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Author for correspondence:
Thomas A. Stewart
e-mail: tomstewart@uchicago.edu

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The origins of adipose fins: an analysis of homoplasy and the serial homology of vertebrate appendages

Thomas A. Stewart[1], W. Leo Smith[2] and Michael I. Coates[1,3]

[1]Department of Organismal Biology and Anatomy, University of Chicago, 1027 E. 57th St., Chicago, IL 60637, USA
[2]Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA
[3]Committee on Evolutionary Biology, University of Chicago, 1025 E. 57th St., Chicago, IL 60637, USA

Adipose fins are appendages found on the dorsal midline between the dorsal and caudal fins in more than 6000 living species of teleost fishes. It has been consistently argued that adipose fins evolved once and have been lost repeatedly across teleosts owing to limited function. Here, we demonstrate that adipose fins originated repeatedly by using phylogenetic and anatomical evidence. This suggests that adipose fins are adaptive, although their function remains undetermined. To test for generalities in the evolution of form in de novo vertebrate fins, we studied the skeletal anatomy of adipose fins across 620 species belonging to 186 genera and 55 families. Adipose fins have repeatedly evolved endoskeletal plates, anterior dermal spines and fin rays. The repeated evolution of fin rays in adipose fins suggests that these fins can evolve new tissue types and increased structural complexity by expressing fin-associated developmental modules in these new territories. Patterns of skeletal elaboration differ between the various occurrences of adipose fins and challenge prevailing hypotheses for vertebrate fin origin. Adipose fins represent a powerful and, thus far, barely studied model for exploring the evolution of vertebrate limbs and the roles of adaptation and generative biases in morphological evolution.

1. Introduction

The fins and limbs of vertebrates are a classic model for studying both homoplasy and serial homology [1–4]. On the basis of position, vertebrate fins can be categorized as two kinds: paired and unpaired. Pectoral and pelvic fins are paired bilaterally and are homologous to tetrapod fore- and hindlimbs, respectively [5]. Caudal, dorsal, anal and adipose fins are unpaired median fins, positioned on the body midline. In vertebrates, the evolution of new fins is rare [5]. Fin number and skeletal anatomy are diagnostic characters for major vertebrate clades, suggesting that these characters are conserved in phylogeny and constrained in development. For instance, pectoral fins appear to have evolved only once, and pelvic fins are a synapomorphy of jawed vertebrates [6,7]. New fins can originate by either the subdivision of an existing fin domain—one module becoming two—as in the dorsal fins of some acanthopterygians [8], or by de novo origin—a new appendage developing in a location where there was not one previously. Pectoral fins are an example of de novo fin origin, the developmental programme of median fins having been recruited from paraxial to lateral plate mesoderm [9,10].

Fins that originate de novo are first observed in the palaeontological record as rudimentary outgrowths, which secondarily evolve greater anatomical and functional complexity [6]. Dermal skeleton appears first and is followed by endoskeleton, the presumed first direct evidence of muscular attachment and active control in fins [6]. The consistency of these patterns across fin systems suggests a common route for evolving new, complex appendicular systems. Although these patterns are discovered from study of the palaeontological record, their generality can be tested through analysis of extant diversity.

Adipose fins are appendages found in more than 6000 species of living teleosts, the major radiation of ray-finned (actinopterygian) fishes [11,12]. Adipose fins are

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defined by their position on the dorsal midline between the dorsal and caudal fins, and also by their anatomy, which appears less complex than the other fins of extant fishes [13]. Generally, adipose fins lack the endoskeleton, dermal skeleton and associated musculature that characterize the other fins found in extant fishes [14,15]. Instead, adipose fins tend to be passive structures supported by rods of collagen oriented along the proximodistal axis of the fin called actinotrichia, which sandwich a subdermal space composed of either adipose tissue, as in some Siluriformes [15–17], or a non-adipose tissue, loosely termed 'connective matrix' [17–19]. Adipose fin diversity is not well characterized, and the evolution, development and function of these structures remain poorly understood.

Hypotheses of adipose fin evolution are rooted in questions of homology and whether adipose fins are adaptive. Garstang [20] postulated that adipose fins were vestigial and homologous to the second dorsal fin that is plesiomorphic in gnathostomes, seen today in *Latimeria* and many chondrichthyans. Bridge [21] similarly concluded from anatomical study that adipose fins were vestigial. But, recognizing a single dorsal fin to be the primitive condition of ray-finned fishes, Bridge argued that adipose fins represented the degeneration of a second dorsal fin, which itself originated by the subdivision of the actinopterygian dorsal fin. Fossils, however, do not support either of these hypotheses. Within ray-finned fishes, structurally elaborated second dorsal fins (i.e. with dermal skeleton, endoskeleton and associated musculature) are found almost exclusively within the Acanthopterygii, which lack adipose fins [8]. Study of the fossil record highlights two lineages of non-acanthopterygian fishes that have evolved two dorsal fins: macrosemiids (e.g. †*Agoultichthys chattertoni* [22]), an extinct clade of ginglymodian fishes [23]; and †*Placidichthys*, an extinct genus of Halecomorphi [24,25]. Thus, most who have considered adipose fin evolution have concluded that the rudimentary appearance of these fins is plesiomorphic [15,19,26–30]. It is generally thought that adipose fins evolved once within the Actinopterygii, usually on the basis of their apparently limited function [19,26,28,29,31,32]. Some have proposed that their phylogenetic distribution might be best explained by homoplasy [15,27]; however, these hypotheses have never been tested.

Recent large-scale phylogenetic analyses are transforming our understanding of the evolution of teleost fishes [33–35], and hypotheses of character evolution must be revisited in the light of these new phylogenies. Here, we test competing hypotheses of adipose-fin origin and conclude that adipose fins have evolved repeatedly. We also characterize adipose fin skeletal anatomy for a diversity of fishes to test for similar patterns of structural elaboration among independent derivations of adipose fins and compare these patterns with what is known from the fossil record of other fins. Adipose fin skeletal evolution is highly homoplastic, differs significantly between instances of adipose fin origination and exhibits patterns of elaboration not observed in the fossil record of other fins. Finally, we discuss how fins, as serial homologues, originate and evolve.

2. Methods

(a) Ancestral-state reconstruction

To test how many times and in which groups adipose fins originated, we reconstructed a phylogeny of ray-finned fishes using the published data from Near *et al.* [34], which is comprised of 7587 base pairs from multiple nuclear genes for 232 actinopterygian fishes and 36 fossil age constraints. Using BEAST [36] with the same strategy as the original study, we recovered a pool of post-burn-in trees with a consensus topology that was congruent and similar in support of Near *et al.* [34] (electronic supplementary material, figure S1). The resulting trees are ultrametric, with branch lengths proportional to time. To account for evolutionary uncertainty, models of ancestral-state reconstruction were run across a distribution of 200 trees sampled randomly from the posterior distribution of post-burn-in trees generated by the Bayesian analysis.

