Little evidence for enhanced phenotypic evolution in early teleosts relative to their living fossil sister group

John T. Clarke[a,b,1], Graeme T. Lloyd[c], and Matt Friedman[b,2]

[a]Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, PA 19104-6316; [b]Department of Earth Sciences, University of Oxford, Oxford OX1 3AN, United Kingdom; and [c]Department of Biological Sciences, Faculty of Science, Macquarie University, North Ryde, NSW 2109, Australia

Edited by Neil H. Shubin, University of Chicago, Chicago, IL, and approved August 19, 2016 (received for review May 6, 2016)

Since Darwin, biologists have been struck by the extraordinary diversity of teleost fishes, particularly in contrast to their closest "living fossil" holostean relatives. Hypothesized drivers of teleost success include innovations in jaw mechanics, reproductive biology and, particularly at present, genomic architecture, yet all scenarios presuppose enhanced phenotypic diversification in teleosts. We test this key assumption by quantifying evolutionary rate and capacity for innovation in size and shape for the first 160 million y (Permian–Early Cretaceous) of evolution in neopterygian fishes (the more extensive clade containing teleosts and holosteans). We find that early teleosts do not show enhanced phenotypic evolution relative to holosteans. Instead, holostean rates and innovation often match or can even exceed those of stem-, crown-, and total-group teleosts, belying the living fossil reputation of their extant representatives. In addition, we find some evidence for heterogeneity within the teleost lineage. Although stem teleosts excel at discovering new body shapes, early crown-group taxa commonly display higher rates of shape evolution. However, the latter reflects low rates of shape evolution in stem teleosts relative to all other neopterygian taxa, rather than an exceptional feature of early crown teleosts. These results complement those emerging from studies of both extant teleosts as a whole and their sublineages, which generally fail to detect an association between genome duplication and significant shifts in rates of lineage diversification.

neopterygian | phylogeny | genome duplication | fossil record | morphological diversification

Numbering ~29,000 species, teleost fishes account for half of modern vertebrate richness. In contrast, their holostean sister group, consisting of gars and the bowfin, represents a mere eight species restricted to the freshwaters of eastern North America (1). This stark contrast between teleosts and Darwin's original "living fossils" (2) provides the basis for assertions of teleost evolutionary superiority that are central to textbook scenarios (3, 4). Classic explanations for teleost success include key innovations in feeding (3, 5) (e.g., protrusible jaws and pharyngeal jaws) and reproduction (6, 7). More recent work implicates the duplicate genomes of teleosts (8–10) as the driver of their prolific phenotypic diversification (8, 11–13), concordant with the more general hypothesis that increased morphological complexity and innovation is an expected consequence of genome duplication (14, 15).

Most arguments for enhanced phenotypic evolution in teleosts have been asserted rather than demonstrated (8, 11, 12, 15, 16; but see ref. 17), and draw heavily on the snapshot of taxonomic and phenotypic imbalance apparent between living holosteans and teleosts. The fossil record challenges this neontological narrative by revealing the remarkable taxonomic richness and morphological diversity of extinct holosteans (Fig. 1) (18, 19) and highlights geological intervals when holostean taxonomic richness exceeded that of teleosts (20). This paleontological view has an extensive pedigree. Darwin (2) invoked a long interval of cryptic teleost evolution preceding the late Mesozoic diversification of the modern radiation, a view subsequently supported by the implicit (18) or explicit (19) association of Triassic–Jurassic species previously recognized as "holostean ganoids" with the base of teleost phylogeny. This perspective became enshrined in mid-20th century treatments of actinopterygian evolution, which recognized an early-mid Mesozoic phase dominated by holosteans *sensu lato* and a later interval, extending to the modern day, dominated by teleosts (4, 20, 21). Contemporary paleontological accounts echo the classic interpretation of modest teleost origins (22–24), despite a systematic framework that substantially revises the classifications upon which older scenarios were based (22–25). Identification of explosive lineage diversification in nested teleost subclades like otophysans and percomorphs, rather than across the group as a whole, provides some circumstantial neontological support for this narrative (26).

In contrast to quantified taxonomic patterns (20, 23, 24, 27), phenotypic evolution in early neopterygians has only been discussed in qualitative terms. The implicit paleontological model of morphological conservatism among early teleosts contrasts with the observation that clades aligned with the teleost stem lineage include some of the most divergent early neopterygians in terms of both size and shape (Fig. 1) (see, for example, refs. 28 and 29). These discrepancies point to considerable ambiguity in initial patterns of phenotypic diversification that lead to a striking contrast in the vertebrate tree of life, and underpins one of the most successful radiations of backboned animals.

Here we tackle this uncertainty by quantifying rates of phenotypic evolution and capacity for evolutionary innovation for the first 160 million y of the crown neopterygian radiation. This late Permian (Wuchiapingian, ca. 260 Ma) to Cretaceous (Albian, ca. 100 Ma) sampling interval permits incorporation of diverse

Significance

The success of teleost fishes, which represent roughly half of all vertebrate species, has attracted attention since Darwin. Numerous scenarios invoke elevated diversification in teleosts facilitated by supposed key innovations, yet claims of teleost exceptionalism are profoundly biased by the evolutionary "snapshot" of living fishes. Analysis of 160 million y (Permian–Early Cretaceous) of evolution in neopterygian fishes reveals that anatomical diversification in Mesozoic teleosts as a whole differed little from their "living fossil" holostean sister group. There is some evidence for evolutionary heterogeneity within teleosts, with early evolving lineages showing the greatest capacity for evolutionary innovation in body shape among Mesozoic neopterygians, whereas members of the modern teleost radiation show higher rates of shape evolution.

Author contributions: J.T.C. and M.F. designed research; J.T.C. performed research; G.T.L. contributed new reagents/analytic tools; J.T.C. and G.T.L. analyzed data; and J.T.C., G.T.L., and M.F. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

Freely available online through the PNAS open access option.

[1]To whom correspondence should be addressed. Email: j.clarke.paleo@gmail.com.

[2]Present address: Museum of Paleontology and Department of Earth and Environmental Science, University of Michigan, Ann Arbor, MI 48108-1079.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1607237113/-/DCSupplemental.

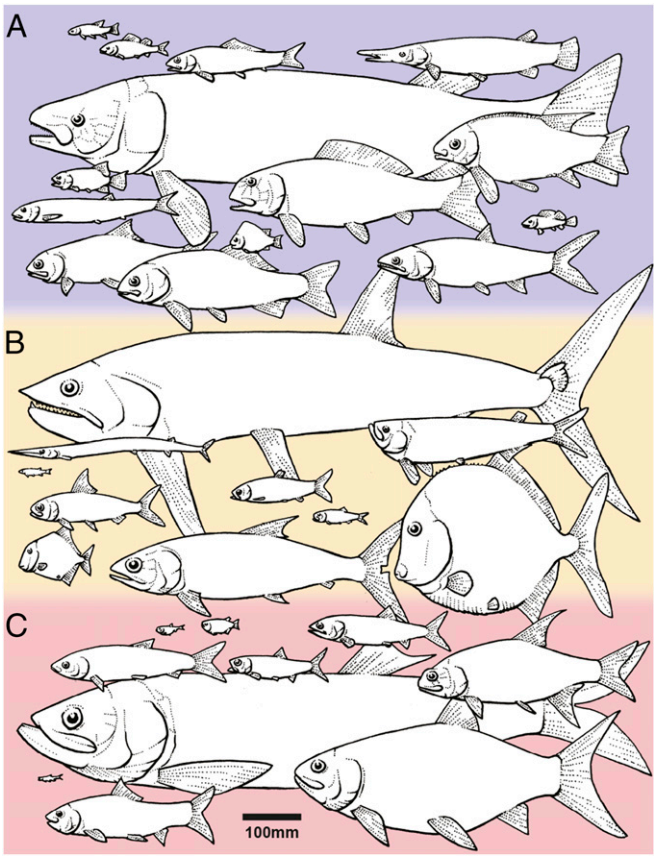

Fig. 1. Phenotypic variation in early crown neopterygians. (*A*) Total-group holosteans. (*B*) Stem-group teleosts. (*C*) Crown-group teleosts. Taxa illustrated to scale.

fossil holosteans and stem teleosts alongside early diverging crown teleost taxa (Figs. 1 and 2*A* and Figs. S1 and S2), resulting in a dataset of 483 nominal species-level lineages roughly divided between the holostean and teleost total groups (Fig. 2*B* and Fig. S2). Although genera are widely used as the currency in paleobiological studies of fossil fishes (30; but see ref. 31), we sampled at the species level to circumvent problems associated with representing geological age and morphology for multiple congeneric lineages. We gathered size [both log-transformed standard length (SL) and centroid size (CS); results from both are highly comparable (Figs. S3 and S4); SL results are reported in the main text] and shape data (the first three morphospace axes arising from a geometric morphometric analysis) (Fig. 2*A* and Figs. S1) from species where possible. To place these data within a phylogenetic context, we assembled a supertree based on published hypotheses of relationships. We assigned branch durations to a collection of trees under two scenarios for the timescale of neopterygian diversification based on molecular clock and paleontological estimates. Together, these scenarios bracket a range of plausible evolutionary timelines for this radiation (Fig. 2*B*). We used the samples of trees in conjunction with our morphological datasets to test for contrasts in rates of, and capacity for, phenotypic change between different partitions of the neopterygian Tree of Life (crown-, total-, and stem-group teleosts, total-group holosteans, and neopterygians minus crown-group teleosts), and the sensitivity of these conclusions to uncertainty in both relationships and evolutionary timescale. Critically, these include comparisons of phenotypic evolution in early crown-group teleosts—those species that are known with certainty to possess duplicate genomes—with rates in taxa characterized largely (neopterygians minus crown teleosts) or exclusively (holosteans) by unduplicated genomes. By restricting our scope to early diverging crown teleost lineages, we avoid potentially confounding signals from highly nested radiations that substantially postdate both genome duplication and the origin of crown teleosts (26, 32). This approach provides a test of widely held assumptions about the nature of morphological evolution in teleosts and their holostean sister lineage.

Results and Discussion

Mesozoic Teleosts Do Not Show Enhanced Phenotypic Diversification. Contrary to expectations ingrained in the neontological literature (3, 4, 8, 9, 12, 13, 15), early teleosts do not possess significantly higher rates of size or shape evolution than holosteans (Fig. 3*A*). We found no significant difference between rates of body size (measured as SL; other measures deliver comparable results) (Figs. S3 and S4) evolution between early members of the holostean and teleost total groups across the majority of sampled topologies under either paleontological or molecular timescales (Fig. 3*A*). In terms of evolution in overall body shape (as indicated by scores on the first three shape axes of our morphospace), we found no consistent signal, whether rates were higher in total-group teleosts or holosteans (Fig. 3*A*). However, total-group holosteans possess significantly higher rates of overall shape change than total-group teleosts in a majority of topologies when these were timescaled to match published divergence-time estimates made using the molecular clock (Fig. 3*A*).

We calculated Blomberg's *K* for specific clades to summarize how efficiently they explore phenotypic space (*Methods*). Because interpretation of *K* in isolation can be misleading (33), it is useful to consider *K* alongside information on evolutionary rate (34) (Table S1). We report *K* values directly here and in subsequent sections, drawing on our comparisons of evolutionary rate to provide necessary context. Table S1 provides more detailed interpretations of *K* using rate information. Concerning size innovation, *K* distributions for the teleost and holostean total-groups overlap considerably on paleontological timescales (Fig. 3*A*), whereas holostean *K* values are distinctly higher than teleost values on molecular timescales (Fig. 3*A*). Taken together with the suggestion of broadly comparable rates of evolution in the two clades (Fig. 3*A* and Table S1), these results imply that total-group holosteans either match or exceed total-group teleosts in their size innovation. (Fig. 3*A* and Table S1). *K* distributions for shape in holosteans and teleosts are comparable regardless of timescale (Fig. 3*A* and Table S1), suggesting they were similarly innovative.

The Broader Holostean Radiation Does Not Fulfill Numerous Living Fossil Expectations. Darwin articulated several concepts of what it means to be a living fossil (2), such as taxa that are "remnants of a once preponderant order," or are "slowly formed" (i.e., showing low rates of lineage diversification or trait evolution). Extant holosteans, which are among Darwin's archetypal living fossils (2), embody these features clearly: they represent the last survivors of a once diverse radiation and demonstrate low rates of lineage diversification (26, 32, 35). The modern genera *Amia*, *Lepisosteus*, and *Atractosteus* show negligible anatomical change since their first appearance in the Late Cretaceous and Paleocene (1, 36), and living gars show low rates of body size evolution (17).

In contrast to this pattern from living species, Mesozoic holosteans show comparable rates of size change to total- (Fig. 3*A*), crown- (Fig. S5*A*), and stem-group teleosts (Fig. S5*B*). These patterns are seen across a majority of topologies regardless of timescale. Rates of shape evolution in holosteans are broadly comparable to those of teleosts, but often exceed those of total-group teleosts on molecular timescales (Fig. 3*A*) and stem teleosts on both timescales (Fig. S5*B*).

