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# Fossils provide better estimates of ancestral body size than do extant taxa in fishes

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**Abstract**

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The use of fossils in studies of character evolution is an active area of research. Characters from fossils have been viewed as less informative or more subjective than comparable information from extant taxa. However, fossils are often the only known representatives of many higher taxa, including some of the earliest forms, and have been important in determining character polarity and filling morphological gaps. Here we evaluate the influence of fossils on the interpretation of character evolution by comparing estimates of ancestral body size in fishes (non-tetrapod craniates) from two large and previously unpublished datasets; a palaeontological dataset representing all principal clades from throughout the Phanerozoic, and a macroecological dataset for all 515 families of living (Recent) fishes. Ancestral size was estimated from phylogenetically based (i.e. parsimony) optimization methods. Ancestral size estimates obtained from analysis of extant fish families are five to eight times larger than estimates using fossil members of the same higher taxa. These disparities arise from differential survival of large-bodied members of early branching lineages, and are not statistical or taphonomic artefacts. Estimates of ancestral size obtained from a limited but judicious selection of fossil fish taxa are more accurate than estimates from a complete dataset of extant fishes.

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## Introduction

The vast majority (> 99%) of species that have ever existed are now extinct (Simpson 1952) and whole branches of the tree of life are known only from fossil forms (e.g. trilobites, placoderms, plesiosaurs). Consequently, fossils represent a unique resource for evolutionary studies. However, interpreting the morphology of fossil taxa is regarded as more subjective and less informative than data derived from living members of the same higher taxon (Patterson 1981; Ax 1987). In particular, the morphology of extant taxa can be studied in greater detail than in fossils, including aspects of soft anatomy, and usually using larger sample sizes. By contrast, and despite occasionally exceptional preservation, fossils are often fragmentary and exhibit large amounts of non-randomly distributed missing data (Wiens 2006). All of these sources of error contribute to uncertainty about the phenotypes and phylogenetic positions of fossil taxa (Gauthier *et al*. 1988; Wilkinson 2003).

Considering even limited sample sizes and problems associated with preservation of individuals, fossils can still provide irreplaceable information regarding the tempo and mode of character evolution. Fossils are often the only exemplars from the earliest radiations in many higher taxa, providing critical information in determining character polarity (Conway Morris 1993; Budd and Jensen 2000; Briggs and Fortey 2005). Because the taxa they represent are often extinct, fossils may represent taxa on shorter genealogical

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branches than their living relatives, and as such are more likely to preserve less derived character states. Fossils often sample lineages closer in time to relatively deep splitting events, and frequently display character state combinations not observed among extant forms (Gauthier *et al.* 1988; Donoghue *et al.* 1989; Wilson 1992; Santini and Tyler 2004). Because of the added information from extinct lineages, inclusion of fossils in phylogenetic analyses has substantially improved understanding of phylogeny (O'Leary 1999; Gatesy and O'Leary 2001), character state evolution (O'Leary 2001) and phylogenetic trends (Finarelli and Flynn 2006; Cobbett *et al.* 2007).

Body size is among the most easily acquired and directly comparable attributes of organisms for which reliable estimates may be obtained from the fossil record (Stanley 1998). Adult body size is also a central feature of organismal design, imposing constraints on many aspects of life history, especially critical scaling functions related to growth, metabolism and fecundity (Peters 1983; Schmidt-Nielsen 1984; Haldane 1985; McNab 2002). Consequently, understanding the evolution of body size can provide insights into the diversification of biological form and function. Changes in body size can have allometric effects on morphology, physiology, behaviour (e.g. activity patterns, thermoregulation), and are widely used as an adaptation to novel physical (e.g. temperature extremes, hypoxia, desiccation) and biotic (e.g. predation, competition) environmental parameters (Hutchinson and Macarthur 1959; Strathdee and Bale 1998; Burness *et al.* 2001; Leaper *et al.* 2001). Importantly, many features associated with body size transcend the particularities of taxonomic design, and as such often exhibit repeated patterns of evolution (Wake 1991; Mabee 2000; Bird and Mabee 2002; Mabee 2002).

Fishes (non-tetrapod craniates) provide numerous examples of taxa and circumstances in which to test theories on the evolution of continuous traits such as size (Albert *et al.* 1999; Knouft and Page 2003). Marine and freshwater fishes represent the largest component of contemporary vertebrate diversity, including more than 50% of all living vertebrate species, and inhabiting most of the Earth's aquatic habitats and geographical regions. Fishes also have a rich palaeontological record from throughout the Phanerozoic, with fossil taxa ranging in body size over more than three orders of magnitude. Moreover, recent discoveries of early Palaeozoic fossils have greatly expanded our knowledge of early vertebrate diversity and phylogeny (see Mallatt and Chen 2003; Shu *et al.* 2003; Janvier *et al.* 2006; references therein).