Models of ancestral-state reconstruction were run treating the adipose fin as a binary character. Each of the 232 terminal taxa were coded for the presence or absence of an adipose fin with reference to specimens at the Field Museum of Natural History (Chicago, IL) and the literature (electronic supplementary material, figure S1). Maximum-likelihood and maximum-parsimony models of ancestral-state reconstruction were run in Mesquite [37]. Two likelihood models were considered: a Markov *k*-state one-parameter (Mk1) probability model, and a Markov *k*-state two-parameter (Mk2) probability model. The Mk1 model defines the rate of transition between states as equal, whereas the Mk2 model allows the rate of transition between two states to differ, allowing for bias in the direction of character state transformation. A likelihood ratio test was used to determine whether MK1 or MK2 models produced a better fit of the data for each of the 200 sampled topologies. The two-rate (Mk2) model of character evolution fit the data significantly better than the one-rate (Mk1) model over all trees (likelihood ratio test: $p < 0.001$, d.f. = 1), and so only results from the Mk2 model are reported. The MK2 model was run both by treating the root state frequencies as equal and root state frequencies equal to equilibrium. Results were consistent for each method, and results are shown only for the model in which root state frequencies are equal to equilibrium.

(b) The evolution of form in adipose fins

To characterize the evolution of form in adipose fins, skeletal anatomy was studied making reference to (i) cleared and stained specimens from the Fishes Collection at the Field Museum of Natural History (Chicago, IL), (ii) photographs of X-rays uploaded to the electronic collections of the California Academy of Sciences (San Francisco, CA) and Le Muséum National d'Histoire Naturelle (Paris, France) and (iii) the literature. A total of 746 specimens belonging to 620 species, 186 genera and 55 families were studied (table 1 and electronic supplementary material, table S1). Additionally, the adipose fin skeleton of *Mochokus niloticus* was characterized by making reference to micro-CT scans, which were made available to us by Dr John Friel, Curator of Fishes at Cornell University's Museum of Vertebrates. The specimen CUMV91386 was methanol-preserved, treated with iodine solution (I2M) following the methods from Metscher [38], and portions of it were CT scanned at 1.2, 3, 12 and 41.5 μM resolution. Mimics (Materialise Inc.) was used to process the data and to generate three-dimensional reconstructions of skeletal anatomy.

3. Results

(a) Adipose fins have evolved repeatedly

All models of ancestral-state reconstruction found support for multiple origins of adipose fins within Teleostei. The Mk2 likelihood model finds support for an origin of adipose fins in the group that includes Siluriformes and Characiformes, and again independently in the Euteleostei excluding Lepidogalaxiidae (figure 1). Specifically, adipose fins were likely absent in the lineage that diverged from the Euteleostei and led to the Otophysi (the clade composed of Siluriformes, Characiformes and Gymnotiformes; figure 1, nodes f,h,i,k,n). Although absence

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Table 1. Summary of specimens examined for adipose fin skeleton. Eschmeyer's catalogue of fishes [12] was used to assign species to families. Ordinal-level designations differ from Eschmeyer according to the tree recovered by Near *et al*. [34]—Osmeriformes have been split into: Osmeriformes, Retropinnidae, Galaxiidae, Argentiniformes, Alepocephaliformes, Lepidogalaxidae. Although some species may have undergone taxonomic revision or synonymization, this summary provides a reasonable indication of coverage.

	families surveyed	families recognized	genera surveyed	species surveyed	valid species
Argentiniformes	2	4	3	5	89
Aulopiformes	5	16	6	12	261
Characiformes	14	22	107	223	2035
Galaxiiformes	1	1	1	1	50
Myctophiformes	2	2	11	16	258
Osmeriformes	3	3	7	10	35
Percopsidae	1	1	2	2	2
Retropinnidae	1	1	2	2	6
Salmoniformes	1	1	5	14	217
Siluriformes	21	37	33	326	3594
Stomiiformes	4	4	9	9	426
total	55	92	186	620	6973
total number of individuals surveyed: 745					

is recovered as unambiguously optimal in only a small fraction of the trees, proportional probabilities consistently show support for adipose fins having been absent. The Mk2 likelihood model also found equivocal support for the hypothesis that adipose fins originated a third time, in the Percopsidae (figure 1, nodes t–v). The parsimony model unambiguously found support for the same three adipose fins origination events (electronic supplementary material, figure S2).

(b) Adipose fins have repeatedly evolved endoskeleton and dermal skeleton

Endoskeleton is found in the adipose fins of three taxonomically distinct groups: *Horabagrus brachysoma* (Siluriformes), Stomiiformes and Myctophiformes (figure 2). In each case, the adipose-fin endoskeleton was composed of a cartilaginous plate, undifferentiated and generally positioned at the posterior of the adipose fin base (figure 2*a*) [14,15]. The presence of stained cartilage varied within genera (i.e. *Neoscopelus* and *Spirinchus*) and even within a species (i.e. *Salangichthys microdon*).

Dermal adipose-fin spines formed from modified midline scutes are found in three taxonomically distinct groups of Siluriformes: a clade within Loricarioidei, which includes Callichthyidae, Astroblepidae and Loricariidae; *Sisor* spp. (Sisoridae); and some Amphilidae (observed in *Phractura*, described in *Andersonia* [40] and *Trachyglanis* [41]; figure 2*b–d*). In each case, spines are anterior to the adipose fin membrane, posteriorly projecting and anteriorly bounded by additional midline scutes.

Fin rays are found in the adipose fins of at least four taxonomically distinct groups of fishes: three catfish groups and at least one characiform (figure 2*e–k*). Siluriformes with adipose fin rays include *Clarotes* spp. (Bagridae) [42,43], *Phractocephalus hemioliopterus* (Pimelodidae) [42] and *Mochokus* spp. (Mochokidae) [40]. Within Characiformes, adipose fin rays were observed in *Colossoma macropomum* (Serrasalminae) and have also been described for *C. brachypomum*, and *Pygocentrus piraya* [44,45]. In all lineages except *Mochokus*, adipose fin rays are described as developing only after fishes have achieved a large adult size [42,44,45]. This may explain why some species previously reported with a rayed-fin phenotype, were not observed with adipose fin rays in our study (e.g. *Clarotes laticeps*, FMNH 50304; *Pygocentrus piraya*, FMNH 69988). *Pygocenrus* is the only genus previously described in the literature with a rayed adipose fin phenotype that we were unable to confirm. If *P. piraya* does indeed exhibit this phenotype, it likely represents a fifth unique origination of adipose fin rays, *Colossoma* and *Pygocentrus* being phylogenetically distinct [46–48].