There is no clear difference in size innovation between holosteans and total- (Fig. 3*A*), crown- (Fig. S5*A*), and stem- (Fig. S5*B*) group teleosts on paleontological timescales (Table S1). On molecular timescales, holostean-size *K* values are marginally larger than those of total- (Fig. 3*A*) and crown-group teleosts (Fig. S5*A*), and clearly larger than stem teleosts (Fig. S5*B*), suggesting holosteans are more innovative in these instances (Table S1). Unlike

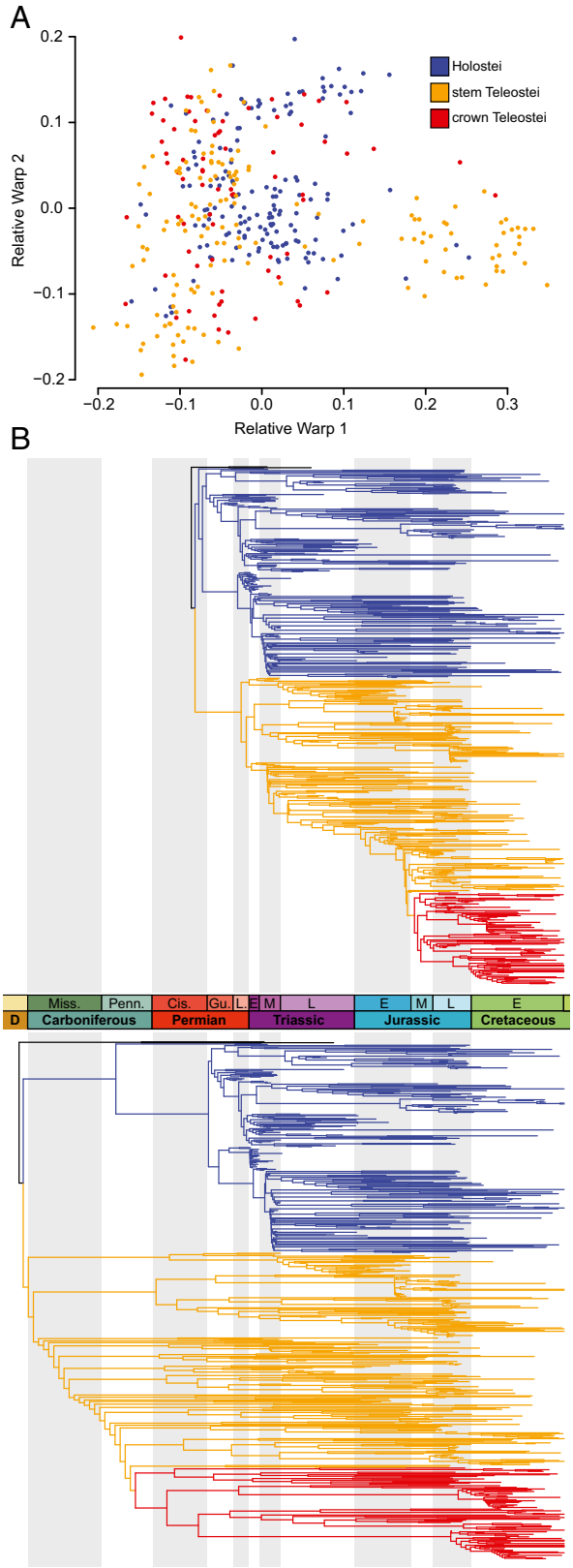

Fig. 2. (*A*) Morphospace of Permian–Early Cretaceous crown Neopterygii. (*B*) One supertree subjected to our paleontological (*Upper*) and molecular (*Lower*) timescaling procedures to illustrate contrasts in the range of evolutionary timescales considered. Colors of points (*A*) and branches (*B*) indicate membership in major partitions of neopterygian phylogeny. Topologies are given in Datasets S4 and S5. See Dataset S6 for source trees.

evolutionary rates and size innovation, there are some scenarios in which holosteans are marginally poorer shape innovators than teleosts. For example, on paleontological timescales, holosteans show marginally less shape innovation than crown teleosts (Fig. S5*A* and Table S1) and appear less innovative than stem teleosts (Fig. S5*B* and Table S1) regardless of timescale.

Crown Teleosts Display Comparable Patterns of Phenotypic Evolution to other Mesozoic Neopterygians. Despite possession of duplicate genomes, we find only ambiguous evidence for elevated shape evolution in early crown teleosts relative to rates in other neopterygian lineages. Rates are significantly higher for only a small majority of topologies on paleontological timescales (Fig. 3*B*), and fewer than half on molecular timescales (Fig. 3*B*). Evidence for higher rates in crown teleosts is even less compelling for size evolution, where a majority of trees display no significant difference in rate between crown teleosts and other neopterygians regardless of timescale (Fig. 3*B*).

Matching our inferences concerning evolutionary rate, we find no clear evidence to support the notion that early crown teleosts are better size or shape innovators than other neopterygian fishes as a whole. Regarding size, crown teleost *K* values are comparable to those of other neopterygians regardless of timescale (Fig. 3*B*), suggesting they are similarly innovative (Table S1). Regarding shape, crown teleost *K* values are either comparable to (on paleontological timescales) (Fig. 3*B*) or marginally lower than (on molecular timescales) (Fig. 3*B*) those of other neopterygians, suggesting they are similarly or less innovative, respectively (Table S1).

Capacity for Innovation and Rates of Phenotypic Change Vary Within the Teleost Total Group. Unremarkable evolutionary patterns across teleosts mask heterogeneities within the teleost total group. For example, crown-group teleosts show significantly elevated rates of shape evolution relative to stem teleosts in a small majority of topologies under both molecular and paleontological timescales (Fig. 3*C*). However, evidence for elevated rates of shape change in crown-group teleosts is by no means unambiguous; we also find no rate difference between crown teleosts and stem teleosts, or significantly higher rates in stem teleosts, in a nontrivial fraction of topologies (Fig. 3*C*). Furthermore, finding higher shape rates in crown teleosts relative to stem taxa does not demonstrate uniquely enhanced shape diversification in crown teleosts, because holosteans also demonstrate higher shape rates than stem teleosts in a similar fraction of topologies (Fig. S5*B*). In contrast to these patterns for shape evolution, we find little evidence for elevated rates of size evolution in crown teleosts relative to members of the stem (Fig. 3*C*).

Possible contrasts in rates of shape evolution between crown teleosts and stem teleosts do not align with patterns of evolutionary innovation. *K* distributions point to moderately (paleontological timescale) or substantially (molecular timescale) lower capacity for evolutionary innovation in members of the crown compared with those on the stem (Fig. 3*C*). Concerning differences in body-size evolution, there is little support for major differences between crown- and stem-group teleosts (Fig. 3*C*).

Tenuous Links Between Genome Duplication and Enhanced Evolutionary Rate and Innovation in Fishes. The staggering ecological and anatomical diversity of extant teleosts, especially in comparison with living nonteleost actinopterygian lineages, has long been taken as prima facie evidence of enhanced capacity for phenotypic evolution in this enormously successful vertebrate radiation (3, 4, 8, 9, 12). Based on a more balanced taxon sample incorporating roughly equal numbers of early teleost and holostean species, we find that evidence for this widely held assumption is at best equivocal. Teleosts as a whole cannot be reliably distinguished from holosteans in terms of either rate of phenotypic change or capacity for evolutionary innovation. The most consistent contrasts we find concern patterns of shape change between crown- and stem-group teleosts, but these do not align: stem teleosts potentially show a higher capacity for evolutionary innovation, whereas crown teleosts are characterized by higher rates of phenotypic change. However, both

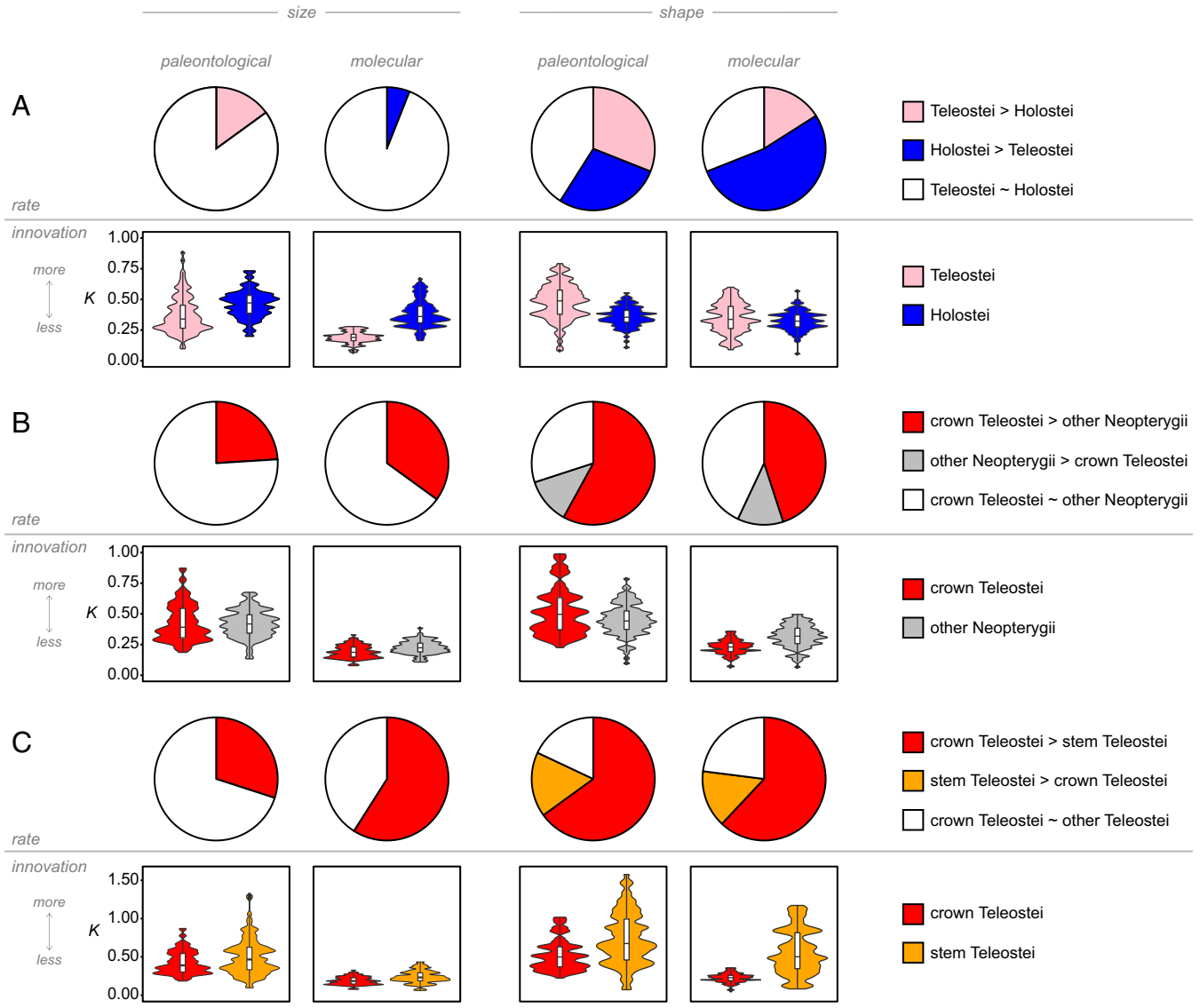

Fig. 3. Comparisons of phenotypic rate and innovation between (*A*) holosteans and teleosts, (*B*) crown teleosts and all other neopterygians, and (*C*) crown teleosts and stem teleosts. Rate results are conveyed with pie charts, where the proportion of sampled supertrees in support of significantly higher rates (as determined from two-way *P* values with $\alpha = 0.05$) in a given neopterygian partition are color coded to match that partition; white sections correspond to supertrees indicating no significant rate differences. Violin plots capturing the distribution of *K* values obtained from 100 sampled supertrees allow for investigation of innovation. Higher *K* values suggest greater phylogenetic signal, and correspondingly, greater innovation, in contrast to the iterative "rediscovery" of similar phenotypes (*Methods*). *K* interpretations are contextualised with rate in Table S1.

must be viewed as ambiguous in light of the multiple pairwise comparisons made between partitions of neopterygian phylogeny.

With the obvious caveat that our paleontological sample excludes some of the most divergent modern teleost body plans, these results call into question the search for key innovations fueling the success of modern teleosts in sum. Many such features of teleost biology have been proposed (3–7), but the duplicate genomes that characterize all living members of this group represent the most popular candidate in recent literature (8, 11–13). The connection between genome duplication and shifts in evolutionary patterns in teleosts has, to date, been addressed in terms of rates of lineage diversification in modern species alone. As with our own examination of phenotypic evolution, these studies yield ambiguous results. Elevated rates of lineage diversification are not uniformly detected for crown teleosts as a whole, but there is a consistent and strong signal for exceptional shifts in rate associated with the hyperdiverse and phylogenetically nested otophysan and percomorph radiations (26, 32, 35). The origin of these clades substantially postdates the teleost-specific whole-genome duplication, which molecular-clock dating of paralogue pairs (10) localizes to the middle of the teleost stem lineage rather than near the origin of the crown radiation (Table S2).

Further polyploid events within actinopterygians provide additional natural experiments for examining the consequences of genome duplications for subsequent patterns of evolutionary diversification. Here, too, results provide little direct support for increased rates of lineage diversification in polyploid groups relative to close relatives that have not undergone duplication events (37). In the case of groups like salmonids, geologically recent ecological shifts—rather than more ancient changes in genomic architecture—appear more closely linked with increased rates of lineage diversification (38, 39). How rates of phenotypic evolution might relate to these polyploid events has not been explored specifically, although at least two lineages characterized largely (Acipenseridae) or exclusively (Salmonidae) by polyploid species show elevated rates of body-size evolution relative to

background actinopterygian rates (17). Thus, although genome duplication represents a seductive and widely enlisted hypothesis for explaining the taxonomic and especially morphological proliferation of clades, a synoptic view of the consequences of polyploid events on rates of lineage diversification and patterns of phenotypic change remains elusive.

Although our results do not strongly suggest any immediate consequences of genome duplication for morphological evolution in early crown-group teleosts, we anticipate that future developments could help to better constrain these patterns. Inferences about rate heterogeneity can vary substantially within our pool of sampled topologies. A more robustly constrained hypothesis of relationships and times of evolutionary divergence among early neopterygians, therefore, represents a first step to more decisive detection of shifts in the nature of morphological evolution across this major radiation, the early history of which has received substantially less systematic attention than more species-poor groups like birds (40–42) and mammals (43–45). Divergence estimates for paralogues (10) provide a loose constraint for the timing of the teleost-specific genome duplication (Table S2), but cannot identify which members of the teleost stem lineage were polyploid. There is the possibility that a paleogenomic approach using the size of osteocyte lacunae to estimate genome sizes in extinct lineages could more precisely pinpoint the phylogenetic position of the genome duplication. In addition to permitting more finely defined contrasts than those applied here, estimation of genome size in fossil teleosts would allow direct investigation of rates of genome reduction following duplication (46).

Methods

Phenotypic Datasets. Phenotypic data were collected from photographs of museum specimens of neopterygians ranging in age from Wuchiapingian (late Permian, ∼260 Ma) to Albian (Early Cretaceous, ∼100 Ma), supplemented by high-quality images in the primary literature. The phenotypic datasets represent a combined total of 1,170 unique specimen images assigned to 483 species.

Our phenotypic datasets are divided into those describing variation in size and those capturing differences in shape. Because of varying degrees of completeness between fossil specimens, these datasets do not contain identical sets of taxa, although the degree of overlap between any two datasets is high. We obtained SL for 949 specimens assigned to 468 species, and CS (based on our constellation of landmarks for geometric morphometic analyses; see below) for 626 individuals assigned to 382 species. Size values within species were averaged, and all resultant species sizes were log-transformed before analysis (SL in Dataset S1; CS in Dataset S2).

We used a 2D geometric morphometric approach using a constellation of 25 landmarks to quantify shape variation (Fig. S6) using the software package tpsDig2 (47). The shape dataset consisted of 774 specimen images assigned to 398 species (Fig. 2*A* and Figs. S1 and S2). Both fixed landmarks and semi-landmarks were used to capture overall body shape and fin position, based on schemes applied previously to living (48) and fossil (31) fishes. Landmarked specimen data were aligned using orthogonal generalized Procrustes superimposition analysis (GPA), permitting shape values to be averaged within species. The averaged species data were then aligned with GPA and subject to a relative warp (RW) analysis in tpsRelw v1.54 (49). Of the four axes that described >5% of overall variation, the first three (RW1 to 3) captured clear biological features (rather than differences potentially related to preservation) and formed the basis of all shape analyses in Dataset S3. RW1 to 3 explained 42.53%, 21.43%, and 13.52% of the variation respectively. The *Supporting Information* details anatomical correlates of these axes (Table S3).

Tree Construction.