To better understand the importance of fossil data in documenting patterns of diversification in relation to body size, we compare estimates of ancestral body size in fishes using phylogenetically based methods of character state optimization applied to two new (previously unpublished) and large datasets. The first is a palaeontological dataset representing all principal clades of non-tetrapod craniates from throughout the Phanerozoic, including exemplars of all the early Ordovician radiations (*c.* 488 Ma; Long 1995; Janvier 1996). The second dataset is a compilation of mean body size for all 515 families of living (Recent) fishes using data from FishBase (Froese and Pauly 2005). A main conclusion is that estimates of ancestral body size obtained from a limited but judicious selection of fossil taxa are more accurate than estimates from an (almost) complete dataset of all extant fishes. The results invite caution when interpreting the conclusions of character state optimization studies based on examination of extant taxa alone. These limitations persist even when the terminal taxa represent a complete (or almost complete) sampling of the living biota, and when they have been analysed in a robust phylogenetic context. These results are a reminder that patterns of organismic diversification arise from the processes of both speciation and extinction, and that only study of fossils allows the sampling of character states in extinct clades.

## Materials and methods

Body size was measured as total length (TL) in centimetres from the tip of the snout to the posterior margin of the caudal fin directly from specimens, published photographs or reconstructions of articulated specimens in primary sources. Appendix 1 presents maximum recorded total length and stratigraphic data for 465 fish species, including 425 species known only as fossils and 40 species in clades for which fossils with reliable size data are lacking (e.g. *Myxine*; *Huso*). Appendix 2 presents statistical measures of size (average total length in cm), size variation (standard deviation, skew, kurtosis), and species richness (N) for all 515 recognized extant fish families, based on data for 24 259 species from FishBase. The taxonomic compositions of these two datasets are summarized in Tables 1 and 2, respectively. Total length is highly correlated with other measures of overall size, including maximum body weight, and size and age to first reproduction (Froese and Binohlan 2000). Among fishes, body mass in grams (g) may be estimated from total length in cm from the empirical equation: $g = 0.0217\,TL^{2.861}$ (Fig. 1).

The fossil taxa included in this analysis were selected to maximize representation of phylogenetically basal craniate lineages (*sensu* Janvier 1996), and include a thorough sampling of higher fish taxa for which reliable estimates of size are currently available. Taxon sampling followed the basal exemplar approach which maximizes representation of phylogenetically basal clades (Prendini 2001; Prendini and Wheeler 2004). The basal-exemplar approach is less sensitive to preservational biases than stratigraphically based taxon-counting methods (Lane *et al.* 2005). This sampling strategy produced a fossil dataset that is broadly representative of the fossil record of fishes as a whole, including members of more than half (51%) of all the 324 fish families known only as fossils (Benton 1993), 26% (164 of 622) of all fish families, living and extinct, known as fossils, and 68% (71 of 105) of all non-teleost actinopterygian genera known only as fossils. Fossil


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**Table 1** Taxonomic summary of the fossil fish database

| Clade | Fossil* | Extant† | Total | Total (%) |
|---|---|---|---|---|
| Cephalochordata | 3 | 1 | 4 | 0.86 |
| Yunnanozoa | 2 | 0 | 2 | 0.43 |
| Hyperotreti | 3 | 7 | 10 | 2.15 |
| Myllokunmingiida | 2 | 0 | 2 | 0.43 |
| Hyperoartia | 5 | 5 | 10 | 2.15 |
| Pteraspidomorphi | 25 | 0 | 25 | 5.38 |
| Thelodonti | 8 | 0 | 8 | 1.72 |
| Anaspida | 6 | 0 | 6 | 1.29 |
| Galeaspida | 7 | 0 | 7 | 1.51 |
| Pituriaspida | 1 | 0 | 1 | 0.22 |
| Osteostraci | 15 | 0 | 15 | 3.23 |
| Furcacaudiformes | 2 | 0 | 2 | 0.43 |
| Placodermi | 39 | 0 | 39 | 8.39 |
| Chondricthyes | 91 | 5 | 96 | 20.65 |
| Acanthodii | 17 | 0 | 17 | 3.66 |
| Sarcopterygii | 38 | 4 | 42 | 9.03 |
| Actinopterygii | 161 | 18 | 179 | 38.49 |
| **Total** | **425** | **40** | **465** | **100.00** |

*Taxa known only as fossils. †Extant taxa for clades lacking fossils with reliable size data (e.g. *Myxine; Huso*). Data are maximum recorded total length (cm), geological age (Epoch or Series), and phylogenetic position, from multiple sources (see text for explanation).