Adipose fin rays are similar in their morphology to the lepidotrichia of other actinopterygian fins. They are composed of segmented and bilaterally paired hemitrichia, but are distinguished by their lack of associated musculature (figure 2*e–k*). In *P. hemioliopterus*, lepidotrichia segments appear to fuse to form non-segmented dermal rods, though segmentation remains visible in the smallest rays (figure 2*g,h*). In some species, adipose fin rays are separated by a thin fin membrane (e.g. *C. macropomum* and *Mochokus* spp.), whereas in other species, adipose fin rays are embedded in a thick fleshy fin (i.e. *Clarotes* spp. and *P. hemioliopterus*). In addition to flexible fin rays, *Clarotes* spp., also develop an anterior spine in large individuals (figure 2*f*). Conflicting accounts have been given as to how this spine develops: either through the elaboration of an anterior fin ray [42] or by the fusion of 'fulcra-like scutes' [43]. Because of this developmental ambiguity, we have not included *Clarotes* spp., among the list of taxa with dermal skeleton derived from dermal scutes. The adipose fin rays of *M. niloticus* are significantly differentiated along the anteroposterior axis. The two anterior-most fin rays are unsegmented, and anterior fin rays have flared bases (figure 2*i,j*).

4. Discussion

Homoplasy is defined as independently derived similarity [49]. It has been studied, thus far, in biological systems as a pattern

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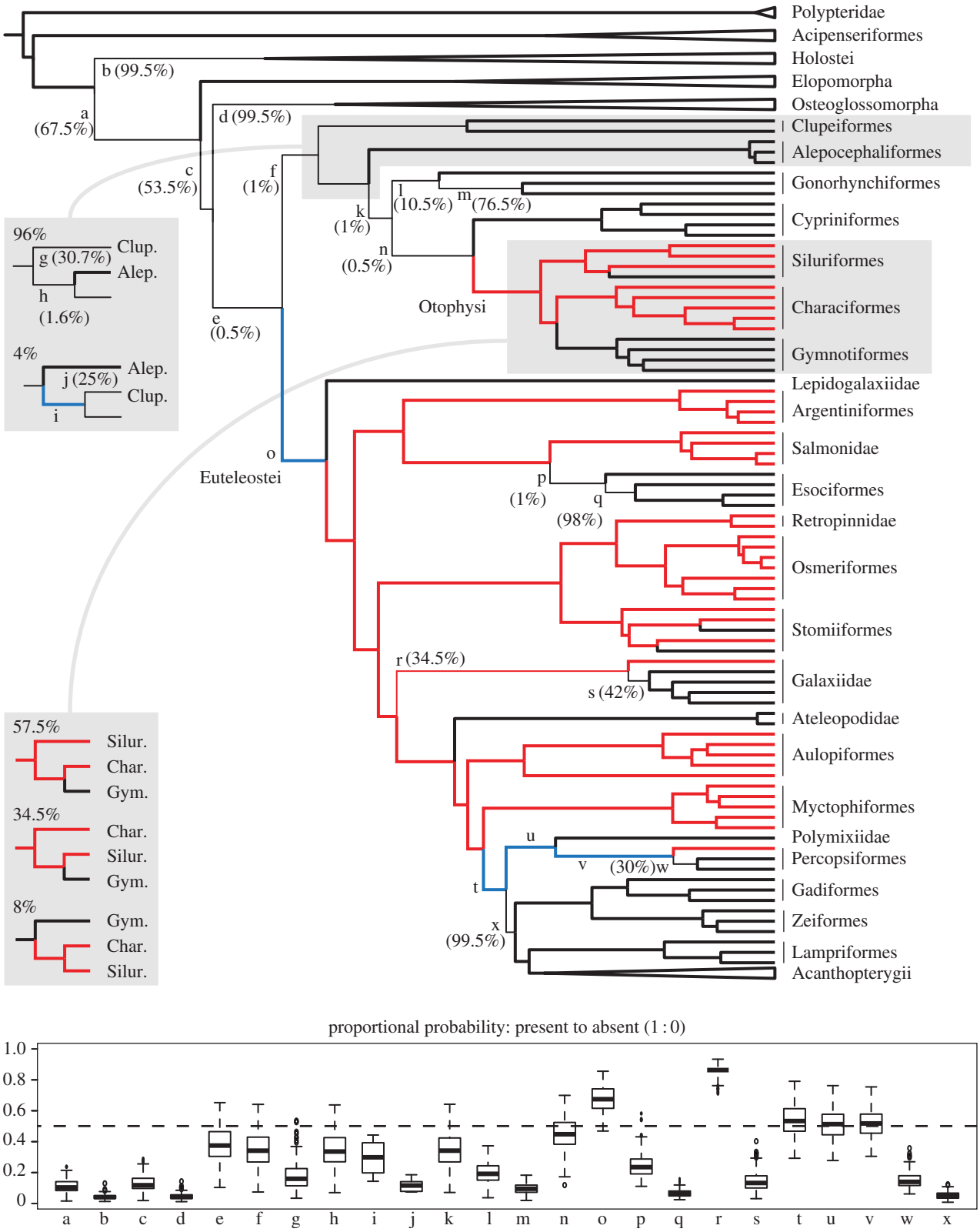

Figure 1. Adipose fins have evolved repeatedly. A summary of results from the Mk2 model of ancestral-state reconstruction run over 200 trees is plotted on a representative tree. Branch colour indicates the state that was recovered as optimal; black, red and blue indicate absent, present and neither, respectively. A particular character state is considered optimal when the log-likelihoods differed by 2 or more, the state with the lower likelihood being rejected. Thick lines indicate that 100% of the trees returned a particular state as optimal. Thin lines indicate that a fraction of the trees recovered that state as optimal. In these cases, the percentage of trees recovering that particular optimal solution is listed adjacent to the node, and a box-and-whisker plot of proportional probabilities, where 1 indicates presence and 0 absence, is shown below. Nodes boxed in grey varied across the distribution of trees. For those nodes, recovered topologies and their corresponding frequencies are shown at the left-hand side with the reconstructed ancestral states for those topologies. Nodes that varied but did not affect reconstructions (e.g. internal relations of the Gymnotiformes) are not indicated here.

that arises between lineages and can reflect the operation of developmental constraints and natural selection [50,51]. Parts of an organism evolve with degrees of independence and can similarly exhibit derived similarity. For example, similarity between the fore- and hindlimbs of crown group tetrapods is a derived condition [7,52]. By studying anatomies that have