Summarizing existing topologies. Because there is no densely sampled phylogenetic hypothesis available for early fossil neopterygians, we adopted a "supertree" approach to produce a sample of trees for comparative analyses. Topologies were constructed using matrix representation with parsimony (MRP), drawing upon 120 source topologies (Dataset S6) to summarize relationships and capture phylogenetic uncertainty among 671 (mostly Mesozoic, but some living) neopterygian species. We adopted MRP because many trees lacked the data matrix used to create them (e.g., ref. 50) or were hand-constructed (e.g., ref. 51). All junior synonyms present in the source trees were replaced by their correct senior synonyms to ensure all taxa were correctly represented in the source topologies. We included a "seed" (i.e., backbone) tree built with reliable taxonomic information that contained every species (52). This process permitted inclusion of large numbers of taxonomically assigned species that have not otherwise been included in a formal phylogenetic analysis. Use of taxonomic information is further vindicated given that paleontological trees derived from taxonomies can deliver comparable results using comparative methods to those derived from cladistic phylogenies (53). The taxonomy seed tree was also treated as a constraint on the supertree analysis to ensure that strongly corroborated placements could not be overruled by the source trees (e.g., holostean monophyly, which is well-supported by modern molecular and morphological analyses, but not recovered by older studies). We purposely left the seed tree poorly resolved to allow source trees to dictate relationships where there is genuine uncertainty. A second constraint was applied to ensure that the relationships between major living teleost clades matched those arising from recent molecular phylogenetic studies (54). To implement both constraints, the nodes (expressed as characters in the MRP matrix) defining the relationships of the taxonomic and molecular trees were upweighted to 1,000 (the maximum) in our MRP data matrix.

Safe taxonomic reduction (55) was performed upon the MRP matrix using Claddis v0.1 (56) before phylogenetic analysis in TNT v1.1 (57). Twenty replicates of new technology searches were performed, saving 1,000 trees each time, with each replicate starting from a random tree. Ten-thousand MPTs were then obtained from these saved replicates, followed by a final search for remaining MPTs with tree bisection and reconnection, delivering a total of 10,500 MPTs. Taxa removed by safe taxonomic reduction were reinserted into every MPT, either into their sole possible position or, if multiple positions were equally likely, one was chosen at random. One-hundred trees were then selected at random from this pool for downstream comparative analyses, with any remaining polytomies randomly resolved using the "multi2di" function in APE (58).

Timescaling topologies. Living species were pruned from our 100 supertrees before timescaling using the timePaleoPhy function of the paleotree package in R (59). As illustrated in Fig. 2*B*, we adopted two end-member timescaling procedures: (*i*) a paleontological timescale to reflect divergence times based solely upon fossils, and (*ii*) a molecular timescale to reflect some of the oldest neopterygian divergence estimates in recent clock studies.

The tip age of every species was randomized (with a uniform distribution) between its oldest potential age (i.e., the oldest lower boundary age of all of the deposits where the species is found) and its oldest reliable minimum age (i.e., the oldest upper boundary age of all of the deposits where the species is found). This randomization procedure was carried out for each tree individually. We used the node-dating procedure of Hedman (60) to provide an estimate for the neopterygian crown node (i.e., the root of the supertree) as the first step in timescaling topologies under our paleontological approach. This approach delivered a mean estimate of 280 Ma for the neopterygian crown, which we set as the root age. For our molecular timescaling procedure, we constrained the age of three nodes based upon the clock estimates of Near et al. (54) (crown Neopterygii: 361.2 Ma; crown Holostei: 271.9 Ma; crown Teleostei: 307.1 Ma). For both paleontolgical and molecular timescaling, we used the "equal" method implemented in timePaleoPhy.

Quantifying Phenotypic Rates. Size rates were quantified using the Bayesian approach of Eastman et al. (61) implemented over 1,000,000 generations, discarding the first 250,000 generations as burn-in. Randomization tests (implemented via the "compare.rates" function of the auteur package in R v2.15.3) provided a two-way *P* value ($\alpha = 0.05$) to test for differences between neopterygian partitions. The Adams (62) method permits estimation of evolutionary rate on multivariate data, and was applied to our shape dataset. Simulation of each supertree topology under a null model of equal rates was used to generate a null distribution of rate ratios for each of our five comparisons. The observed rate ratio for a given comparison can then be compared with the simulated distribution of rate ratios to derive a two-way *P* value to test for differences between two sets of taxa ($\alpha = 0.05$).

Quantifying Phenotypic Innovation. Blomberg's *K* quantifies whether closely related taxa in a clade of interest are either more ($K > 1$) or less similar ($K < 1$) with respect to a trait value than expected under a Brownian motion model of evolution ($K = 1$). Therefore, a more innovative clade (i.e., one that is efficient at exploring new regions of trait space) should have a larger *K* value than a less innovative clade. This is because the lineages of an innovative clade should spread apart from one another, occupying different regions of trait space so that more closely related taxa appear more similar in trait value than more distantly related taxa. A less-innovative clade should express lower *K* values, as multiple lineages overlap and re-explore similar phenotypes, eroding phylogenetic signal. Variation in rate of phenotypic change between focal groups can, however, distort this simple relationship. For example, in a clade that shows high rates of phenotypic change relative to its boundaries in

phenotypic space, *K* can be degraded (33, 34). *K* values are interpreted to reflect innovation in the main text with appropriate caveats given potential differences in rate, with all comparisons further contextualized in Table S1.

ACKNOWLEDGMENTS. We thank L. Sallan, R. Benson, R. Close, and L. Soul for useful discussion; and the collections managers, curators, and research scientists at numerous institutions for their assistance and access to fossil specimens. This work was supported by a Palaeontological Association Whittington Award and a Natural Environment Research Council Cohort grant (to J.T.C.); Australian Research Council Grant DE140101879 (to G.T.L.); Philip Leverhulme Prize PLP 2012-130 (to M.F.); Natural Environment Research Council Award NE/I005536/1 (to M.F.); and the John Fell Fund (M.F.).

1. Grande L (2010) An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holostei. (American Society of Ichthyologists and Herpetologists, Copeia, Lawrence, KS) 10(2A).
2. Darwin C (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (John Murray, London), 1st Ed.
3. Pough FH, Heiser JB, McFarland WN (1996) *Vertebrate Life*, 4th ed. (Prentice Hall, Upper Saddle River, NJ).
4. Colbert EH (1969) *Evolution of Vertebrates* (Wiley, New York), 2nd Ed.
5. Motta PJ (1984) Mechanics and functions of jaw protrusion in teleost fishes—A review. *Copeia* 1984(1):1–18.
6. Collazo A, Bolker JA, Keller R (1994) A phylogenetic perspective on teleost gastrulation. *Am Nat* 144(1):133–152.
7. Collazo A (1996) Evolutionary correlations between early development and life history in plethodontid salamanders and teleost fishes. *Am Zool* 36(2):116–131.
8. Hoegg S, Brinkmann H, Taylor JS, Meyer A (2004) Phylogenetic timing of the fish-specific genome duplication correlates with the diversification of teleost fish. *J Mol Evol* 59(2):190–203.
9. Crow KD, Stadler PF, Lynch VJ, Amemiya C, Wagner GP (2006) The "fish-specific" Hox cluster duplication is coincident with the origin of teleosts. *Mol Biol Evol* 23(1):121–136.
10. Hurley IA, et al. (2007) A new time-scale for ray-finned fish evolution. *Proc Biol Sci* 274(1609):489–498.
11. Wittbrodt J, Meyer A, Schartl M (1998) More genes in fish? *BioEssays* 20(6):511–515.
12. Meyer A, Van de Peer Y (2005) From 2R to 3R: Evidence for a fish-specific genome duplication (FSGD). *BioEssays* 27(9):937–945.
13. Glasauer SMK, Neuhauss SCF (2014) Whole-genome duplication in teleost fishes and its evolutionary consequences. *Mol Genet Genomics* 289(6):1045–1060.
14. Freeling M, Thomas BC (2006) Gene-balanced duplications, like tetraploidy, provide predictable drive to increase morphological complexity. *Genome Res* 16(7):805–814.
15. Van de Peer Y, Maere S, Meyer A (2009) The evolutionary significance of ancient genome duplications. *Nat Rev Genet* 10(10):725–732.
16. Postlethwait J, Amores A, Cresko W, Singer A, Yan YL (2004) Subfunction partitioning, the teleost radiation and the annotation of the human genome. *Trends Genet* 20(10):481–490.
17. Rabosky DL, et al. (2013) Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. *Nat Commun* 4:1958.
18. Kner R (1866) *Betrachtungen über die Ganoiden, als Natürliche Ordnung* (Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Wien), pp 519–536.
19. Woodward AS (1901) *Catalogue of the Fossil Fishes in the British Museum (Natural History). Part IV. Trustees of the British Museum* (Natural History, London).
20. Thomson KS (1977) The pattern of diversification among fishes. *Developments in Palaeontology and Stratigraphy*, ed Hallam A (Elsevier, Amsterdam), pp 377–404.
21. Romer AS (1966) *Vertebrate Paleontology* (Univ of Chicago Press, Chicago), 3rd Ed.
22. Arratia G (1997) Basal teleosts and teleostean phylogeny. *Palaeo Ichthyologica* 7:5–168.
23. Guinot G, Cavin L (2015) 'Fish' (Actinopterygii and Elasmobranchii) diversification patterns through deep time. *Biol Rev Camb Philos Soc* 25:2314–2318.
24. Romano C, et al. (2016) Permian-Triassic Osteichthyes (bony fishes): Diversity dynamics and body size evolution. *Biol Rev Camb Philos Soc* 91(1):106–147.
25. Patterson C (1977) The contributions of paleotnology to teleostean phylogeny. *Major Patterns in Vertebrate Evolution*, eds Hecht MK, Goody PC, Hecht BM (Plenum, New York), pp 579–643.
26. Santini F, Harmon LJ, Carnevale G, Alfaro ME (2009) Did genome duplication drive the origin of teleosts? A comparative study of diversification in ray-finned fishes. *BMC Evol Biol* 9:194.
27. McCune AR, Schaeffer B (1986) Triassic and Jurassic fishes patterns of diversity. *The Beginning of the Age of Dinosaurs: Faunal Change across the Triassic-Jurassic Boundary; Symposium Held in Conjunction with the 44th Annual Meeting of the Society of Vertebrate Paleontology, Berkeley, California, USA, October 31, 1984*, ed Padian K (Cambridge Univ Press, Cambridge, UK), pp 171–182.
28. Friedman M, et al. (2010) 100-million-year dynasty of giant planktivorous bony fishes in the Mesozoic seas. *Science* 327(5968):990–993.
29. Poyato-Ariza FJ, Wenz S (2002) A new insight into pycnodontiform fishes. *Geodiversitas* 24(1):139–248.
30. Forey PL, Fortey RA, Kenrick P, Smith AB (2004) Taxonomy and fossils: A critical appraisal. *Philos Trans R Soc Lond B Biol Sci* 359(1444):639–653.
31. Friedman M (2010) Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous extinction. *Proc Biol Sci* 277(1688):1675–1683.
32. Alfaro ME, et al. (2009) Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc Natl Acad Sci USA* 106(32):13410–13414.
33. Revell LJ, Harmon LJ, Collar DC (2008) Phylogenetic signal, evolutionary process, and rate. *Syst Biol* 57(4):591–601.
34. Hopkins MJ, Smith AB (2015) Dynamic evolutionary change in post-Paleozoic echinoids and the importance of scale when interpreting changes in rates of evolution. *Proc Natl Acad Sci USA* 112(12):3758–3763.
35. Near TJ, et al. (2014) Boom and bust: Ancient and recent diversification in bichirs (Polypteridae: Actinopterygii), a relictual lineage of ray-finned fishes. *Evolution* 68(4):1014–1026.
36. Grande L, Bemis WE (1998) A comprehensive phylogenetic study of Amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. *Society of Vertebrate Paleontology Memoir,* 4:1–690.
37. Zhan SH, Glick L, Tsigenopoulos CS, Otto SP, Mayrose I (2014) Comparative analysis reveals that polyploidy does not decelerate diversification in fish. *J Evol Biol* 27(2):391–403.
38. Alexandrou MA, Swartz BA, Matzke NJ, Oakley TH (2013) Genome duplication and multiple evolutionary origins of complex migratory behavior in Salmonidae. *Mol Phylogenet Evol* 69(3):514–523.
39. Macqueen DJ, Johnston IA (2014) A well-constrained estimate for the timing of the salmonid whole genome duplication reveals major decoupling from species diversification. *Proc Biol Sci* 281(1778):20132881.
40. Fountaine TMR, Benton MJ, Dyke GJ, Nudds RL (2005) The quality of the fossil record of Mesozoic birds. *Proc Biol Sci* 272(1560):289–294.
41. O'Connor JK, Zhou Z (2013) A redescription of *Chaoyangia beishanensis* (Aves) and a comprehensive phylogeny of Mesozoic birds. *J Syst Palaeontology* 11(7):889–906.
42. Lee MSY, Worthy TH (2012) Likelihood reinstates Archaeopteryx as a primitive bird. *Biol Lett* 8(2):299–303.
43. Luo Z-X (2007) Transformation and diversification in early mammal evolution. *Nature* 450(7172):1011–1019.
44. Zheng X, Bi S, Wang X, Meng J (2013) A new arboreal haramiyid shows the diversity of crown mammals in the Jurassic period. *Nature* 500(7461):199–202.
45. Luo Z-X, Gatesy SM, Jenkins FA, Jr, Amaral WW, Shubin NH (2015) Mandibular and dental characteristics of Late Triassic mammaliaform Haramiyavia and their ramifications for basal mammal evolution. *Proc Natl Acad Sci USA* 112(51):E7101–E7109.
46. Inoue J, Sato Y, Sinclair R, Tsukamoto K, Nishida M (2015) Rapid genome reshaping by multiple-gene loss after whole-genome duplication in teleost fish suggested by mathematical modeling. *Proc Natl Acad Sci USA* 112(48):14918–14923.
47. Rohlf FJ (2013) TPSdig2, v.2.17 (Department of Ecology and Evolution, SUNY at Stony Brook, Stony Brook, NY).
48. Kerschbaumer M, Sturmbauer C (2011) The utility of geometric morphometrics to elucidate pathways of cichlid fish evolution. *Int J Evol Biol* 2011:290245.
49. Rohlf FJ (2014) tpsRelw, v1.54 (Department of Ecology and Evolution, SUNY at Stony Brook, Stony Brook, NY).
50. Lambers PH (1995) The monophyly of the Caturidae (Pisces, Actinopterygii) and the phylogeny of the Halecomorphi. *Geobios* 28:201–203.
51. Taverne L (2011) Osteology and phylogenetic relationships of Steurbautichthys ("Pholidophophorus") aequatorialis gen. nov (Teleostei, "Holidophoriformes") from the Middle Jurassic of Kisangani, Democratic Republic of Congo. Osteologie et relations phylogenetiques de Steurbautichthys ("Pholidophophorus") aequatorialis gen. nov. (Teleostei, "Pholidophoriformes") du Jurassique moyen de Kisangani, en Republique Democratique du Congo. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Sciences de la Terre* 81:129–173.
52. Bininda-Emonds ORP, Sanderson MJ (2001) Assessment of the accuracy of matrix representation with parsimony analysis supertree construction. *Syst Biol* 50(4):565–579.
53. Soul LC, Friedman M (2015) Taxonomy and phylogeny can yield comparable results in comparative paleontological analyses. *Syst Biol* 64(4):608–620.
54. Near TJ, et al. (2012) Resolution of ray-finned fish phylogeny and timing of diversification. *Proc Natl Acad Sci USA* 109(34):13698–13703.
55. Wilkinson M (1995) Coping with abundant missing entries in phylogenetic inference using parsimony. *Syst Biol* 44(4):501–514.
56. Lloyd GT (2016) Estimating morphological diversity and tempo with discrete character-taxon matrices: Implementation, challenges, progress, and future directions. *Biol J Linn Soc Lond* 118:131–151.
57. Goloboff PA, Farris JS, Nixon KC (2008) TNT, a free program for phylogenetic analysis. *Cladistics* 24(5):774–786.
58. Paradis E, Claude J, Strimmer K (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* 20(2):289–290.
59. Bapst DW (2012) paleotree: An R package for paleontological and phylogenetic analyses of evolution. *Methods Ecol Evol* 3(5):803–807.
60. Hedman MM (2010) Constraints on clade ages from fossil outgroups. *Paleobiology* 36(1):16–31.
61. Eastman JM, Alfaro ME, Joyce P, Hipp AL, Harmon LJ (2011) A novel comparative method for identifying shifts in the rate of character evolution on trees. *Evolution* 65(12):3578–3589.
62. Adams DC (2014) Quantifying and comparing phylogenetic evolutionary rates for shape and other high-dimensional phenotypic data. *Syst Biol* 63(2):166–177.
63. Bookstein FL (1986) Size and shape spaces for landmark data in two dimensions. *Stat Sci* 1:238–242.
64. Edgecombe GD, Legg DA (2014) Origins and early evoloution of arthropods. *Palaeontology* 57(3):457–468.
65. Clarke JT, Warnock RCM, Donoghue PCJ (2011) Establishing a time-scale for plant evolution. *New Phytol* 192(1):266–301.
66. Dornburg A, Townsend JP, Friedman M, Near TJ (2014) Phylogenetic informativeness reconciles ray-finned fish molecular divergence times. *BMC Evol Biol* 14:169.
67. Bapst DW (2013) A stochastic rate-calibrated method for time-scaling phylogenies of fossil taxa. *Methods Ecol Evol* 4(8):724–733.