**Table 2** Taxonomic summary of the extant fish species database. Data are maximum recorded total length (cm) and taxonomic affiliation for more than 24 000 species from Froese and Pauly (2005)

| Clade | Orders | Families | Species | Total (%) |
|---|---|---|---|---|
| Hyperotreti | 1 | 1 | 69 | 0.28 |
| Hyperoartia | 1 | 2 | 40 | 0.16 |
| Chondrichthyes | 13 | 46 | 826 | 3.40 |
| Sarcopterygii | 3 | 4 | 10 | 0.04 |
| Actinopterygii | 45 | 462 | 23 314 | 96.10 |
| **Total** | **63** | **515** | **24 259** | **100.00** |

species were dated to epoch or series (e.g. Upper Devonian, Palaeocene) with geological dates from Gradstein *et al.* (2004). Conodonts were excluded from analysis due to uncertainties in body size and detailed phylogenetic information (Donoghue and Sansom 2002; Janvier 2003; Dong *et al.* 2005; Northcutt 2005; Wickstrom & Donoghue 2005). Hyperoartia data are from Janvier and Lund (1983), Gess *et al.* (2006) and Janvier *et al.* (2006). Triassic neoselachians are known only from teeth and were excluded from analysis (Underwood 2006). Sarcopterygian data are largely from Clouthier and Forey (1991), Cloutier 1996), Cloutier and Ahlberg (1996) and Clouthier (1997). Actinopterygian data are largely from Coates (1998), Dietze (2000), Arratia (1997, 1999), Arratia and Cloutier (2002), Arratia and Clouthier (2004), Lund (2000) and Friedman and Blom (2006). Carboniferous actinopterygians are not considered

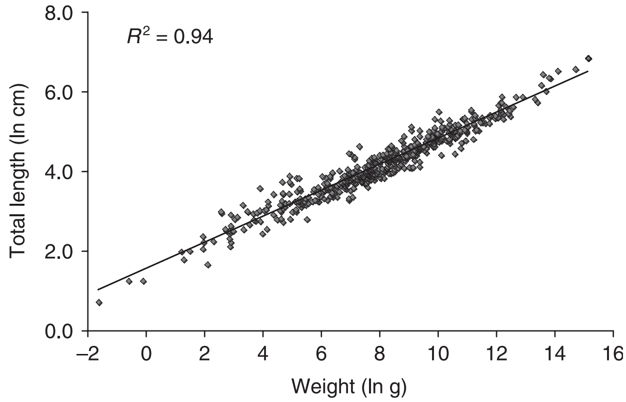


**Fig. 1**—Length and weight are significantly correlated in fishes. Data are maximum recorded total length (cm) and mass (g) for 517 extant fish species. The slope of the regression (m = 0.3267) on this log–log plot is close to the theoretically expected value 0.33 (i.e. mass = length$^3$). Size data from FishBase (Froese and Pauly 2005).

to be closely related to crown Actinopteri giving a long branch (*c.* 371–301 Ma).

The taxa examined provide sufficiently broad temporal ($10^7$–$10^8$ MY) and taxonomic ($10^2$–$10^4$ species) scopes to avoid non-random sampling errors arising from community assembly processes, convergent evolution or investigator bias (Ackerly 2000; Pollock *et al.* 2002). Due to the limited number of known fossils closely related to certain extant basal fish clades, size data for 13 terminal taxa are presented as an average of extant species from FishBase. These clades include the seven extant myxiniform genera, the two extant petromyzontiform genera, one extant dipnoan (*Protopterus* with six spp.), and five extant actinopterygians (*Polypterus, Acipenser, Scaphyrinchus, Psuedoscaphyrinchus, Clupea*). Taxa for which morphologically mature specimens are not known were excluded, as were taxa for which adult body size cannot be reliably estimated from known fossilized fragments (e.g. †*Polymerolepis margaritifera*, †*Lophosteus* sp.). Mature specimens are recognized by osteological criteria when available, that is, the shape of bones in the sphenoid and palatoquadrate regions of the skull, and the scapulocoracoid region of the pectoral girdle (Arratia 1997). Size of some Palaeozoic forms was estimated from large body fragments (e.g. †*Andinaspis suarezorum*, †*Pituriaspis doylei*; Janvier, pers. comm.).

Composite tree topologies were constructed from literature sources. The phylogeny of principal craniate clades (i.e. with initial radiations during the Lower Ordovician, *c.* 488–472 Ma; Fig. 2), of 465 fossil species, and of the 515 extant fish families (Fig. 3), largely follow Janvier (1996, 2003) and Long (1995), and references therein, with certain emendations noted by taxon in Appendix 1. These sources were used to a construct a tree topology for fossil fishes with 843 branches and 86 polytomies, or a tree that is *c.* 91% resolved.

†extinct taxa known only as fossils.

