1948;1378:1–32.
72. Schaeffer B. The Triassic coelacanth fish *Diplurus*, with observations on the evolution of the Coelacanthini. *Bull AMNH*. 1952;99(2):1–67.
73. Schaeffer B, McDonald NG. Redfieldiid fishes from the Triassic-Liassic Newark Supergroup of eastern North America. *Bull AMNH*. 1978;159(4):129–74.
74. Schaeffer B. The Triassic coelacanth fish *Diplurus*, with observations on the evolution of the Coelacanthini. *Bull Am Mus Nat Hist*. 1952;99:27–75.
75. Schluter D. *The ecology of adaptive radiation*. Oxford: OUP; 2000.
76. Shainin VE. New coelacanth fishes from the Triassic of New Jersey. *J Paleontol*. 1943;17(3):271–5.
77. Simões TR, Caldwell MW, Pierce SE. Sphenodontian phylogeny and the impact of model choice in Bayesian morphological clock estimates of divergence times and evolutionary rates. *BMC Biol*. 2020;18(1):1–30.
78. Simpson GG, *The major features of evolution*. In: *The Major Features of Evolution*. Columbia University Press. 71; 1953.
79. Smith JLB. A living fish of Mesozoic type. *Nature*. 1939;143:455.
80. Smoot JP. Sedimentary facies and depositional environments of early Mesozoic Newark Supergroup basins, eastern North America. *Palaeogeogr Palaeoclimatol Palaeoecol*. 1991;84:369–423.
81. Soto M, De Carvalho MS, Maisey JG, Perea D, Silva JD. Coelacanth remains from the Late Jurassic–? Earliest Cretaceous of Uruguay: the southernmost occurrence of the Mawsoniidae. *J Vertebr Paleontol*. 2012;32(3):530–7.
82. Stanley SM. A theory of evolution above the species level. *Proc Natl Acad Sci*. 1975;72(2):646–50.
83. Toriño P, Soto M, Perea D. A comprehensive phylogenetic analysis of coelacanth fishes (Sarcopterygii, Actinistia) with comments on the composition of the Mawsoniidae and Latimeriidae: evaluating old and new methodological challenges and constraints. *Hist Biol*. 2021;33(12):3423–43.
84. Tschopp E, Napoli JG, Wencker L, Delfino M, Upchurch P. How to render species comparable taxonomic units through deep time: a case study on intraspecific osteological variability in extant and extinct lacertid lizards. *Syst Biol*. 2021. <https://doi.org/10.1093/sysbio/syab078/6380963>.
85. Van Houten FB. Cyclic sedimentation and the origin of analcime-rich Upper Triassic Locketong Formation, west-central New Jersey and adjacent Pennsylvania. *Am J Sci*. 1962;260:561–76.
86. Venkatesh B, Lee AP, Ravi V, Maurya AK, Lian MM, Swann JB, Ohta Y, Flajnik MF, Sutoh Y, Kasahara M, Hoon S. Elephant shark genome provides unique insights into gnathostome evolution. *Nature*. 2014;505(7482):174–9.
87. Wendruff AJ, Wilson MV. A fork-tailed coelacanth, *Rebellatrix divaricerca*, gen. et sp. nov. (Actinistia, Rebellatricidae, fam. nov.), from the Lower Triassic of Western Canada. *J Vertebr Paleontol*. 2012;32(3):499–511.
88. Wickham H. *ggplot2: elegant graphics for data analysis*. Cham: Springer; 2016.
89. Wu CS, Chaw SM, Huang YY. Chloroplast phylogenomics indicates that *Ginkgo biloba* is sister to cycads. *Genome Biol Evol*. 2013;5(1):243–54.

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