Supporting Information

Clarke et al. 10.1073/pnas.1607237113

Major Axes of Shape Variation and Their Anatomical Correlates

All relative warp axes that individually account for >5% of the variation across the species sampled are displayed in Table S3. Morphospaces derived from the first three axes, containing all 398 Mesozoic neopterygian species in our shape dataset, are presented in Fig. S1. Images of sampled fossil specimens are also included in Fig. S1 to illustrate the anatomical correlates of shape axes. The positions of major neopterygian clades in morphospace are indicated by different colors in Fig. S2. Major teleost clades are presented in Fig. S2*A* and major holostean clades in Fig. S2*B*.

RW1 captures 42.53% of the variance, reflecting changes from slender-bodied taxa to deep-bodied taxa (Fig. S1 and Table S3). Highly positive scores on RW1 are dominated by Pycnodontiformes (Fig. S2*A*). The most negative scores on RW1 (highly slender bodies) belong to Aspidorhynchiformes (Fig. S2*A*).

RW2, representing 21.43% of variance, captures the position of the dorsal fin relative to the anal fin (Fig. S1 and Table S3). Those taxa with highly positive scores have dorsal fins that insert far anterior to the anal fin. Highly positive scores are dominated by the Macrosemiiformes (a clade of stem gars; Fig. S2*B*), although numerous crown teleosts, stem teleosts, and halecomorphs also share this region (Fig. S2). Highly negative scores characterize taxa whose dorsal fin inserts more posteriorly than the anal fin, the most extreme example of which is the pachycormid *Euthynotus incognitus*. Other Pachycormiformes, as well as Aspidorhynchiformes, Ichthyodectiformes, "pholidophoriforms," and Osteoglossomorpha possess highly negative scores (Fig. S2).

RW3 explains 13.52% of variance and captures variation in the length of the dorsal fin base (Fig. S1 and Table S3). Highly positive scores characterize taxa with small dorsal fin bases relative to the length of the dorsal body surface, and include Ellimichthyiforms (Clupeomorpha); some pholidophoriforms and a few Ginglymodi and Halecomorphi (Fig. S2). The most negative scores (less than –0.2) are restricted to Macrosemiiformes (Fig. S2*B*).

RW4, representing only 6.10% of the variation, appears to summarize ventral-dorsal flexion, commonly exhibited by some fish after death. Although care was taken to remove highly distorted taxa from the dataset, some expressing mild degrees of bending clearly remain, and appear to inform this axis. Therefore, we do not analyze variation in RW4, and instead focus upon RW1 to 3.

SL vs. CS Comparisons

CS offers a measure of size independent of shape (63), whereas SL does not. Therefore, we may expect to observe some differences in the analytical results derived from these two types of dataset. When the SL dataset is pruned to match the CS dataset for taxon sampling, it yields near identical results regarding evolutionary rate regardless of timescale choice (Fig. S3). The same is also true of innovation, where K distributions in taxonomic comparisons are very similar for both the pruned SL and CS datasets (Fig. S4). The larger SL dataset produces highly similar rate and innovation results compared with the CS and pruned SL dataset (Figs. S3 and S4). The only minor differences observed occur exclusively in rate, where the larger SL dataset recovers significantly higher rates in crown and total group teleosts in a higher proportion of trees than the CS and pruned SL datasets, regardless of timescale choice (Fig. S3). However, these small differences have almost no influence on our interpretations, because there is only a single instance where the increased frequency of high rate results changes the overall conclusion for a comparison: the crown teleost vs. stem teleost comparison on molecular timescales. Here, the larger SL dataset delivers a majority of trees where crown teleosts possess significantly higher rates than stem teleosts, whereas the CS and pruned SL datasets find this result in a large minority (Fig. S3).

Overall, these results suggest that choice of size metric is relatively unimportant for our dataset, and that the overall size and taxonomic samplings of the dataset are more likely to influence subsequent results, despite those factors having a relatively small influence here. Nevertheless, choice of metric may be important for other datasets (e.g., different groups of organisms or datasets of other biological/nonbiological structures), because it is possible to envisage scenarios where the choice of size metric would matter. For example, it is possible that two fishes, identical in SL, could differ greatly in CS if their shapes differed greatly, such as between an extremely deep-bodied taxon (e.g., Opah) and a highly shallow-bodied taxon (e.g., needlefish). This discrepancy could present downstream effects on analyses if a hypothetical "clade A" contained deep-bodied taxa that regularly evolved into shallow-bodied taxa of similar SL (and vice versa), whereas "clade B" consisted solely of similar sized deep-bodied taxa. As a result, these two clades may show similar rates of evolution using SL but different rates using CS (because clade A would be expected to possess much higher rates of CS change). In our own data, the fact that SL and CS datasets deliver near identical results suggests such transitions are rare enough not to create such issues. This theory matches what we expect given the topology of our tree, where organisms that contrast the most in shape, such as highly deep-bodied (e.g., Pycnodontiformes) and shallow-bodied taxa (e.g., Aspidorhychiformes), form distinct, distantly related clades, meaning rates will rarely be calculated upon transitions between these distinct shape clusters.

The Importance of Timescale and Topology

Examination of Fig. 3 and Figs. S4 and S5 clearly demonstrates the ability for evolutionary timescale and topology to alter specific rate and innovation analyses. For example, timescale can dictate whether crown teleosts show higher size rates than stem teleosts in a minority or a majority of trees (Fig. 3*C*), whereas topology can dictate whether holosteans or teleosts are more likely to possess higher rates of shape evolution (Fig. 3*A*). Furthermore, the observation that molecular and paleontological timescales can deliver differing results has considerable implications for paleontology because the vast majority of analyses in the field are, often by necessity, conducted solely upon paleontological timescales. Therefore, where possible (when crown nodes are present in paleontological trees to which various molecular estimates could be applied) it should prove enlightening to incorporate the full range of known timescale uncertainty, especially in cases where large mismatches still persist between clock and rock estimates, such as for arthropods (e.g., ref. 64) or land plants (e.g., ref. 65). Similarly, paleontological analyses that do not contain crown nodes may benefit from the introduction of additional timescale uncertainty, to discover the temporal limits of their findings.

Our analyses also provide insight into the relative importance of timescale versus topology for understanding Mesozoic neopterygian evolution. Although neopterygian timescales have estimated the origin of crown teleosts to range anywhere from the Carboniferous to the Lower Jurassic (54, 66), we demonstrate that even the most dramatic timescale differences under our current methodology have little bearing upon our main findings.

Instead, the pool of sampled topologies typically set the range of outcomes for a given analysis (Fig. 3 and Fig. S5), while changes to the timescale subtly adjust the proportions of each potential outcome, rather than bringing about conclusive outcomes in favor of one or another hypothesis (Fig. 3 and Fig. S5). These observations suggest refinement of the fossil neopterygian phylogentic framework could be more important to Mesozoic-specific questions than additional revisions to the neontological neopterygian timescale. However, this does not undermine the importance of timescale (indeed, changes to the topology themselves alter the timescale by altering branch durations), but simply highlights that reductions in uncertainty will be primarily delivered by improvements to paleontological topology and timescale, obtainable via more systematic studies of fishes and the creation of paleontological databases that will permit use of probabilistic timescaling approaches (67).

Estimating the Position of the Genome Duplication upon the Teleost Stem

Hurley et al. (10) performed a molecular clock analysis on the basis of four paralogous genes. This approach allowed them to date not only the major divergences between taxa, but the divergence between the paralogs themselves, providing an estimate for the timing of the genome duplication event. Hurley et al. (10) performed clock analyses upon both a halecostome and a holostean topology, and although the holostean topology is preferable in the light of recent analyses (e.g., refs. 1 and 54); see also figure 2 in ref. 10), both topologies still provide an estimate for the origin of the teleost stem lineage. Different paralogue groups (a and b) also provide two independent estimates for the age of the teleost crown (an estimate from "a" paralogues and a separate estimate derived only from "b" paralogues); we averaged these to provide a single crown estimate. Finally, a clock estimate between the pairs of paralogues (a vs b) delivered an absolute age estimate for the genome duplication event. Altogether, these analyses delivered both the total duration of the teleost stem, and an absolute estimate for the genome duplication event. For three analyses (tables 3–5 in the supplement of ref. 10) it was therefore possible to calculate the relative timing of the genome duplication on the teleost stem, providing estimates of 62%, 54%, and 64%, respectively, yielding an average estimate of 60% (Table S2). Therefore, current estimates suggest that the duplication occurred just over half way up the teleost stem lineage.

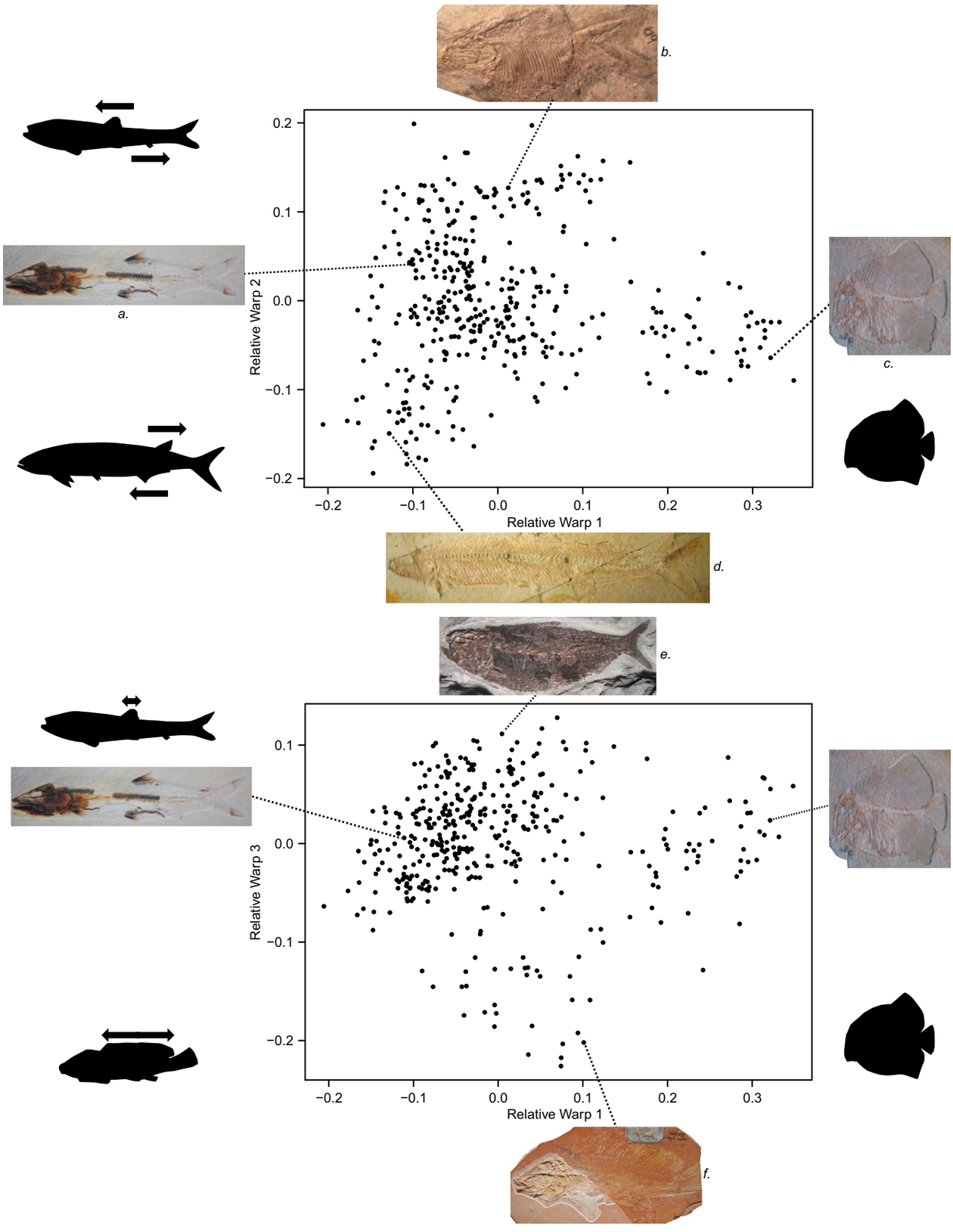

Fig. S1. Morphospace of 398 Permian–Early Cretaceous Neopterygii. Three major axes of shape variation are presented. Silhouettes and accompanying arrows illustrate the main anatomical correlates of these principal axes, as described in Table S3. Actual fossil specimens represented in the dataset are also displayed to visualize the extremities of morphospace axes. Fossil taxa as follows: (*a*) *Bavarichthys incognitus*; (*b*) *Ellimmichthys longicostatus*; (*c*) *Turbomesodon relegans*; (*d*) *Allothrissops salmoneus*; (*e*) *Pholidophorus germanicus*; (*f*) *Macrosemius fourneti*.