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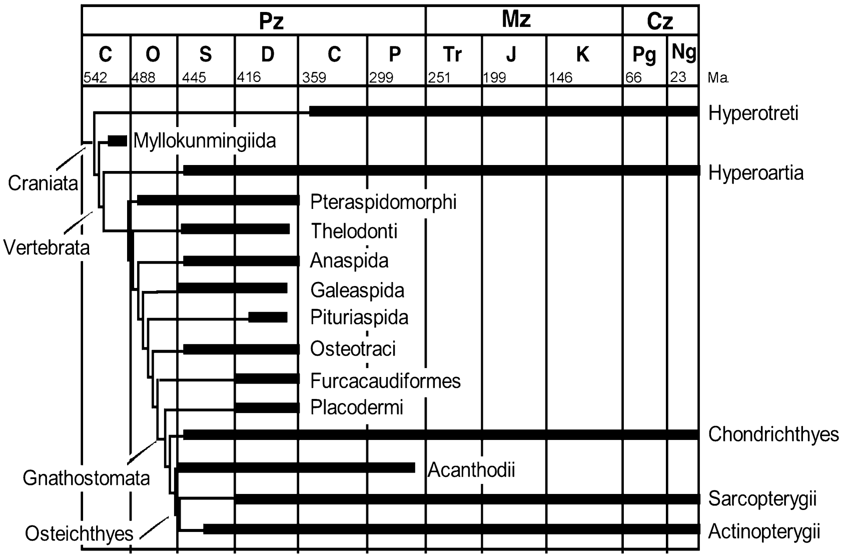


**Fig. 2**—Interrelationships and stratigraphic ranges of the principal craniate clades (i.e. Ordovician radiations *c.* 488 Ma (Long 1995; Janvier 1996; Table 1). Thick lines represent known stratigraphic ranges. Extant craniates represent just five of the 14 principal craniate clades. In terms of numbers of clades and species, Actinopterygii (ray-finned fishes) dominates the marine ichthyofauna from the Carboniferous (*c.* 363 Ma) to the Recent, the global freshwater ichthyofauna from the Upper Cretaceous (*c.* 100 Ma) to the Recent, and includes 96.1% of living fish species.

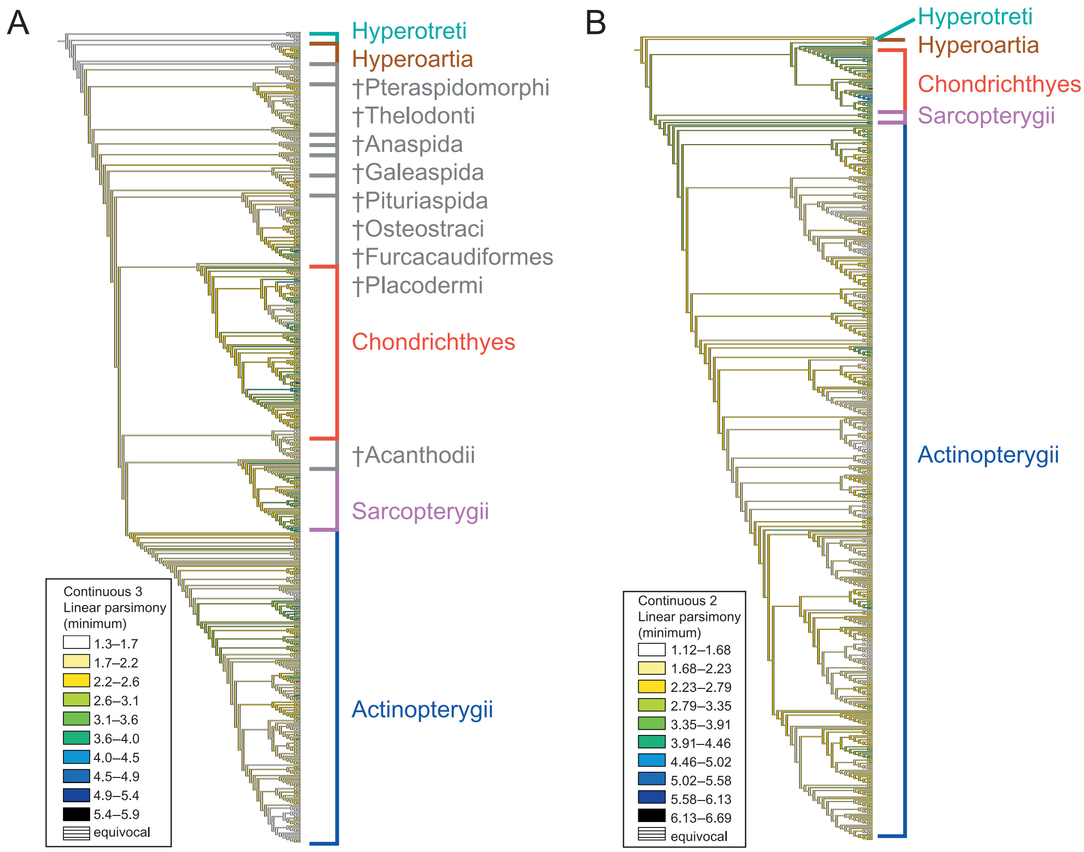


**Fig. 3**—Phylogenetic hypotheses of fish taxa with size-change optimized at all internal tree branches using Linear Parsimony (LP). —**A**. 465 fossil species, representing all 14 principal craniate clades (Ordovician radiations), with size optimized at 926 branches. —**B**. 515 extant fish families representing five principal craniate clades, with size optimized at 1031 branches. Tree topologies from Long (1995), Janvier (1996), Appendix 1 and references therein. Names of extinct clades (†) in grey font; extant clades in coloured fonts. Size data in cm log transformed before analyses. Branch lengths in MY estimated from stratigraphic data.