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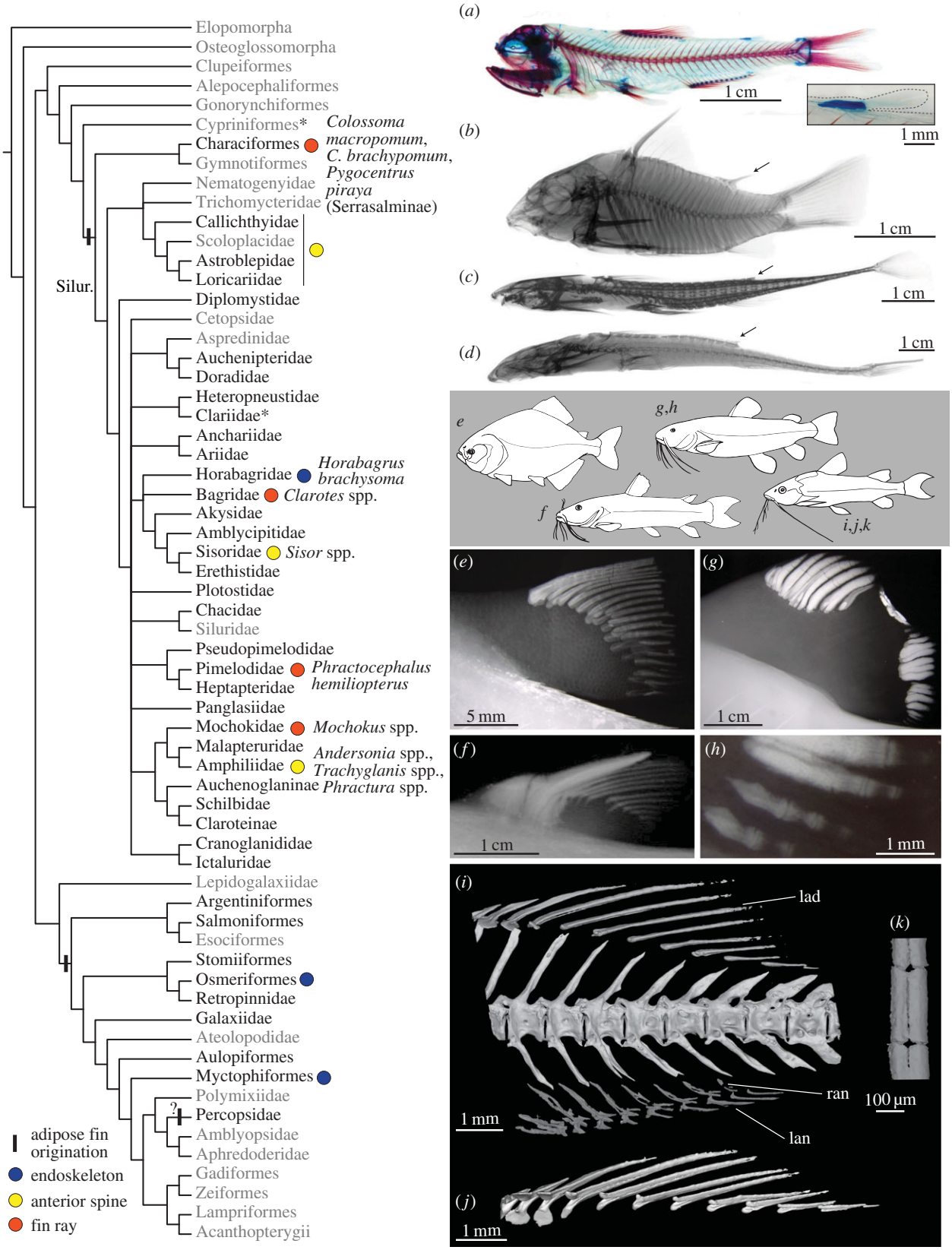

Figure 2. The evolution of adipose fin skeleton is highly homoplastic. Distribution of adipose fin skeleton is mapped onto the phylogeny of Near *et al.* [34], which has been appended with the phylogeny of Siluriformes, modified from Sullivan *et al.* [39]. Adipose fin origination events recovered by ancestral-state reconstruction are shown on the phylogeny. Asterisks indicate additional groups that may have evolved adipose fins independently. Groups lacking adipose fins are distinguished with grey font. Cypriniformes is marked in grey, despite the observation of an adipose fin in *Paracobitis rhadinaeus*, because the rest of the 4000+ species in this clade lack adipose fins. Cartilage discs, anterior dermal spines, and fin rays have evolved repeatedly in adipose fins. (*a*) Example of adipose fin endoskeleton, *Diaphus garmani*, FMNH 64632. (*b–d*) Photographs of X-rays for representative species with anterior dermal spines. (*b*) *Corydoras sychri*, SU 51295; (*c*) *Sisor torosus*, CAS 96629; (*d*) *Phractura clauseni*, MNHN 1960-0148. (*e–k*) Photographs of X-rays for representative species with adipose fin rays; line drawings of whole bodies are in the grey panel. (*e*) *Colossoma macropomum*, FMNH 56826. (*f*) *Clarotes bidorsalis*, MNHN 1938-0139. (*g*) *Phractocephalus hemioliopterus*, FMNH 58032. (*h*) The posterior-most and smallest fin rays from panel (*g*) at a higher magnification. (*i–k*) *Mochokus niloticus* CT scans. lad, lepidotrichia of the adipose fin; ran, radials of the anal fin; lan, lepidotrichia of the anal fin. (*k*) A portion of the seventh adipose fin ray viewed anteriorly showing segmented and bilaterally paired hemitrichia. Photos in panels (*b,d*) reproduced with permission from the California Academy of Science. Photos in panels (*c*) and (*f*) reproduced with permission from the Le Muséum National d'Histoire Naturelle.

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evolved repeatedly, both between lineages and within an organism, we might discover common trajectories and logic in the routes by which adaptive landscapes are navigated.

(a) Adipose fins have evolved repeatedly

New hypotheses of actinopterygian phylogeny provide consensus on the relationships of major actinopterygian clades [33–35]. Our result, that adipose fins have evolved repeatedly, is based on the phylogenetic hypothesis of Near *et al.* [34] and appears robust relative to minor topological changes among euteleosts [35]. A few analyses have found Characiformes to be paraphyletic, with Siluriformes nested within Characiformes [53,54]. Although our analysis does not include trees of this topology, characiform paraphyly is unlikely to change our result. The analysis presented here includes trees of three alternative topologies of the Otophysi, the clade composed of Gymnotiformes, Characiformes and Siluriformes. Each of the three topologies recover the same result that adipose fins originated in a common ancestor of Characiformes and Siluriformes.