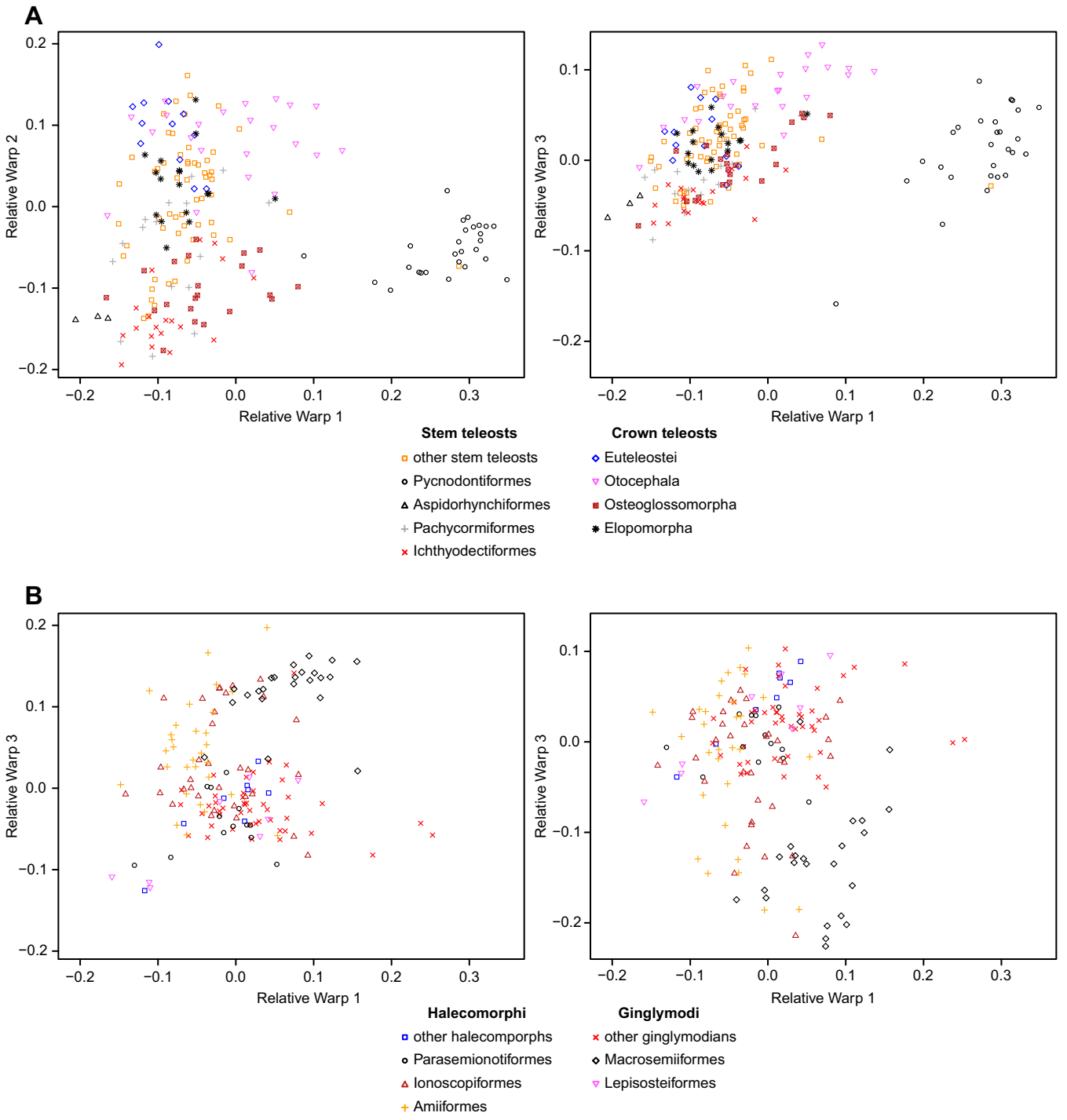

Fig. S2. Morphospace of 398 Permian–Early Cretaceous Neopterygii, illustrating the major clades of (*A*) teleosts and (*B*) holosteans.

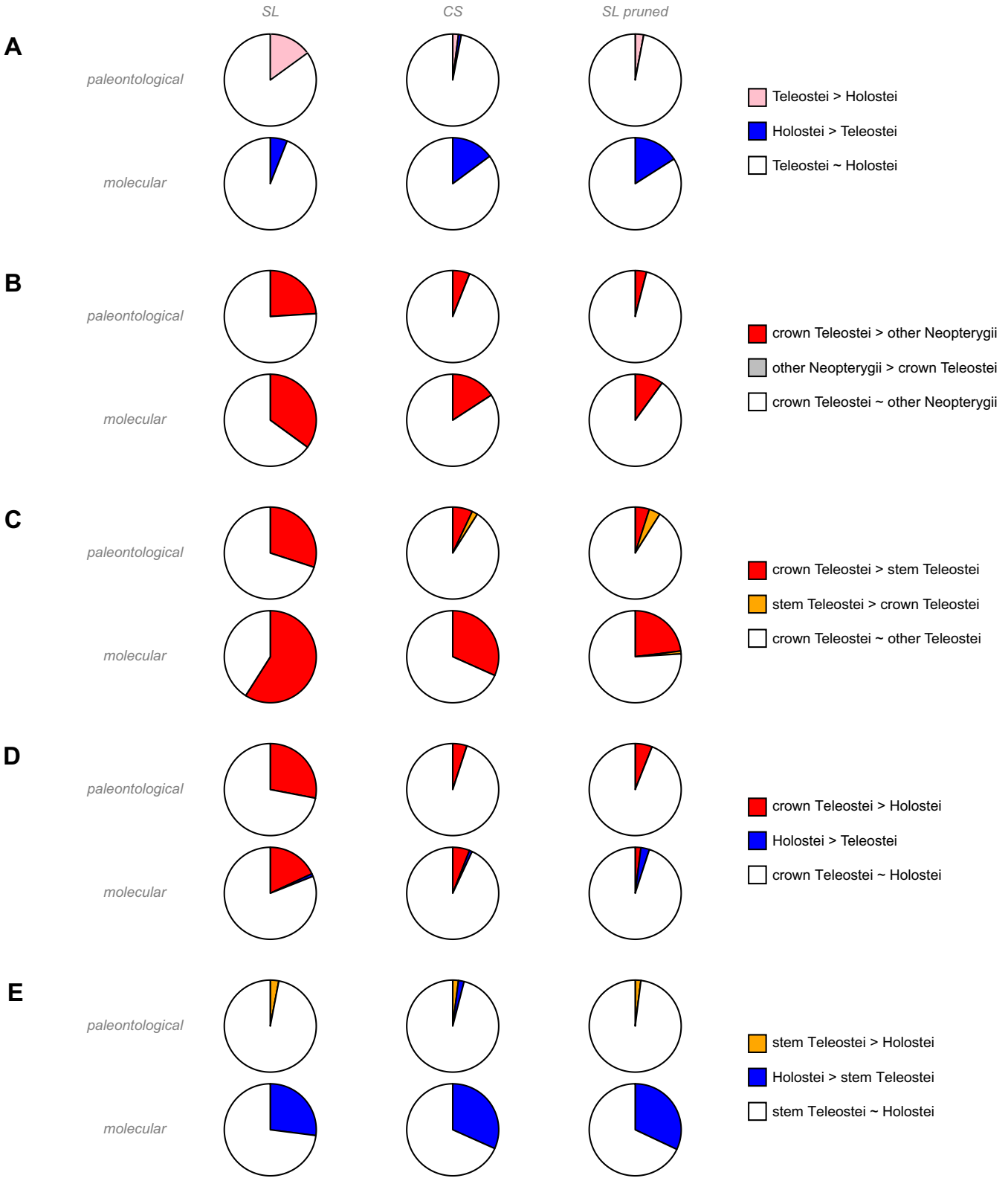

Fig. S3. Comparisons of size rates between (*A*) holosteans and teleosts, (*B*) crown teleosts and all other neopterygians, (*C*) crown teleosts and stem teleosts, (*D*) crown teleosts and holosteans, and (*E*) stem teleosts and holosteans. Comparisons were made using the full-size SL dataset, a CS dataset, and a smaller SL dataset pruned to exactly match the taxon sampling of the CS dataset. Identical taxon sampling leads the CS and pruned SL datasets to yield near identical results. Although the larger SL dataset results often differ slightly, the overall conclusion from each pairwise comparison (i.e., which outcome is the most likely in an overall majority of trees) is identical in all but one comparison (*E*, under molecular timescales).

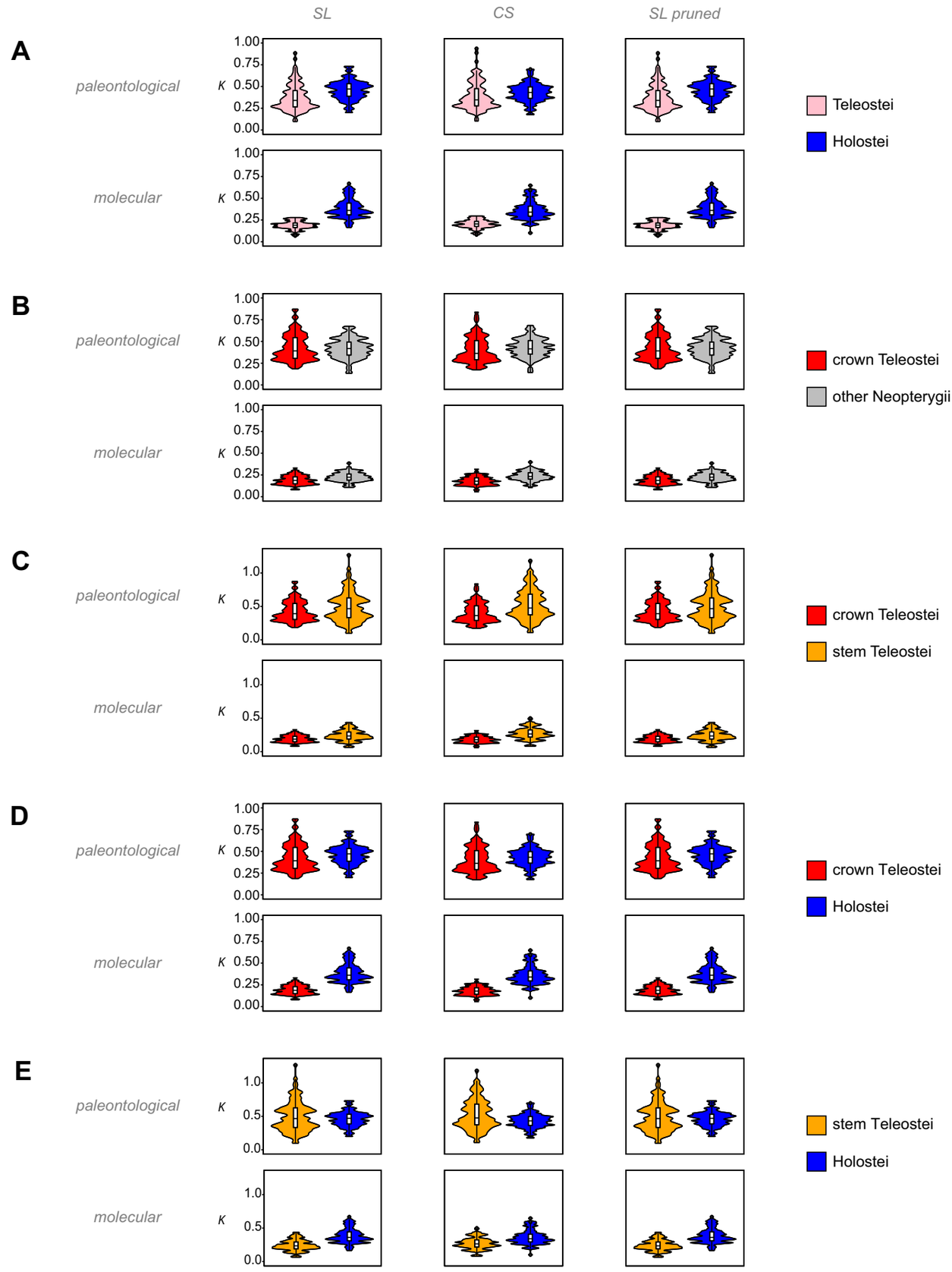

Fig. S4. Comparisons of size innovation between (*A*) holosteans and teleosts, (*B*) crown teleosts and all other neopterygians, (*C*) crown teleosts and stem teleosts, (*D*) crown teleosts and holosteans, and (*E*) stem teleosts and holosteans. Comparisons were made using the full-size SL dataset, a CS dataset, and a smaller SL dataset pruned to exactly match the taxon sampling of the CS dataset. Comparisons of size innovation are presented for *K* value distributions of the three datasets resemble each other closely.