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Two chordate outgroup taxa were used to root the size optimizations: Cephalochordata and Yunnanozoa (Mallatt and Chen 2003). The phylogenetic positions of †*Haikouichthys* as a non-craniate deuterostome follows Shu (2003).

Linear and least squared parsimony (LSP) methods were employed to optimize ancestral size using the MESQUITE v.1.06 software package (Maddison & Maddison 2006). Linear Parsimony (LP) minimizes the total amount of trait change along tree branches such that the cost of a change from state x to y is $|x - y|$ (Swofford and Maddison 1987). LSP, also referred to as Squared-Change Parsimony, follows a Brownian motion model of evolutionary change in which the cost of a change from state x to state y is $(x - y)^2$ (Maddison 1991). LP differs from LSP and model-based (i.e. Bayesian and Likelihood) approaches to character state optimization in that it permits the reconstruction of discontinuous events, or of large changes in trait values (Butler and Losos 1997; Pagel 1999). Although evolutionary change is often considered as gradual, large differences in trait values between internal tree nodes may result from a variety of real biological processes, including punctuated evolution (Pagel *et al.* 2006) or extinction of taxa with intermediate trait values (Butler and Losos 1997; Albert *et al.* 1998). LP also permits the reconstruction of ambiguous ancestral state values when data are insufficient to provide an unambiguous resolution. Nevertheless, estimates of mean size among fossil fishes per epoch using LP and LSP are significantly correlated ($P < 0.0001$; Fig. 4). All ancestral reconstruction methods assume that trait evolution is conservative enough for node reconstruction techniques to be useful, even in the face of large standard errors (Polly 2001).

Ancestral trait optimization was performed using 10 replicates on arbitrarily fully resolved trees using MACCLADE 4.07 (Maddison and Maddison 2005). The qualitative results of this analysis were similar in all replicates of arbitrary node resolution. Available methods of character state reconstruction are limited to estimating ancestral trait values from within the limits of those observed in terminal taxa. LP analysis may therefore perform poorly at detecting a consistent underlying trend like Cope's rule. The reader is referred to Albert (2006) for a discussion of the limits and assumptions of different ancestral trait reconstruction methods. Stratigraphic data of fossils were used to constrain minimum age estimates for internal tree branches (Benton and Donoghue 2007). Branch lengths were estimated from stratigraphic data from fossils following Benton (1993, 2005). Branch lengths were estimated as the absolute difference in MY between nodes. In several taxa known only from Recent organisms, branch lengths were estimated from biogeographical information among sister taxa (see Appendix 1).