There is equivocal evidence that Gymnotiformes might have primitively possessed adipose fins. A fossil gymnotiform was interpreted as having an adipose fin [55]; however, this interpretation has been challenged [56,57]. It has also been proposed that the 'dorsal filament' [58], an appendage found on the dorsal midline of some apteronotid gymnotiformes, which lacks a skeleton and musculature, is a transformed adipose fin. Assessment of this hypothesis yielded inconclusive results [59]. Regardless, when the entire Otophysi clade is reconstructed as primitively possessing adipose fins, our reconstructions still support the hypothesis that adipose fins in this group evolved independently from those in the Euteleosti.

Although adipose fins usually are composed of soft tissue and preserve poorly, these fins have been identified in a number of fossils as body outlines. In each case, they are found on fishes belonging to families known already to possess adipose fins [60–62]. If adipose fins originated only once in teleost fishes, we would expect to find evidence of their loss in multiple lineages; however, this is not the case. For example, fossil Gonorynchiformes, which are abundant and often exquisitely preserved [63], are never observed with an adipose fin. Thus, although the occurrence of adipose fins in fossils was not coded in our analysis of ancestral-state reconstruction, we argue that treating these data independently is very likely to impede our ancestral-state reconstruction, because the distribution of fossil fishes with adipose fins is congruent with what is predicted by our model. Finally, the only non-acanthopterygian actinopterygian fishes known to have elaborated second dorsal fins are the macrosemiids [22] and *Placidichthys* [24,25]. Both these Mesozoic holostean clades are nested deeply within groups otherwise characterized by the presence of a single dorsal fin. This suggests further instances of distinct fin origination, but in these examples perhaps by subdivision of the primary dorsal outgrowth.

In addition to the number of originations recovered by ancestral-state reconstruction, detailed analysis of adipose-fin variation within major actinopterygian clades suggests that adipose fins might have originated twice more, in Cypriniformes and in Clariidae (Siluriformes). The cypriniform *Paracobitis rhadinaeus* is described with a 'soft fin' between the dorsal and caudal fins [18,64]. Originally described in the appropriately named genus *Adiposia*, the anatomy of its posterior fin is reminiscent of the adipose fin of the madtom catfish, *Noturus exilis*, and its structure is similar in its histology to other adipose fins: a superficial epidermal layer covers fibrous rods, likely actinotrichia, which run proximo-distally and posteriorly and sandwich a core of 'connective tissue' [18]. Related species have been described with similar, but less prominent, extensions of the midline anterior to the caudal fin on both the dorsal and ventral midline [65]. *Paracobitis rhadinaeus* is nested deep within the Cypriniformes [66], a clade that includes over 4000 species otherwise lacking adipose fins [11], and this structure thus originated within Cypriniformes. Additionally, within the Clariidae, a group of air-breathing catfishes, there is phylogenetic and anatomical evidence that adipose fins may have been lost and subsequently re-evolved. Only three of the 14 clariid genera possess adipose fins: *Heterobranchus*, *Dinotopterus* and *Encheloclarias* [67]. Initially, it was proposed that these fishes represented the primitive Clariidae condition, the possession of an adipose fin and that the rest of the family had lost the fin [68]. However, a recent phylogeny of clariid catfishes recovers *Heterobranchus* and *Dinotopterus* nested well within a clade of clariids lacking adipose fins [69]. The adipose fins of *Heterobranchus* and *Dinotopterus* are anatomically unique when compared with all other adipose fins. Remarkably, they are supported by neural spines, which extend to the distal margin of the fin [67,70]. Whether this distinct anatomy reflects the independent derivation of an adipose fin of unique morphology or secondary modification of a more typical adipose fin is unclear. Regrettably, *Encheloclarias* is not included in recent molecular phylogenetic analyses, and it remains to be seen how its placement might affect interpretations of adipose fin evolution within the group.

(b) Are adipose fins adaptive?

The repeated evolution of adipose fins raises the question—what, if any, is the adaptive function of adipose fins? Homoplasy is not unto itself evidence of adaptation, as it can reflect non-adaptive processes [51,71]. However, natural selection readily purges fishes of their fins. For example, pelvic fins have been lost at least 80 times in teleosts alone [72]. The maintenance of adipose fins for millions of years and the discovery of unanticipated structural complexity in some fins [15,19] implies functionality. Attempts have been made to identify adipose fin function through an eco-morphological approach [30], but fishes with adipose fins may be too varied in their ecologies for such an approach to be broadly informative. Adipose fins are found on fishes ranging in size from centimetres to metres in length; on fishes from diverse ecosystems, ranging from montane rivers to the deep sea and on fishes occupying nearly every trophic level that fishes hold, ranging from planktivores, to molluscivores and piscivores. Discovering the adaptive function of adipose fins might be best achieved through biomechanical modelling and experimental functional approaches, as in Reimche & Temple [29]. Accumulating evidence suggests that some adipose fins function to direct pre-caudal flow or serve as a flow sensor (reviewed in reference [19]). These hypotheses are not mutually exclusive and, given the diversity of adipose fins in their size, positioning and composition, may not capture the full repertoire of adipose fin functions.

(c) Homoplasy in the adipose fin skeletal evolution

Adipose fins have evolved several kinds of skeleton, and each has evolved repeatedly. Endoskeleton appears to have evolved

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in adipose fins three times. This study highlights what is known about adipose fin endoskeletal elements, but likely underestimates the occurrence and therefore, too, the diversity of endoskeletal supports. It is notable that X-rays did not detect any adipose-fin endoskeleton, even in species expected to have them, for example, those species belonging to a genus in which endoskeleton had been previously described (electronic supplementary material, table S1). It is also noteworthy that Alcian blue does not always stain the acidic polysaccharides (e.g. glycosaminoglycans) in cartilages. For example, the adipose fin endoskeleton of *H. brachysoma* was identified by analysis of histological sections and does not stain with Alcian blue [15].

Two kinds of dermal skeleton have evolved in adipose fins. First, anterior spines derived from modified scutes have evolved in adipose fins three times, each time in the Siluriformes. Only one siluriform group, the Doradidae, has evolved dermal plates, but not an adipose fin spine [73]. Prominent spines at anterior boundary of fins are common in early gnathostomes [5], which often exhibit similarly enlarged scales and scutes immediately anterior to the fin spine (e.g. *Guiyu oneiros* [74]). Second, fin rays have evolved in adipose fins at least four times, but only in characiforms and siluriforms. Adipose fin rays may evolve as a saltatory change. Two abnormal individuals, both siluriformes, have been reported with adipose fins possessing lepidotrichia [28,75]. These apparently spontaneous transformations imply that simple developmental or genetic changes can generate rayed-fin morphology in some adipose fins.