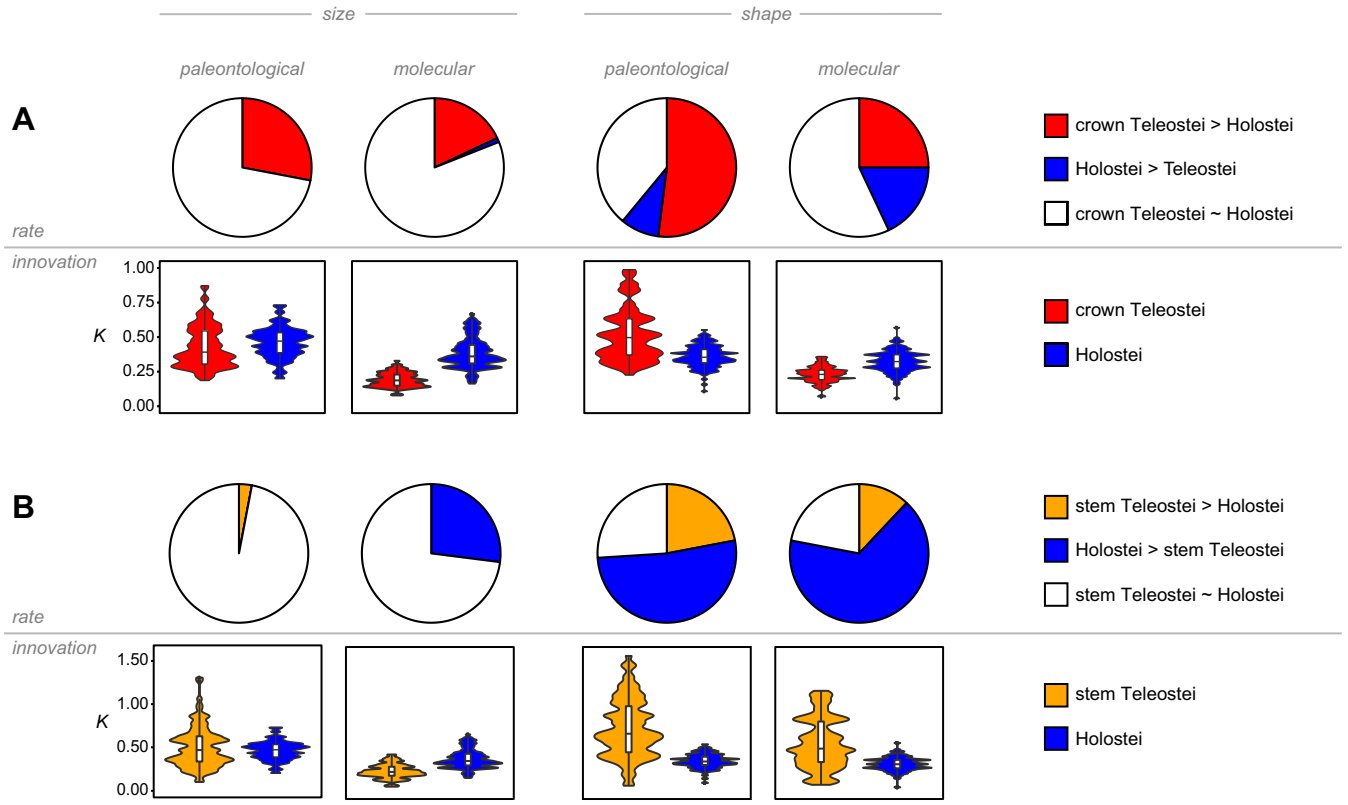

Fig. S5. Comparisons of phenotypic rate and innovation between (*A*) holosteans and crown teleosts; (*B*) holosteans and stem teleosts. Rate results are conveyed with pie charts, where the proportion of sampled supertrees in support of significantly higher rates (as determined from two-way *P* values with $\alpha = 0.05$) in a given neopterygian partition are color-coded to match that partition; white sections correspond to supertrees indicating no significant rate differences. Violin plots capturing the distribution of *K* values obtained from 100 sampled supertrees allow for investigation of innovation. Higher *K* values suggest greater phylogenetic signal, and correspondingly, greater innovation, in contrast to the iterative "rediscovery" of similar phenotypes (*Methods*). *K* interpretations are contextualized with the rate in Table S1.

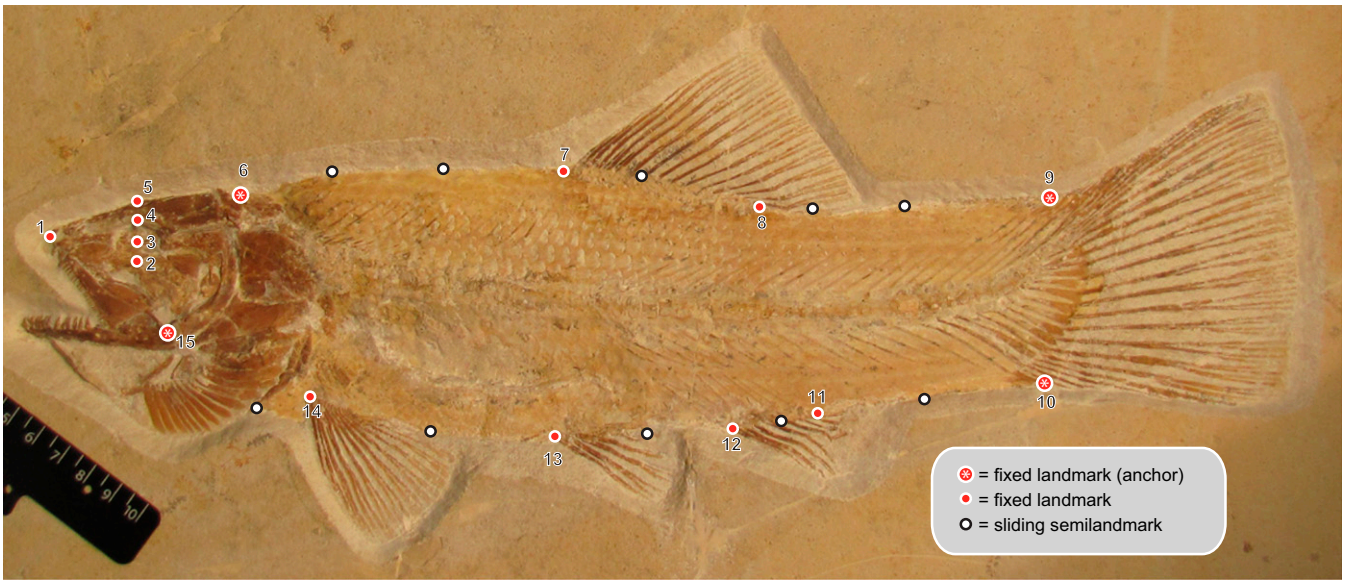

Fig. S6. Landmark scheme used to quantify shape. Fixed landmarks are marked by red circles; semilandmarks are marked by black circles with white fill. Red circles containing a white asterisk act as anchor points for the semilandmarks in-between. Fixed landmarks document: 1) anterior tip of the upper jaw (premaxilla); 2) the central, ventral surface of the orbit; 3) the center of the orbit; 4) the central, dorsal surface of the orbit; 5) the dorsal surface of the skull immediately above the eye; 6) postero-dorsal tip of braincase; 7) anterior insertion of dorsal fin; 8) posterior insertion of dorsal fin; 9) dorsal surface representation of the last vertebral centra; 10) ventral surface representation of the last vertebral centra; 11) posterior insertion of anal fin; 12, anterior insertion of anal fin; 13) anterior insertion of the pelvic fin; 14) anterior insertion of the pectoral fin; 15) lower jaw joint. Landmarked specimen is *Amiopsis lepidota* (SMNS 80251) from the Staatliches Museum für Naturkunde, Stuttgart.

Table S1. Innovation interpretations, based upon *K* value distributions, contextualized with rate

Figure	Comparison	Trait	Timescale	Rate result	K result	Innovation interpretation	Implication of rate on innovation interpretation
Fig. 3*A*	Teleosts vs. Holosteans	Size (SL)	Paleontological	Comparable rates in a majority of trees	*K* distributions overlap considerably	Comparable innovation	Comparable rates of size evolution increase our confidence that teleosts and holosteans are similarly innovative.
Fig. 3*A*	Teleosts vs. Holosteans	Size (SL)	Molecular	Comparable rates in a majority of trees	Holostean distribution higher	Holosteans more innovative	Comparable rates of size evolution increase our confidence that holosteans are more innovative than teleosts.
Fig. 3*A*	Teleosts vs. Holosteans	Shape (RW1-3)	Paleontological	Higher rates in holosteans or teleosts equally probable, although no significant difference is the most common outcome	*K* distributions overlap considerably	Comparable innovation	There is the potential for rate differences to influence the innovation interpretation. For instance, if holosteans truly possessed higher rates, this may have lowered their *K* values. However, it is equally likely that teleosts possessed higher rates, and so teleosts *K* values may have been lowered. Comparable rates were also the most likely outcome, increasing our confidence that that these two groups are similarly innovative. Rate may also have had no influence.
Fig. 3*A*	Teleosts vs. Holosteans	Shape (RW1-3)	Molecular	Higher holostean rates in a slim majority of trees	*K* distributions overlap considerably	Comparable innovation	There is the potential for rate differences to influence the innovation interpretation. For instance, high shape rates in holosteans may have lowered their *K* values, leading them to appear as comparable innovators to teleosts. Rate may also have had no influence.
Fig. 3*B*	Crown teleosts vs. all other neopterygians	Size (SL)	Paleontological	Comparable rates in a majority of trees	*K* distributions overlap considerably	Comparable innovation	Comparable rates of size evolution increase our confidence that crown teleosts and other neopterygians (stem teleosts + holosteans) are similarly innovative.
Fig. 3*B*	Crown teleosts vs. all other neopterygians	Size (SL)	Molecular	Comparable rates in a majority of trees	*K* distributions overlap considerably	Comparable innovation	Comparable rates of size evolution increase our confidence that crown teleosts and other neopterygians are similarly innovative.
Fig. 3*B*	Crown teleosts vs. all other neopterygians	Shape (RW1-3)	Paleontological	Higher crown teleost rates in a slim majority of trees	*K* distributions overlap considerably	Comparable innovation	There is the potential for rate differences to influence the innovation interpretation. For instance, the potential for high shape rates in crown teleosts may have lowered their *K* values, making them appear as comparable innovators to other neopterygians. Rate may also have had no influence.
Fig. 3*B*	Crown teleosts vs. all other neopterygians	Shape (RW1-3)	Molecular	No single outcome seen in a majority of trees. Higher crown teleost rates, and no significant difference in rate, are equally probable	Other neopterygian (stem teleost + holostean) distribution very marginally higher	Other neopterygians (stem teleosts + holosteans) very marginally more innovative	There is the potential for rate differences to influence the innovation interpretation. For instance, high shape rates in crown teleosts, a common outcome short of a majority, may have lowered their *K* values, making them appear marginally less innovative than other neopterygians. However, it is equally likely that there is either no difference in rate, or even that other neopterygians actually possessed higher rates. If either of the last two scenarios are correct, we could be even more confidence that our innovation interpretation is correct. Rate may also have had no influence.
Fig. 3*C*	Crown teleosts vs. stem teleosts	Size (SL)	Paleontological	Comparable rates in a majority of trees	*K* distributions overlap considerably	Comparable innovation	Comparable rates of evolution increase our confidence that crown and stem teleosts are similarly innovative.
Fig. 3*C*	Crown teleosts vs. stem teleosts	Size (SL)	Molecular	Higher crown teleost rates in a slim majority of trees	*K* distributions overlap considerably	Comparable innovation	There is the potential for rate differences to influence the innovation interpretation. For instance, if crown teleosts truly possessed higher rates, these may have lowered their *K* values to appear comparable to those of stem teleosts. Rate may also have had no influence.
Fig. 3*C*	Crown teleosts vs. stem teleosts	Shape (RW1-3)	Paleontological	Higher crown teleost rates in a slim majority of trees	*K* distributions overlap considerably	Comparable innovation	There is the potential for rate differences to influence the innovation interpretation. For instance, if crown teleosts truly possessed higher rates, these may have lowered their *K* values to appear comparable to those of stem teleosts. Rate may also have had no influence.
Fig. 3*C*	Crown teleosts vs. stem teleosts	Shape (RW1-3)	Molecular	Higher crown teleost rates in a slim majority of trees	Stem teleost distribution higher	Stem teleosts more innovative	There is the potential for rate differences to influence the innovation interpretation. For instance, high shape rates in crown teleosts may have lowered their *K* values, making them appear less innovative relative to stem teleosts. Rate may also have had no influence.

Table S1. Cont.

Figure	Comparison	Trait	Timescale	Rate result	K result	Innovation interpretation	Implication of rate on innovation interpretation
Fig. S5*A*	Crown teleosts vs. Holosteans	Size (SL)	Paleontological	Comparable rates in a majority of trees	*K* distributions overlap considerably	Comparable innovation	Comparable rates of size evolution increase our confidence that crown teleosts and holosteans are similarly innovative.
Fig. S5*A*	Crown teleosts vs. Holosteans	Size (SL)	Molecular	Comparable rates in a majority of trees	Holostean distribution higher	Holosteans more innovative	Comparable rates of size evolution increase our confidence that holosteans are more innovative than crown teleosts.
Fig. S5*A*	Crown teleosts vs. Holosteans	Shape (RW1-3)	Paleontological	Higher crown teleost rates in a slim majority of trees	Crown teleost distribution marginally higher	Crown teleosts marginally more innovative	Crown teleosts appear marginally more innovative despite displaying higher rates in a slim majority of trees (which we would expect might degrade *K*), granting even greater confidence that crown teleosts are marginally more innovative. Comparable rates, seen in a large minority of trees, would increase our confidence that crown teleosts were marginally more innovative.
Fig. S5*A*	Crown teleosts vs. Holosteans	Shape (RW1-3)	Molecular	Comparable rates in a majority of trees	Holostean distribution marginally higher	Holosteans marginally more innovative	Comparable rates of shape evolution increase our confidence that holosteans are marginally more innovative than crown teleosts.
Fig. S5*B*	Stem teleosts vs. Holosteans	Size (SL)	Paleontological	Comparable rates in a majority of trees	*K* distributions overlap considerably	Comparable innovation	Comparable rates of size evolution increase our confidence that stem teleosts and holosteans are similarly innovative.
Fig. S5*B*	Stem teleosts vs. Holosteans	Size (SL)	Molecular	Comparable rates in a majority of trees	Holostean distribution marginally higher	Holosteans marginally more innovative	Comparable rates of size evolution increase our confidence that holosteans are marginally more innovative than stem teleosts.
Fig. S5*B*	Stem teleosts vs. Holosteans	Shape (RW1-3)	Paleontological	Higher holostean rates in a slim majority of trees	Stem teleost distribution higher	Stem teleosts more innovative	There is the potential for rate differences to influence the innovation interpretation. For instance, high shape rates in holosteans may have lowered their *K* values, making them appear less innovative than stem teleosts. Rate may also have had no influence.
Fig. S5*B*	Stem teleosts vs. Holosteans	Shape (RW1-3)	Molecular	Higher holostean rates in a majority of trees	Stem teleost distribution higher	Stem teleosts more innovative	There is the potential for rate differences to influence the innovation interpretation. For instance, high shape rates in holosteans may have lowered their *K* values, making them appear less innovative than stem teleosts. Rate may also have had no influence.

Table S2. Relative time of the genome duplication event upon the teleost stem lineage

Hurley et al. (10) supplementary table no.	Stem teleost origin age (i.e., neopterygian or halecostomi age, Ma)	Stem teleost end age (i.e., crown teleost node age, Ma) 1	Stem teleost end age (i.e., crown teleost node age, Ma) 2	Average Stem teleost end age (i.e., crown teleost node age, Ma)	Duration of the teleost stem lineage (Ma)	Genome duplication estimate (absolute age, Ma)	Relative genome duplication timing between the start and end of the teleost stem (%)
Table 3	311	219	269	244	67	269	62.68
Table 4	317	222	250	236	81	273	54.32
Table 5	324	217	244	230.5	93.5	264	62.17
Average:							60.39

All dates required to calculate the relative timings of the genome duplication (far right column) are taken from the supplementary information from Hurley et al. (10).

Table S3. The first four axes derived from a relative warp analysis and their anatomical correlates

RW axis	% Variance	Anatomical correlate (positive scores)	Anatomical correlate (negative scores)
1	42.53	Slender body form	Deep body form
2	21.43	Dorsal fin inserts close to the head, anal fin inserts close to tail.	Dorsal fin inserts closer to the tail, anal fin inserts close to midlength of body.
3	13.52	Large dorsal fin base.	Short dorsal fin base.
4	6.10	Ventral-dorsal flexion (i.e., bend). Distal parts point downward.	Ventral-dorsal flexion (i.e., bend). Distal parts point upwards.