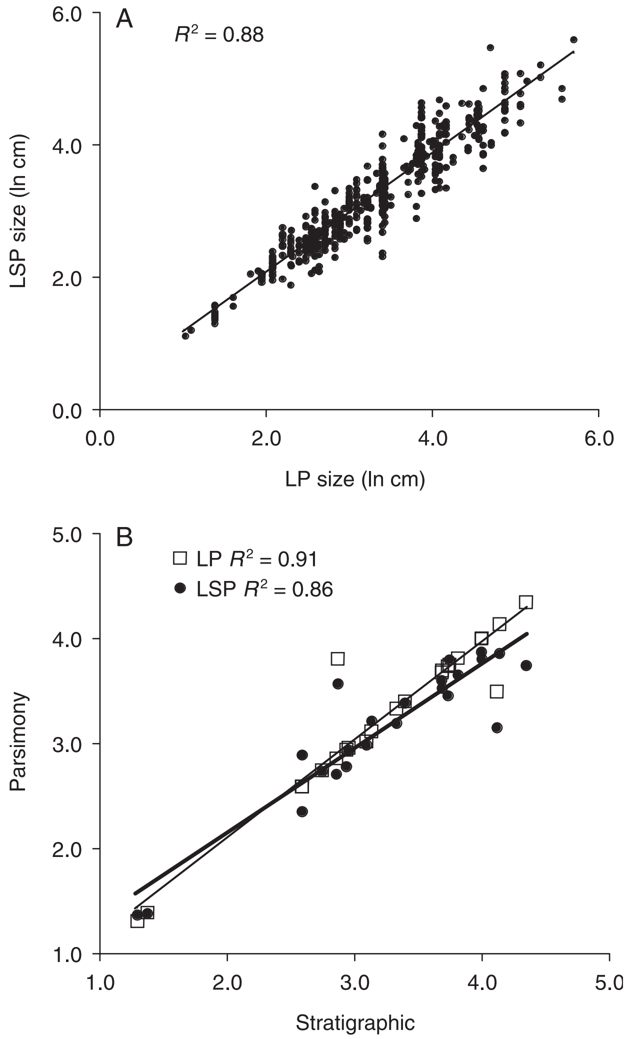


**Fig. 4**—Estimates of mean body size (ln cm) per epoch from phylogenetic optimization (LP and LSP) and stratigraphic (non-phylogenetic) methods. Stratigraphic estimates assessed directly as average log-transformed body size data of fossils per epoch. Phylogenetic estimates assessed as averages of interior node values per epoch using LP and LSP optimization on the phylogeny of fossil fishes (Fig. 3A). All $R^2$ values are significant at $P < 0.0001$. Note stratigraphic estimates are more highly correlated with LP than LSP, due to the averaging nature of squared-change optimization.

## Results and discussion

Ancestral size estimates obtained from analysis of the 515 extant fish families are five to eight times larger than estimates using fossil members of the same higher taxa (Fig. 5). This result is consistent for all of the 14 craniate clades with origins during the Lower Ordovician, including taxa with broad disparities in date of clade origin (*c.* 550–450 Ma), clade duration (*c.* 50–500 MY), body size at origin (*c.* 5–25 cm), habitat (i.e. marine, freshwater, euryhaline) and geography (i.e. tropical, extratropical, cosmopolitan). Plesiomorphic size estimates from the fossil dataset for Craniata, Hyperotreti, Vertebrata and Hyperartia are 5.0–8.0 cm, as compared with 45–50 cm from the extant dataset for these same taxa. Similarly, plesiomorphic size estimates from the

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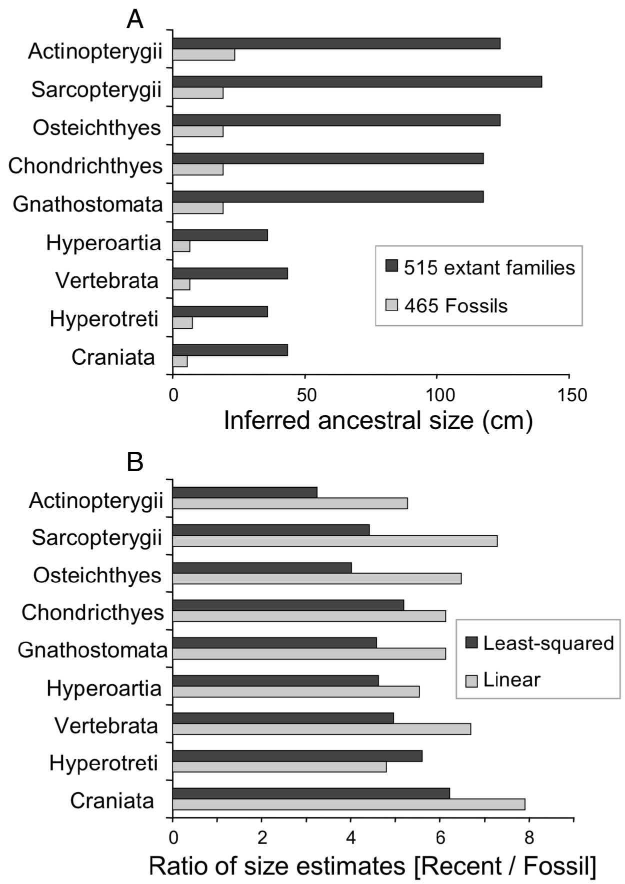


**Fig. 5**—Ancestral size estimates from analysis of extant fishes (515 extant families) are five to eight times larger than estimates using fossil members of the same higher taxa. —**A**. Inferred ancestral sizes using LP optimization. —**B**. Size estimates from extant (= Recent) vs. fossil members of the same higher taxa using LP and LSP optimization. Note the averaging effect of LSP results in somewhat less disparity in size estimate from Recent and fossil taxa.

fossil dataset for Gnathostomata, Chondrichthyes, Osteichthyes, Sarcopterygii and Actinopterygii are 20–25 cm, as compared with 120–140 cm from the extant dataset. Clearly there has been a strong filter on the size distribution of living taxa. A similar bias in the persistence of taxa with larger sizes has been observed in mammalian carnivores (Finarelli and Flynn 2006).