Patterns of dermal skeletal evolution differ dramatically between adipose fin originations. Dermal skeleton has evolved independently in adipose fins at least seven times, but it has only evolved within the clade that includes characiforms and siluriforms, never within euteleosts. Different patterns of dermal skeletal evolution might reflect differences between these two groups in how adipose fins develop. Regrettably, studies of adipose fin development are limited. Bender & Moritz [76] characterized the timing of adipose fin development in several species and, intriguingly, identified two major developmental modes, which they call characiform and salmoniform types. Development of the characiform type is characterized by adipose fin outgrowth after the complete reduction of the larval fin fold. By contrast, salmoniform-type development is characterized by adipose fins apparently developing as a remnant of the larval fin fold. If these different developmental modes are broadly representative of adipose fins in the Otophysi and Euteleostei, then it would be further evidence of their independent origins and might explain differences in their propensity to evolve dermal skeleton.

(d) The origin of vertebrate fins and limbs

Vertebrates seem to be constrained in their ability to evolve new fins and limbs. When new fins do evolve, they originate either by the subdivision of an existing fin domain or de novo. Fully elaborated de novo fins are observed in malformed fishes with some frequency [77–80]; however, this seems not to be a realized route of evolutionary innovation. Rather, fins that originate de novo are primitively rudimentary in form and function, secondarily evolving greater structural and functional complexity [6].

Primitively, adipose fins lack endoskeleton, dermal skeleton and associated musculature. Each of these components has evolved in the adipose fins of some lineages (this study and [15]). Adipose fins can evolve new tissue types and increased structural complexity by expressing fin-associated developmental modules in this new territory. This is best exemplified by the repeated evolution of fin rays in adipose fins, and has been proposed for adipose fin endoskeleton [14] and musculature [15]. Broadly, high degree of developmental similarity, and thus serial homology, between fins may be a derived feature, general outgrowths converging on similar forms owing to common functional demands and biases in the generation of morphological variation.

Studies of the palaeontological record have identified a common pattern of elaboration in de novo vertebrate fins, with dermal skeleton evolving first and endoskeleton evolving second [6]. Our analysis challenges the general nature of this pattern. In adipose fins, endoskeleton repeatedly evolves in the absence of dermal skeleton. Dermal and endoskeleton, therefore, need not evolve in a hierarchical pattern; the capacity to evolve one is not dependent on the presence of the other. Multiple routes of elaboration are possible.

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References

1. Lankester E. 1870 On the use of the term homology in modern zoology, and the destinction between homogenetic and homoplastic agreements. *Ann. Mag. Nat. Hist.* **6**, 35–43.
2. Owen R. 1849 *On the nature of limbs: a discourse delivered on Friday, February 9, at an Evening Meeting of the Royal Institution of Great Britain*. London, UK: J. van Voorst.
3. Hall BK. 1994 *Homology: the hierarchical basis of comparative biology*, 1st edn. San Diego, CA: Academic Press.
4. Patterson C. 1982 Morphological characters and homology. In *Problems of phylogenetic reconstruction* (eds K Joysey, A Friday), pp. 21–74. London, UK: Academic Press.
5. Janvier P. 1996 *Early vertebrates*. Oxford, UK: Clarendon Press.
6. Coates MI. 1994 The origin of vertebrate limbs. *Development* 169–180.
7. Coates M. 2003 The evolution of paired fins. *Theory Biosci.* **122**, 266–287. (doi:10.1007/s12064-003-0057-4)
8. Mabee PM, Crotwell PL, Bird NC, Burke AC. 2002 Evolution of median fin modules in the axial skeleton of fishes. *J. Exp. Zool. B Mol. Dev. Evol.* **294**, 77–90. (doi:10.1002/jez.10076)
9. Coates MI, Cohn MJ. 1998 Fins, limbs, and tails: outgrowths and axial patterning in vertebrate evolution. *Bioessays* **20**, 371–381. (doi:10.1002/(SICI)1521-1878(199805)20:5<371::AID-BIES4>3.0.CO;2-R)
10. Freitas R, Zhang G, Cohn MJ. 2006 Evidence that mechanisms of fin development evolved in the midline of early vertebrates. *Nature* **442**, 1033–1037. (doi:10.1038/nature04984)
11. Nelson JS. 2006 *Fishes of the world*, 4th edn. Hoboken, NJ: John Wiley & Sons, Inc.
12. Eschmeyer W, Fricke R. 2013 Species by family/subfamily. Catalog of Fishes. electronic version (accessed 1 August 2013).