Other Supporting Information Files

Dataset S1 (CSV)
Dataset S2 (CSV)
Dataset S3 (CSV)
Dataset S4 (TXT)
Dataset S5 (TXT)
Dataset S6 (PDF)

Source trees used to construct the neopterygian supertrees

Our supertrees, provided as text files (change the .txt extension to .tre for use in phylogenetic packages) are available for both the paleontological timescaling approach (Dataset S4) and the molecular timescaling approach (Dataset S5). These supertrees were constructed on the basis of the source trees listed below:

Alvarado-Ortega 2004 Fig.10 (1)

Alvarado-Ortega & Brito 2011 (2)

Alvarado-Ortega & Espinosa-Arrubarrena 2008 Fig. 8 part 2 (3)

Alvarado-Ortega et al. 2008 Fig. 8a (4)

Arratia 2013 (5)

Arratia 1994 Fig. 9 (6)

Arratia 1995 Fig. 1b (7)

Arratia 1995 Fig. 1c (7)

Arratia 1996 Fig. 4 (8)

Arratia 1996 Fig. 5 (8)

Arratia 1996 Fig. 6a (8)

Arratia 1997 Fig. 100 (9)

Arratia 1997 Fig. 101 (9)

Arratia 1997 Fig. 102 (9)

Arratia 1999 Fig. 19 (10)

Arratia 1999 Fig. 20 (10)

Arratia 1999 Fig. 21 (10)

Arratia 1999 Fig. 22 (10)

Arratia 2000a Fig. 20 (11)

Arratia 2000a Fig. 21 (11)

Arratia 2000b Fig. 21 (12)

Arratia 2008 Fig. 7 (13)

Arratia et Thies 2001 (14)

Arratia et Tischlinger 2010 (15)

Bonde 1996 Fig. 4 (16)

Brito 1997 Fig. 57 (17)

Brito et Alvarado 2008 (18)

Brito et al. 2008 (19)

Bryant 1987 (20)

Cavin 2001 Fig. 16 (21)

Cavin 2010 Fig. 1a (22)

Cavin 2010 Fig. 1b (22)

Cavin et Brito 2001 (23)

Cavin et Suteethorn 2006 Fig. 4 (24)

Cavin et Suteethorn 2006 Fig. 5a (24)

Cavin et Suteethorn 2006 Fig. 5b (24)

Cavin et al. 2007 Fig. 9 left (25)

Cavin et al. 2007 Fig. 9 right (25)

Cavin et al. 2012 Fig. 40 (26)

Cavin et al. 2013 (27)

Chalifa et Tchernov 1982 (28)

Cumbaa & Murray 2008 Fig. 12 (29)

Cumbaa & Murray 2008 Fig. 12 dotted tree (29)

Deesri 2013 Fig. 21L (30)

Figueiredo et al. 2012 Fig. 3 (31)

Forey 2004 Fig. 13 (32)

Friedman 2012 Fig. S1 (33)

Friedman et al. 2010 Fig. S13 (34)

Gardiner et al. 1996 Fig. 1 (35)

Gardiner et al. 1996 Fig. 3 (35)

Gardiner et al. 1996 Fig. 4 (35)

González-Rodríguez et al. 2004 Fig. 9a (36)

González-Rodríguez et al. 2004 Fig. 9b (36)

Gonzalez-Rodriqguez et Reynoso 2004 Fig. 7 (37)

Grande 1982 Fig. 20 (38)

Grande 1996 Fig. 2 (39)

Grande 1996 Fig. 3 (39)

Grande 2010 (40)

Grande et Bemis 1998 App. C (41)

Grande et Bemis 1998 App. F (41)

Grande et Grande 2008 Fig. 8 (42)

Grande et Poyato-Ariza 1999 Fig. 2 (43)

Hilton 2003 (44)

Hurley et al. 2007 (45)

Kear 2007 (46)

Lambers 1995 (47)

Li 1996 Fig. 4 (48)

Li et Wilson 1996 IoF Fig. 2 (49)

Li et Wilson 1996 JVP Fig. 7 (50)

Li et Wilson 1999 Fig. 3 (51)

Li et al. 1997a (52)

Li et al. 1997b Fig. 8 (53)

Liston 2008 Fig. 10 (54)

Lopez-Arbarello 2012 Fig. 16 (55)

Lopez-Arbarello 2012 Fig. 17 (55)

Maisey & Moody 2001 (56)

Maisey 1991 p154 (57)

Maisey 1991 p168 (57)

Maisey 1991 p189 (57)

Maisey 1991 p206 (57)

Maisey 1991 p282 (57)

Murray et Wilson 2009 Fig. 8 (58)

Murray et Wilson 2009 Fig. 9 (58)

Near et al. 2012 (59) – acted as molecular constraint tree

Nursall 1996 Fig. 4 MF1 (60)

Nursall 1996 Fig. 18 MF1 (60)

Nursall et Capasso 2004 MF3 (61)

Olsen 1984 (62)

Olsen et McCune 1991 Fig. 17a (63)

Olsen et McCune 1991 Fig. 17b (63)

Patterson 1977 Fig. 19 (64)

Patterson et Rosen 1977 Fig. 54 (65)

Poyato-Ariza & Wenz 2002 Fig. 43 (66)

Poyato-Ariza & Wenz 2005 Fig. 10L (67)

Poyato-Ariza & Wenz 2005 Fig. 10R (67)

Poyato-Ariza 1996 (68)

Poyato-Ariza 1996b Fig. 22 (69)

Poyato-Ariza et Wenz 2004 Fig. 15 (70)

Shen 1996 Fig. 2 (71)

Shen 1996 Fig. 3 (71)

Shen 1996 Fig. 4 (71)

Stewart 1999 MF2 (72)

Taverne 2000 (73)

Taverne 2011 (74)

Taverne et Chanet 2000 (75)

Taxonomic constraint tree

Wen et al. 2012 Fig. 5a (76)

Wen et al. 2012 Fig. 5b (76)

Wen et al. 2012 Fig. 6 (76)

Wilson & Murray 2008 Fig. 8 (77)

Xu & Chang 2009 (78)

Xu & Gao 2011 (79)

Xu et Wu 2011 (80)

Xu et al. 2012 (81)

Yabumoto 2008 Fig. 11a (82)

Yabumoto 2008 Fig. 11b (82)

Yabumoto 2008 Fig. 11c (82)

Zaragüeta-Bagils 2004 Fig. 7 (83)

Zhang 2004 (84)

Zhang et Jin 1999 Fig. 6 (85)

1. Alvarado-Ortega J (2004) Description and relationships of a new ichthyodectiform fish from the Tlayua Formation (Early Cretaceous : Albian), Puebla, Mexico. *Journal of Vertebrate Paleontology* 24(4):802-813.
2. Alvarado-Ortega J & Brito PM (2011) A NEW SPECIES OF ARARIPICHTHYS (TELEOSTEI, ELOPOCEPHALA) FROM THE TLAYUA FORMATION (CRETACEOUS, ALBIAN), MEXICO. *Journal of Vertebrate Paleontology* 31(6):1376-1381.
3. Alvarado-Ortega J & Espinosa-Arrubarrena L (2008) A new genus of ionoscopiform fish (Halecomorphi) from the Lower Cretaceous (Albian) lithographic limestones of the Tlayua quarry, Puebla, Mexico. *Journal of Paleontology* 82(1):163-175.
4. Alvarado-Ortega J, Ovalles-Damian E, & Arratia G (2008) A review of the interrelationships of the order Ellimmichthyiformes (Teleostei: Clupeomorpha). *Mesozoic Fishes 4. Homology and Phylogeny. Proceedings of the international meeting Miraflores de la Sierra, 2005*, eds Arratia G, Schultze H-P, & Wilson MVH (Verlag Dr. F. Pfeil), pp 257-278.
5. Arratia G (2013) MORPHOLOGY, TAXONOMY, AND PHYLOGENY OF TRIASSIC PHOLIDOPHORID FISHES (ACTINOPTERYGII, TELEOSTEI). *Journal of Vertebrate Paleontology* 33:1-138.
6. Arratia G (1994) PHYLOGENETIC AND PALEOGEOGRAPHIC RELATIONSHIPS OF THE VARASICHTHYID GROUP (TELEOSTEI) FROM THE LATE JURASSIC OF CENTRAL AND SOUTH-AMERICA. *Revista Geologica De Chile* 21(1):119-165.
7. Arratia G (1995) Importance of specific fossils in teleostean phylogeny. *Geobios Memoire Special (Villeurbanne)* 19:173-176.
8. Arratia G (1996) Reassessment of the phylogenetic relationships of certain Jurassic teleosts and their implications on teleostean phylogeny. *Mesozoic fishes. Systematics and*

Paleoecology. Proceedings of the international meeting Eichstatt, 1993, eds Arratia G & Günter V (Verlag Dr. Friedrich Pfeil, München, Germany), pp 219-242.
9. Arratia G (1997) Basal teleosts and teleostean phylogeny. *Palaeo Ichthyologica* 7:5-168.
10. Arratia G (1999) The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements. *Mesozoic fishes 2. Systematics and Fossil Record. Proceedings of the international meeting, Buckow, 1997*, eds Arratia G & Schultze HP (Verlag Dr. Friedrich Pfeil), pp 265-334.
11. Arratia G (2000) New teleostean fishes from the Jurassic of southern Germany and the systematic problems concerning the 'pholidophoriforms'. *Palaeontologische Zeitschrift* 74(1-2):113-143.
12. Arratia G (2000) Remarkable teleostean fishes from the Late Jurassic of southern Germany and their phylogenetic relationships. *Mitteilungen aus dem Museum fuer Naturkunde in Berlin Geowissenschaftliche Reihe* 3:137-179.
13. Arratia G (2008) The varasichthyid and other crossognathiform fishes, and the Break-up of Pangaea. *Fishes and the Break-up of Pangaea* 295:71-92.
14. Arratia G & Thies D (2001) A new teleost (Osteichthyes, Actinopterygii) from the Early Jurassic Posidoizia shale of Northern Germany. *Mitteilungen aus dem Museum für Naturkunde zu Berlin, Geowissenschaftliche Reihe* 4:167-187.
15. Arratia G & Tischlinger H (2010) The first record of Late Jurassic crossognathiform fishes from Europe and their phylogenetic importance for teleostean phylogeny. *Fossil Record* 13(2):317-341.
16. Bonde N (1996) Osteoglossids (Teleostei: Osteoglossomorpha) of the Mesozoic. Comments on their interrelationships. *Mesozoic fishes. Systematics and Paleoecology. Proceedings of the international meeting Eichstatt, 1993*, eds Arratia G & Günter V (Verlag Dr. Friedrich Pfeil, München, Germany), pp 273-284.
17. Brito PM (1997) Review of the Aspidorhynchidae (Pisces, Actinopterygii) of the Mesozoic: Osteology, phylogenetic relations, environmental and biogeographic data. *Geodiversitas* 19(4):681-772.
18. Brito PM & Alvarado-Ortega J (2008) A new species of Placidichthys (Halecomorphi: Ionoscopiformes) from the Lower Cretaceous Marizal Formation, northeastern Brazil, with a review of the biogeographical distribution of the Ophiopsidae. *Fishes and the Break-up of Pangaea* 295:145-154.
19. Brito PM, Yabumoto Y, & Grande L (2008) NEW AMIID FISH (HALECOMORPHI: AMIIFORMES) FROM THE LOWER CRETACEOUS CRATO FORMATION, ARARIPE BASIN, NORTHEAST BRAZIL. *Journal of Vertebrate Paleontology* 28(4):1007-1014.
20. Bryant LJ (1988) A New Genus and Species of Amiidae (Holostei; Osteichthyes) from the Late Cretaceous of North America, with Comments on the Phylogeny of the Amiidae. *Journal of Vertebrate Paleontology* 7(4):349-361.
21. Cavin L (2001) Osteology and phylogenetic relationships of the teleost Goulmimichthys arambourgi Cavin, 1995, from the Upper Cretaceous of Goulmima, Morocco. *Eclogae Geologicae Helvetiae* 94(3):509-535.
22. Cavin L (2010) Diversity of Mesozoic semionotiform fishes and the origin of gars (Lepisosteidae). *Naturwissenschaften* 97(12):1035-1040.
23. Cavin L & Brito P (2001) A new Lepisosteidae (Actinopterygii, Ginglymodi) from the Cretaceous of the Kem Kem beds, Southern Morocco. *Bulletin de la Société géologique de France* 172(5):661-670.
24. Cavin L & Suteethorn V (2006) A new semionotiform (Actinopterygii, Neopterygii) from Upper Jurassic Lower Cretaceous deposits of north-east Thailand, with comments on the relationships of semionotiforms. *Palaeontology* 49:339-353.
25. Cavin L*, et al.* (2007) The first sinamiid fish (Holostei, Halecomorpha) from Southeast Asia (Early Cretaceous of Thailand). *Journal of Vertebrate Paleontology* 27(4):827-837.