Which of the two datasets, palaeontological or contemporary provides more accurate estimates of size evolution among the principal craniate clades? Three features of craniate phylogeny and diversity suggest that information from fossils is more reliable for this purpose. First, the plesiomorphic size estimates of Craniata obtained from LP optimization of the fossil dataset are similar to the sizes (*c.* 3–5 cm) of closely related (fossil and extant) craniate outgroups (Mallatt and Chen 2003). Second, the extant diversity of fish clades represents only a fraction of the original (Ordovician) craniate radiations (Webby *et al.* 2004), being limited to just five of the six clades that survived the Late Devonian crisis (*c.* 375 Ma; Fig. 2). This extinction event was a strong filter on the size as well as taxonomic composition of surviving fish faunas (Janvier 1996; McGhee 1996). Third, having persisted for longer periods of geological time, living members of a clade may be expected to have accrued on average more changes than lineages of the same clade cut short by extinction. As a result, fossil species often preserve plesiomorphic states with more fidelity than related extant species (Donoghue *et al.* 1989).

Why are size estimates derived from analysis of living fishes so much larger than those derived from fossil representatives of the same higher taxa? Such disparities could arise from systematic biases in methods used to assemble the fossil dataset or conduct the optimization analysis, reflecting taphonomic or statistical artefacts from size-selective preservation, recovery or identification of fossils. Alternatively, the disparities might arise from real differences in the evolutionary histories of taxa which have become extinct vs. those which have persisted to the Recent. Consideration of the available data suggests the different estimates of ancestral body size result from the persistence of phylogenetically basal taxa with large size among living fish clades. This result also reinforces the claim that early branching lineages do not necessarily retain primitive or ancestral traits (Crisp and Cook 2005).

The disparity in body size estimates from the fossil and extant datasets does not appear to be a taphonomic artefact arising from size-selective preservational biases. Size-related biases on the preservation, recovery and identification of fossils may provide potentially confounding signals in inferring size evolution from palaeontological data (Barton and Wilson 2005; Northwood 2005). Large specimens are more subject to disarticulation and dispersal through hydrodynamic transport and physical wear through abrasion (Long and Langer 1995; Butler and Schroeder 1998; Butler 2004). As a result, large fishes are less likely to be preserved as intact skeletons, and preserved isolated elements are less likely to be recovered and identified, thus hindering accurate estimates of body size. In this regard, Phanerozoic escalation of predation and bioturbation rates (Vermeij 1994) could influence long-term trends in the size-frequency distributions of fossil fishes through time. On the other hand, larger skeletal elements are usually more robust, more resistant to abrasion, and often have more readily observed diagnostic morphologies. As a result they are more likely to be preserved, recovered and correctly identified (Behrensmeyer 1978; Kidwell and Flessa 1995; Alroy 2000). Indeed large-bodied taxa are better represented in many vertebrate palaeofaunas (Cooper *et al.* 2006; Valentine *et al.* 2006), and may actually serve to inflate perceptions of trends to larger size. The aggregate effect of these confounding taphonomic influences on size evolution remains poorly understood (Madin *et al.* 2006).

Global patterns of diversity may also reflect variation in the nature of the fossil record and fossil bearing sediments (Alroy


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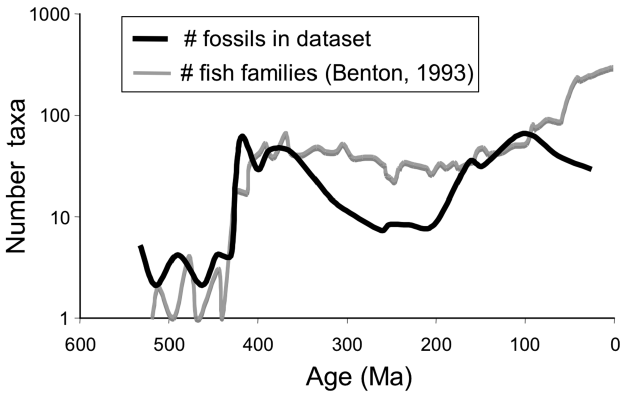


**Fig. 6**—Numbers of taxa per epoch in the fossil fish dataset (Appendix 1). The limited number of Late Palaeozoic (*c.* 318–251 Ma) fossils reflects a major trough in documented ichthyofaunas from the Pennsylvanian to Permian (Hurley *et al.* 2007). Family level diversity for 645 fish families from Benton (1993, 2005).

*et al.* 2001). For example, the dearth of fossil fish taxa from the Pennsylvanian to the Permian (318–251 Ma; Fig. 6) corresponds to a major trough in fish diversity and documented ichthyofaunas known from this interval (Sepkoski 2002; Hurley *et al.* 2007). Among stratigraphic intervals examined (Table 1), there are no significant correlations between mean body size and species richness or the proportion of articulated skeletons ($P > 0.1$). Madin *et al.* (2006) found that escalatory trends did not drive Phanerozoic macroevolutionary patterns in a large dataset of fossil benthic marine invertebrates. Similarly, body size has not been found to be correlated with other long-term geological trends, for example, sedimentary rock volume (Peters and Foote 2001; Crampton *et al.* 2003), bioturbation rates (Crimes and Droser 1992; Vermeij 1993) or mean size of top predators (Janvier 1996; Twitchett *et al.* 2005). In combination we take these results as evidence that taphonomic effects have not been the primary factor influencing the assessment of size distributions of fossil fishes over the Phanerozoic.