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13. Harder W. 1975 *Anatomy of fishes*, 2nd edn. Stuttgart, Germany: Eschweizerbartsche Verlagshuchhandlung.
14. Matsuoka M, Iwai T. 1983 Adipose fin cartilage found in some teleostean fishes. *Jpn. J. Ichthyol.* **30**, 37–46.
15. Stewart TA, Hale ME. 2013 First description of a musculoskeletal linkage in an adipose fin: innovations for active control in a primitively passive appendage. *Proc. R. Soc. B* **280**, 20122159. (doi:10.1098/rspb.2012.2159)
16. Alves RM, Pereira BF, Pitol DL, Senhorini JA, Rocha RdeC, Caetano FH. 2011 Histology, histochemistry and stereology of the adipose fin of *Prochilodus lineatus*. *Microsc. Res. Tech.* **75**, 615–619. (doi:10.1002/jemt.21099)
17. Weisel GF. 1968 The salmonoid adipose fin. *Copeia* **1968**, 626–627. (doi:10.2307/1442040)
18. Annandale N, Hora L. 1920 The fishes of Seistan. *Rec. Indian Museum* **18**, 151–203.
19. Buckland-Nicks JA, Gillis M, Reimchen TE. 2011 Neural network detected in a presumed vestigial trait: ultrastructure of the salmonid adipose fin. *Proc. R. Soc. B* **279**, 553–563. (doi:10.1098/rspb.2011.1009)
20. Garstang W. 1931 A phyletic classification of Teleostei. *Proc. Leeds Philos. Lit. Soc. Sci. Sect.* **2**, 240–261.
21. Bridge T. 1904 Fishes (exclusive of the systematic account of Teleostei). In *The Cambridge natural history* (eds S Harmer, A Shipley), pp. 141–537. New York, NY: Macmillan and Co.
22. Murray A, Wilson M. 2009 A new Late Cretaceous macrosemiid fish (Neopterygii, Halecostomi) from Morocco, with temporal and geographical range extensions for the family. *Palaeontology* **52**, 429–440. (doi:10.1111/j.1475-4983.2009.00851.x)
23. López-Arbarello A. 2012 Phylogenetic interrelationships of ginglymodian fishes (Actinopterygii: Neopterygii). *PLoS ONE* **7**, e39370. (doi:10.1371/journal.pone.0039370)
24. Brito PM. 2000 A new halecomorph with two dorsal fins, *Placidichthys bidorsalis* n. g., n. sp. (Actinopterygii: Halecomorphi) from the Lower Cretaceous of the Araripe Basin, northeast Brazil. *C.R. Acad. Sci., Ser. IIa: Sci. Terre Planets* **331**, 749–754. (doi:10.1016/S1251-8050(00)01477-4)
25. 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. *Geol. Soc. Lond. Spec. Publ.* **295**, 145–154. (doi:10.1144/SP295.9)
26. Jordan DS. 1905 *A guide to the study of fishes*. New York, NY: H. Holt and Company.
27. Vasnetzov W. 1947 The question of the role of the mechanism of development in the formation of species. *Zool. J. Moscow* **26**, 105–108.
28. Sandon H. 1956 An abnormal specimen of *Synodontis membranaceus* (Teleosti, Siluroidea) with a discussion on the evolutionary history of the adipose fin in fishes. *Proc. Zool. Soc. Lond.* **127**, 453–460. (doi:10.1111/j.1096-3642.1956.tb00481.x)
29. Reimchen TE, Temple NF. 2004 Hydrodynamic and phylognetic aspects of the adipose fin in fishes. *Can. J. Zool.* **82**, 910–916. (doi:10.1139/z04-069)
30. Temple N, Reimchen T. 2008 Adipose fin condition and flow regime in catfish. *Can. J. Zool.* **86**, 1079–1082. (doi:10.1139/Z08-086)
31. Kosswig C. 1965 Die Fettflosse der Knochenfische (besonders der Characiden). Morphologie, Funktion, phylogenetische Bedeutung. *J. Zool. Syst. Evol. Res.* **3**, 284–329. (doi:10.1111/j.1439-0469.1965.tb00942.x)
32. Patterson C, Rosen D. 1977 Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bull. Am. Mus. Nat. Hist.* **158**, 81–172.
33. Li J, Xia R, McDowall R, Lopez J, Lei G, Fu C. 2010 Phylogenetic position of the enigmatic *Lepidogalaxias salamandroides* with comment on the orders of lower euteleostean fishes. *Mol. Phylogenet. Evol.* **57**, 932–936. (doi:10.1016/j.ympev.2010.07.016)
34. Near TJ, Eytan RI, Dornburg A, Kuhn KL, Moore JA, Davis MP, Wainwright PC, Friedman M, Smith WL. 2012 Resolution of ray-finned fish phylogeny and timing of diversification. *Proc. Natl Acad. Sci. USA* **109**, 13 698–13 703. (doi:10.1073/pnas.1206625109)
35. Betancur-R R *et al*. 2013 The tree of life and a new classification of bony fishes. *PLoS Curr. Tree of Life* Apr 18, Edition 1, 1–45. (doi:10.1371/currents.tol.53ba26640df0ccaee75bb 165c8c26288)
36. Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012 Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* **29**, 1969–1973. (doi:10.1093/molbev/mss075)
37. Maddison W, Maddison D. 2011 Mesquite: a modular system for evolutionary analysis, v. 2.75.
38. Metscher BD. 2009 MicroCT for comparative morphology: simple staining methods allow high-contrast 3D imaging of diverse non-mineralized animal tissues. *BMC Physiol.* **9**, 1–14. (doi:10.1186/1472-6793-9-11)
39. Sullivan JP, Lundberg JG, Hardman M. 2006 A phylogenetic analysis of the major groups of catfishes (Teleostei: Siluriformes) using *rag1* and *rag2* nuclear gene sequences. *Mol. Phylogenet. Evol.* **41**, 636–662. (doi:10.1016/j.ympev.2006.05.044)
40. Boulenger GA. 1900 On some little-known African silurid fishes of the subfamily Doradinae. *Ann. Mag. Nat. Hist.* **7**, 520–530. (doi:10.1080/00222930008678421)
41. Harry R. 1953 A contribution to the classification of the African catfishes of the family Amphiliidae, with description of collections from Cameroon. *Rev. Zool. Bot. Afr.* **47**, 177–232.
42. Günther A. 1864 *Catalogue of the fishes of the British Museum*. London, UK: Taylor and Francis.
43. Boulenger G. 1907 *The fishes of the Nile*. London, UK: H Rees, Ltd.
44. Gery J. 1977 *Characoids of the world*. Neptune City, NJ: TFH Publications Inc.
45. Eigenmann CH. 1915 The Serrasalminae and Mylinae. *Ann. Carnegie Mus.* **9**, 226–272.
46. Machado-Allison A, Fink W, Antonio M. 1989 Revisión del género *Serrasalmus* (Lacepede, 1803) y géneros relacionados de Venezuela: I. Notas sobre la morfología y sistemática de *Pristobrycon striolatus* (Steindachner, 1908). *Acta Biol. Venez.* **12**, 140–171.
47. Orti G, Petry P, Porto JIR, Jegu M, Meyer A. 1996 Patterns of nucleotide change in mitochondrial ribosomal RNA genes and the phylogeny of piranhas. *J. Mol. Evol.* **42**, 169–182. (doi:10.1007/BF02198843)
48. Ortí G, Sivasundar A, Dietz K, Jégu M. 2008 Phylogeny of the Serrasalmidae (Characiformes) based on mitochondrial DNA sequences. *Genet. Mol. Biol.* **31**, 343–351. (doi:10.1590/S1415-47572008000200030)
49. Gould SJ. 2002 *The structure of evolutionary theory*. Cambridge, MA: The Belknap Press of Harvard University Press.
50. Wake DB, Wake MH, Specht CD. 2011 Homoplasy: from detecting pattern to determining process and mechanism of evolution. *Science* **331**, 1032–1035. (doi:10.1126/science.1188545)
51. Losos JB. 2011 Convergence, adaptation and constraint. *Evolution* **65**, 1827–1940. (doi:10.1111/j.1558-5646.2011.01289.x)
52. Jarvik E. 1980 *Basic structure and evolution of vertebrates*. London, UK: Academic Press.
53. Mauguit Q, Olivier D, Vandewalle N, Vandewalle P. 2010 Ontogeny of swimming movements in bronze corydoras (*Corydoras aeneus*). *Can. J. Zool.* **88**, 378–389. (doi:10.1139/Z10-012)
54. Nakatani M, Miya M, Mabuchi K, Saitoh K, Nishida M. 2011 Evolutionary history of Otophysi (Teleostei), a major clade of the modern freshwater fishes: Pangaean origin and Mesozoic radiation. *BMC Evol. Biol.* **11**, 177. (doi:10.1186/1471-2148-11-177)
55. Gayet M, Meunier F, Krischbaum F. 1994 *Ellisella krischbaumi* (Gayet & Meunier, 1991), gymnotiforme fossile de Bolivie et ses relationes phylogenetiques au sein des formes actuelles. *Cybium* **18**, 273–306.
56. Albert JS, Fink WL. 2007 Phylogenetic relationships of fossil neotropical electric fishes (Osteichthys: Gymnotiformes) from the upper Miocene of Bolivia. *J. Vert. Paleontol.* **27**, 17–25. (doi:10.1671/0272-4634(2007)27[17:PROFNE]2.0.CO;2)
57. Albert J. 2001 Species diversity and phylogenetic systematics of American knifefishes (Gymnotiformes, Teleostei). *Misc. Publ. Mus. Zool. Univ. Michigan* **190**, 1–129.
58. Ellis MM. 1913 The gymnotid eels of tropical America. *Mem. Carnegie Mus.* **6**, 109–195.
59. Franchina CR, Hopkins CD. 1996 The dorsal filament of the weakly electric Apteronotidae (Gymnotiformes; Teleostei) is specialized for electroreception. *Brain Behav. Evol.* **47**, 165–178. (doi:10.1159/000113236)
60. Buchheim HP, Surdam RC. 1977 Fossil catfish and the depositional environment of the Green River