26. Cavin L, Forey PL, & Giersch S (2013) Osteology of Eubiodectes libanicus (Pictet & Humbert, 1866) and some other ichthyodectiformes (Teleostei): phylogenetic implications. *Journal of Systematic Palaeontology* 11(2):115-177.
27. Cavin L, Deesri U, & Suteethorn V (2013) Osteology and relationships of Thaiichthys nov gen.: a Ginglymodi from the Late Jurassic - Early Cretaceous of Thailand. *Palaeontology* 56(1):183-208.
28. Chalifa Y & Tchernov E (1982) PACHYAMIA-LATIMAXILLARIS NEW-GENUS NEW-SPECIES ACTINOPTERYGII AMIIDAE FROM THE CENOMANIAN OF JERUSALEM ISRAEL. *Journal of Vertebrate Paleontology* 2(3):269-285.
29. Cumbaa SL & Murray AM (2008) New Late Cretaceous pachyrhizodontid and enchodontoid fishes and associated ichthyofauna from the Northwest Territories, Canada. *Mesozoic fishes 4. Homology and Phylogeny. Proceedings of the international meeting Miraflores de la Sierra, 2005*, eds Arratia G, Schultze H-P, & Wilson MVH (Verlag Dr. Friedrich Pfeil), pp 229-256.
30. Deesri U, Lauprasert K, Suteethorn V, Wongko K, & Cavin L (2014) A new species of the ginglymodian fish Isanichthys from the Late Jurassic Phu Kradung Formation, northeastern Thailand. *Acta Palaeontologica Polonica* 59(2):313-331.
31. de Figueiredo FJ, Gallo V, & Leal MEC (2012) Phylogenetic relationships of the elopomorph fish dagger Paraelops cearensis Silva Santos revisited: Evidence from new specimens. *Cretaceous Research* 37:148-154.
32. Forey PL (2004) A three-dimensional skull of a primitive clupeomorph from the Cenomanian English Chalk and implications for the evolution of the clupeomorph acustico-lateralis system. *Mesozoic Fishes 3. Systematics, Paleoenvironments and Biodiversity. Proceedings of the 3rd International Meeting, Serpiano, 2001*, eds Arratia G & Tintori A (Verlag Dr. Friedrich Pfeil, München, Germany), pp 75-100.
33. Friedman M (2012) Parallel evolutionary trajectories underlie the origin of giant suspension-feeding whales and bony fishes. *Proceedings of the Royal Society B-Biological Sciences* 279(1730):944-951.
34. Friedman M*, et al.* (2010) 100-Million-Year Dynasty of Giant Planktivorous Bony Fishes in the Mesozoic Seas. *Science* 327(5968):990-993.
35. Gardiner BG, Maisey JG, & Littlewood DTJ (1996) Interrelationships of basal neopterygians. *Interrelationships of Fishes.*, eds Stiassny MLJ, Parenti LR, & Johnson GD (Academic Press, San Diego), pp 117–146.
36. Gonzalez-Rodriguez K, Applegate SP, & Espinosa-Arrubarrena L (2004) A new world Macrosemiid (Pisces : Neopterygii-Halecostomi) from the Albian of Mexico. *Journal of Vertebrate Paleontology* 24(2):281-289.
37. GONZÁLEZ-RODRÍGUEZ K & REYNOSO V-H (2004) A new Notagogus (Macrosemiidae, Halecostomi) species from the Albian Tlayúa Quarry, Central Mexico. *Mesozoic Fishes 3. Systematics, Paleoenvironments and Biodiversity. Proceedings of the 3rd International Meeting, Serpiano, 2001*, eds Arratia G & Tintori A (Verlag Dr. Friedrich Pfeil, München, Germany).
38. Grande L (1982) A revision of the fossil genus Diplomystus: with comments on the interrelationships of clupeomorph fishes. *American Museum novitates* (2728).
39. Grande T (1996) The interrelationships of fossil and Recent gonorynchid fishes with comments on two Cretaceous taxa from Israel. *Mesozoic Fishes. Systematics and Fossil Record. Proceedings of the international meeting, Buckow, 1997*, eds Arratia G & Günter V (Verlag Dr. Friedrich Pfeil, München, Germany), pp 299-318.
40. Grande L (2010) An empirical synthetic pattern study of gars (Lepisosteiformes) and closely related species, based mostly on skeletal anatomy. The resurrection of Holostei. *Copeia* (2A):1-863.

41. Grande L & Bemis WE (1998) A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. *Journal of Vertebrate Paleontology* 18(1):1-696.
42. Grande T & Lance G (2008) Reevaluation of the gonorynchiform genera Ramallichthys, Judeichthys and Notogoneus, with comments on the families Charitosomidae and Gonorynchidae., (Verlag Dr. Friedrich Pfeil, München, Germany), pp 295-310.
43. Grande T & Poyato-Ariza FJ (1999) Phylogenetic relationships of fossil and Recent gonorynchiform fishes (Teleostei : Ostariophysi). *Zoological Journal of the Linnean Society* 125(2):197-238.
44. Hilton EJ (2003) Comparative osteology and phylogenetic systematics of fossil and living bony-tongue fishes (Actinopterygii, Teleostei, Osteoglossomorpha). *Zoological Journal of the Linnean Society* 137(1):1-100.
45. Hurley IA*, et al.* (2007) A new time-scale for ray-finned fish evolution. *Proceedings of the Royal Society B-Biological Sciences* 274(1609):489-498.
46. Kear BP (2007) First record of a pachycormid fish (Actinopterygii : Pachycormiformes) from the Lower Cretaceous of Australia. *Journal of Vertebrate Paleontology* 27(4):1033-1038.
47. Lambers PH (1995) The monophyly of the Caturidae (Pisces; Actinopterygii) and the phylogeny of the Halecomorphi. *Geobios* (M.S. n° 19):201-203.
48. Li GQ (1996) A new species of Late Cretaceous osteoglossid (Teleostei) from the Oldman Formation of Alberta, Canada, and its phylogenetic relationships. *Mesozoic Fishes. Systematics and Paleoecology. Proceedings of the international meeting, Buckow, 1997*, eds Arratia G & Günter V (Verlag Dr. Friedrich Pfeil, München, Germany), pp 285-298.
49. Li GQ & Wilson MVH (1996) Phylogeny of osteoglossomorpha. *Interrelationships of fishes*, eds Stiassny M, Parenti L, & Johnson G (Academic Press, San Diego), pp 163-174.
50. Li GQ & Wilson MVH (1996) The discovery of heterotidinae (Teleostei: Osteoglossidae) from the paleocene Paskapoo formation of Alberta, Canada. *Journal of Vertebrate Paleontology* 16(2):198-209.
51. Li G-Q & Wilson MVH (1999) Early divergence of Hiodontiformes sensu stricto in East Asia and phylogeny of some Late Mesozoic teleosts from China. *Mesozoic fishes 2. Systematics and fossil record. Proceedings of the international meeting, Buckow, 1997.*, eds Arratia G & Schultze HP (Verlag Dr. Friedrich Pfeil, München, Germany), pp 369-384.
52. Li GQ, Grande L, & Wilson MVH (1997) The species of Phareodus (Teleostei: Osteoglossidae) from the Eocene of North America and their phylogenetic relationships. *Journal of Vertebrate Paleontology* 17(3):487-505.
53. Li GQ, Wilson MVH, & Grande L (1997) Review of Eohiodon (Teleostei: Osteoglossomorpha) from western North America, with a phylogenetic reassessment of Hiodontidae. *Journal of Paleontology* 71(6):1109-1124.
54. Liston J (2008) A review of the characters of the edentulous pachycormiforms Leesichthys, Asthenocormus and Martillichthys nov. gen. *Mesozoic fishes 4. Homology and Phylogeny. Proceedings of the international meeting Miraflores de la Sierra, 2005*, (Verlag Dr. Friedrich Pfeil, München, Germany), pp 181-198.
55. Lopez-Arbarello A (2012) Phylogenetic Interrelationships of Ginglymodian Fishes (Actinopterygii: Neopterygii). *Plos One* 7(7).
56. Maisey JG & Moody JM (2001) A review of the problematic extinct teleost fish Araripichthys, with a description of a new species from the Lower Cretaceous of Venezuela. *American Museum Novitates* 3324:1-27.
57. Maisey J (1991) *Santana Fossils: An Illustrated Atlas* (T.F.H. Publications, Neptune City).
58. Murray AM & Wilson MVH (2009) A NEW LATE CRETACEOUS MACROSEMIID FISH (NEOPTERYGII, HALECOSTOMI) FROM MOROCCO, WITH TEMPORAL AND GEOGRAPHICAL RANGE EXTENSIONS FOR THE FAMILY. *Palaeontology* 52:429-440.

59. Near TJ*, et al.* (2012) Resolution of ray-finned fish phylogeny and timing of diversification. *Proceedings of the National Academy of Sciences of the United States of America* 109(34):13698-13703.
60. Nursall JR (1996) The phylogeny of pycnodont fishes. *Mesozoic fishes. Systematics and Paleoecology. Proceedings of the international meeting Eichstatt, 1993*, eds Arratia G & Günter V (Verlag Dr. Friedrich Pfeil, München, Germany), pp 125-152.
61. Nursall JR & Capasso L (2004) Gebrayelichthys (novum), an extraordinary genus of neopterygian fishes from the Cenomanian of Lebanon. *Mesozoic fishes 3. Systematics, Paleoenvironments and Biodiversity. Proceedings of the 3rd International Meeting, Serpiano, 2001*, eds Arratia G & Tintori A (Verlag Dr. Friedrich Pfeil, München, Germany), pp 317-340.
62. Olsen PE (1984) The skull and pectoral girdle of the parasemionotid fish Watsonulus eugnathoides from the Early Triassic Sakamena Group of Madagascar, with comments on the relationships of the holostean fishes. *Journal of Vertebrate Paleontology* 4(3):481-499.
63. Olsen PE & McCune AR (1991) Morphology of the Semionotus elegans species group from the Early Jurassic part of the Newark Supergroup of Eastern North America with comments on the family Semionotidae (Neopterygii). *Journal of Vertebrate Paleontology* 11(3):269-292.
64. Patterson C (1977) The contributions of paleotnology to teleostean phylogeny. *Major Patterns in Vertebrate Evolution*, eds Hecht MK, Goody PC, & Hecht BM (Plenum Press, New York), pp 579–643.
65. Patterson C & Rosen DE (1977) REVIEW OF ICHTHYODECTIFORM AND OTHER MESOZOIC TELEOST FISHES AND THE THEORY AND PRACTICE OF CLASSIFYING FOSSILS. *Bulletin of the American Museum of Natural History* 158(2):83-172.
66. Poyato-Ariza FJ & Wenz S (2002) A new insight into pycnodontiform fishes. *Geodiversitas* 24(1):139-248.
67. Poyato-Ariza FJ & Wenz S (2005) Akromystax tilmachiton gen. et sp nov., a new pycnodontid fish from the Lebanese Late Cretaceous of Haqel and en Nammoura. *Journal of Vertebrate Paleontology* 25(1):27-45.
68. Poyato-Ariza FJ (1996) The phylogenetic relationships of Rubiesichthys gregalis and Gordichthys conquensis (Ostariophysi, Chanidae), from the Early Cretaceous of Spain. *Mesozoic fishes. Systematics and Paleoecology. Proceedings of the international meeting Eichstatt, 1993*, eds Arratia G & Günter V (Verlag Dr. Friedrich Pfeil, München, Germany), pp 329-348.
69. Poyato-Ariza FJ (1996) A revision of the ostariophysan fish family Chanidae, with special reference to the Mesozoic forms. *Palaeo Ichthyologica* 6.
70. Poyato-Ariza FJ & Wenz S (2004) The new pycnodontid fish genus Turbomesodon and a revision of Macromesodon based on new material from the Lower Cretaceous of Las Hoyas, Cuenca, Spain. *Mesozoic fishes 3: Systematics, Paleoenvironments and Biodiversity. Proceedings of the 3rd International Meeting, Serpiano, 2001*, eds Arratia G & Tintori A (Verlag Dr. Friedrich Pfeil, München, Germany), pp 341-378.
71. Shen M (1996) Fossil “osteoglossomorphs” from East Asia and their implications for teleostean phylogeny. *Mesozoic fishes. Systematics and Paleoecology. Proceedings of the international meeting, Buckow, 1997*, eds Arratia G & Günter V (Verlag Dr. Friedrich Pfeil, München, Germany), pp 285-298.
72. Stewart JD (1999) A new genus of Saurodontidae (Teleostei: Ichthyodectiformes) from the Upper Cretaceous rocks of the Western Interior of North America. *Mesozoic fishes 2. Systematics and Fossil Record. Proceedings of the international meeting, Buckow, 1997*, eds Arratia G & Schultze HP (Verlag Dr. Friedrich Pfeil, München, Germany), pp 369-384.
73. Taverne L (2001) Position systématique et relations phylogénétiques de Paraclupavus ("Leptolepis") caheni, téléostéen marin du Jurassique moyen de Kisangani (Calcaires de Songa, étage de Stanleyville), République Démocratique du Congo. *Museé royal de l'Afrique*

centrale, Tervuren (Belg.), Département du Géologie et Mineralogie, Rapportes Annual (1999-2000):55-76.

74. Taverne L (2011) Osteology and phylogenetic relationships of Steurbautichthys ("Pholidophophorus") aequatorialis gen. nov (Teleostei, "Pholidophoriformes") from the Middle Jurassic of Kisangani, Democratic Republic of Congo. Osteologie et relations phylogenetiques de Steurbautichthys ("Pholidophophorus") aequatorialis gen. nov. (Teleostei, "Pholidophoriformes") du Jurassique moyen de Kisangani, en Republique Democratique du Congo *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Sciences de la Terre* 81:129-173.
75. Taverne L & Chanet B (2000) Faugichthys loryi n. gen., n. sp. (Teleostei, Ichthyodectiformes) de l'Albien terminal (Crétacé inférieur marin) du vallon de la Fauge (Isère, France) et considérations sur la phylogénie des Ichthyodectidae. *Geodiversitas* 22(1):23-34.
76. Wen W*, et al.* (2012) A new basal actinopterygian fish from the Anisian (Middle Triassic) of Luoping, Yunnan Province, Southwest China. *Acta Palaeontologica Polonica* 57(1):149-160.
77. Wilson MVH & Murray AM (2008) Osteoglossomorpha: phylogeny, biogeography, and fossil record and the significance of key African and Chinese fossil taxa. *Fishes and the Break-up of Pangaea. Geological Society, London, Special Publications.*, eds Cavin L, Longbottom A, & Richter M), Vol 295, pp 185-219.
78. Xu G-H & Chang M-M (2009) Redescription of dagger Paralycoptera wui Chang & Chou, 1977 (Teleostei: Osteoglossoidei) from the Early Cretaceous of eastern China. *Zoological Journal of the Linnean Society* 157(1):83-106.
79. Xu G-H & Gao K-Q (2011) A new scanilepiform from the Lower Triassic of northern Gansu Province, China, and phylogenetic relationships of non-teleostean Actinopterygii. *Zoological Journal of the Linnean Society* 161(3):595-612.
80. Xu G & Wu F (2012) A deep-bodied ginglymodian fish from the Middle Triassic of eastern Yunnan Province, China, and the phylogeny of lower neopterygians. *Chinese Science Bulletin* 57(1):111-118.
81. Xu G-H, Zhao L-J, Gao K-Q, & Wu F-X (2013) A new stem-neopterygian fish from the Middle Triassic of China shows the earliest over-water gliding strategy of the vertebrates. *Proceedings of the Royal Society B-Biological Sciences* 280(1750).
82. Yabumoto Y (2008) A new Early Cretaceous osteoglossomorph fish from Japan, with comments on the origin of the Osteoglossiformes. *Mesozoic Fishes 4. Homology and Phylogeny. Proceedings of the international meeting Miraflores de la Sierra, 2005*, eds Arratia G, Schultze H-P, & Wilson M (Verlag Dr. F. Pfeil, München, Germany), pp 217-228.
83. ZARAGÜETA BAGILS R (2004) Basal clupeomorphs and ellimmichthyiform phylogeny. *Mesozoic Fishes 3. Systematics, Paleoenvironments and Biodiversity. Proceedings of the 3rd International Meeting, Serpiano, 2001*, eds TINTORI A & ARRATIA G (Verlag Dr. F. Pfeil, München, Germany), pp 391–404.
84. Zhang JY (2004) New fossil osteoglossomorph from Ningxia, China. *Journal of Vertebrate Paleontology* 24(3):515-524.
85. Zhang JY & Fan J (1999) A revision of †Tongxinichthys MA 1980 (Teleostei: Osteoglossomorpha) from the Lower Cretaceous of northern China. *Mesozoic fishes 2. Systematics and Fossil Record. Proceedings of the international meeting, Buckow, 1997*, eds Arratia G & Schultze HP (Verlag Dr. Friedrich Pfeil, München, Germany), pp 385–396.