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Formation, Wyoming. *Geology* **5**, 196–198. (doi:10.1130/0091-7613(1977)5<196:FCATDE>2.0.CO;2)

61. Watanabe K, Uyeno T. 1999 Fossil bagrid catfishes from Japan and their zoogeography, with description of a new species, *Pseudobagrus ikiensis*. *Ichthyol. Res.* **46**, 397–412. (doi:10.1007/bf02673982)
62. Chalifa Y. 1989 New species of *Enchodus* (Pisces: Enchodontoidei) from the Lower Cenomanian of Ein-Yabrud, Israel. *J. Paleontol.* **63**, 356–364. (doi:10.2307/1305507)
63. Fara E, Gayetand M, Taverne L. 2010 The fossil record of gonorhynchiformes. In *Gonorynchiformes and Ostariophysan relationships: a comprehensive review* (eds T Grande, FJ Poyato-Ariza, R Diogo). Enfield, NH: Science Publishers.
64. Hora SL, Silas EG. 1920 Fishes of the high altitude of the Himalays and Central Asia. *Bull. Nat. Inst. Sci. India* **9**, 288–290.
65. Prokofiev AM. 2010 Morphological classification of loaches (Nemacheilinae). *J. Ichthyol.* **50**, 827–913. (doi:10.1134/s0032945210100012)
66. Mayden RL *et al*. 2009 Reconstructing the phylogenetic relationships of the earth's most diverse clade of freshwater fishes: order Cypriniformes (Actinopterygii: Ostariophysi): a case study using multiple nuclear loci and the mitochondrial genome. *Mol. Phylogenet. Evol.* **51**, 500–514. (doi:10.1016/j.ympev.2008.12.015)
67. Teugels GG, Adriaens D. 2003 Taxonomy and phylogeny of Clariidae—an overview. In *Catfishes*, vol. 1 (eds G Arratia, B Kapoor, M Chardon, R Diogo), pp. 265–287. Enfield, NH: Science Publishers.
68. Boulenger G. 1907 A revision of the African Silurid fishes of the subfamily Clariinae. *Proc. Zool. Soc. Lond.* **77**, 1062–1097. (doi:10.1111/j.1469-7998.1907.tb06968.x)
69. Agnese JF, Teugels GG. 2005 Insight into the phylogeny of African Clariidae (Teleostei, Siluriformes): implications for their body shape evolution, biogeography, and taxonomy. *Mol. Phylogenet. Evol.* **36**, 546–553. (doi:10.1016/j.ympev.2005.03.028)
70. Teugels G. 1983 La structure de la nageoire adipeuse dans les genres *Dinotopterus*, *Heterobranchus* et *Clarias* (Pisces; Siluriformes; Clariidae). *Cybium* **7**, 11–14.
71. Stayton C. 2006 Testing hypotheses of convergence with multivariate data: morphological and functional convergence among herbivorous lizards. *Evolution* **60**, 824–841.
72. Yamanoue Y, Setiamarga DHE, Matsuura K. 2010 Pelvic fins in teleosts: structure, function and evolution. *J. Fish Biol.* **77**, 1173–1208. (doi:10.1111/j.1095-8649.2010.02674.x)
73. de Pinna MC. 1996 A phylogenetic analysis of the Asian catfish families Sisoridae, Akysidae, and Amblycipitidae, with a hypothesis on the relationships of the neotropical Aspredinidae (Teleostei, Ostariophysi). *Fieldania Zool.* **84**, 1–56.
74. Zhu M, Zhao W, Jia L, Lu J, Qiao T, Qu Q. 2009 The oldest articulated osteichthyan reveals mosaic gnathostome characters. *Nature* **458**, 469–474. (doi:10.1038/nature07855)
75. Tave D, Ramsey JS, Grizzle JM. 1990 Channel catfish with a rayed adipose fin. *J. Aquat. Anim. Health* **2**, 71–73. (doi:10.1577/1548-8667(1990)002<0071:CCWARA>2.3.CO;2)
76. Bender A, Moritz T. 2013 Developmental residue and developmental novelty—different modes of adipose-fin formation during ontogeny. *Zoosyst. Evol.* **89**, 209–214. (doi:10.1002/zoos.201300007)
77. Seligmann CG. 1898 Supernumerary dorsal fin in a trout. *J. Pathol. Bacteriol.* **5**, 314–315. (doi:10.1002/path.1700050311)
78. Crossman EJ. 1961 Grass pickerel, *Esox americanus vermiculatus*, with supernumary fins. *Copeia* **1961**, 235–236. (doi:10.2307/1440012)
79. Welch EB, Hull M, Katz M. 1962 A trout with two dorsal fins. *Trans. Am. Fish. Soc.* **92**, 67–68. (doi:10.1577/1548-8659(1963)92[67:ATWTDF]2.0.CO;2)
80. Raadik TA. 1993 A specimen of *Salmo trutta* (Pisces: Salmonidae) possessing an additional dorsal fin. *J. Fish Biol.* **42**, 811–812. (doi:10.1111/j.1095-8649.1993.tb00389.x)