If, as predicted by Cope's rule, there was a persistent and general tendency to increase body size within lineages, ancestral size estimates obtained from analysis of terminal (fossil or extant) taxa would be systematically overestimated (Stanley 1973; Polly 1998; Hone and Benton 2005). For example, estimates from terminal taxa are limited to the range of values observed, and are not capable of estimating ancestral values smaller than that of the smallest terminal taxon. This overestimate in the value of internal tree nodes would arise regardless of optimization method used (i.e. LP vs. LSP). However, among 23 Phanerozoic epochs, estimates of internal node values from LP and LSP approaches are significantly correlated ($P < 0.001$) with those of a direct statigraphic approach that does not use phylogenetic methods (Fig. 4). In other words, the principal qualitative results of this study are similar regardless of the parsimony-based optimization approach employed.

The phylogenetic distribution of body size among living fishes strongly suggests a history in which the surviving members of basal taxa attain much larger sizes than did their fossil relatives. Among the principal craniate clades that emerged during the Ordovician and which have survived to the Recent, in all cases the living representatives are substantially larger than are the earliest fossils. To cite some examples, extant hagfishes (Myxiniformes, avg. 51 cm, $n = 69$ species) are larger than the Pennsylvanian †*Myxinkela siroka* (7 cm) or †*Myxineides gononorum* (15 cm), extant lampreys (Petromyzontiformes, avg. 31 cm, $n = 40$ species) are larger than the Mississippian †*Hardistiella montanensis* (10 cm) or Pennsylvanian †*Mayomyzon pieckoensis* (6 cm), extant heterodontiform sharks (avg. 118 cm, $n = 8$ species) are larger than the Jurassic †*Heterodontus falcifer* (28 cm) or †*Paracestracion zitteli* (15 cm), extant coelacanths (avg. 154 cm, $n = 2$ species) are larger than the Middle Devonian †*Miguashaia bureau* (50 cm) or Upper Devonian †*Diplurus newarki* (25 cm), extant lungfishes (Dipnomorpha, avg. 111 cm, $n = 8$ species) are larger than the Upper Devonian †*Rhinodipterus ulrichi* (28 cm), and extant non-teleost actinopterygians (avg. 165 cm, $n = 53$ species) are larger than Palaeozoic actinopterygians (e.g. Lower Devonian †*Dialipina salgueiroensis* at 25 cm, Middle Devonian †*Cheirolepis tralii* at 25 cm, Middle Devonian †*Stegotrachelys finlayi* at 10 cm, or Middle Devonian †*Moythomasia nitida* at about 10 cm). Some Palaeozoic actinopterygians did attain somewhat larger sizes (although not approaching modern values), especially during the Middle Devonian (e.g. †*Cheirolepis canadensis*, 55 cm) and Upper Devonian (e.g. †*Howqualepis rostridens*, 95 cm). Large size in these taxa is apparently derived (Lund and Poplin 2002; Arratia and Cloutier 2002; Arratia and Clouthier 2004; Friedman and Blom 2006).

To summarize, the available information pertaining to body size and phylogeny among the principal clades of fishes indicates differential survival of large-bodied members of early branching lineages. It is important to note these results pertain to phylogenetic patterns only, and do not directly address potential underlying evolutionary processes. In other words, we were not able to reject hypotheses of long-term anagenetic change (e.g. Cope's rule; Hone and Benton 2005), or of the effects of body size on relative rates of diversification (Brown 1999; Gillooly *et al.* 2001). The patterns of size evolution observed in fishes closely resemble those of other vertebrate clades examined to date with comparable taxonomic and temporal resolution (Gardezi and da Silva 1999; Laurin 2004; Smith *et al.* 2004; Webster *et al.* 2004).


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**Appendix 1. The fossil fish dataset.** Size and stratigraphic data for 465 fish species, including 425 species known only as fossils and 40 extant taxa for clades lacking fossils with reliable size information. Data for 15 extant taxa presented as averages from a total of 160 species as follows: 7 Myxiniformes (69 spp.); 2 Petromyzontiformes (40 spp.); *Protopterus* (6 spp.); *Polypterus* (17 spp.); *Acipenser* (18 spp.); *Scaphyrinchus* (2 sp.); *Pseudoscaphyrinchus* (3 spp.); *Clupea* (5 spp.). Minimum geological ages (Ma) from stratigraphic data to Series or Epoch from (Benton 1993) (Benton 2005). Taxa arranged according to conventional phylogenetic sequence. TL, maximum known total length (cm).

| Class | Taxon | Horizon | Min. Age | TL (cm) | Reference |
|---|---|---|---|---|---|
| Cephalochordata | † *Cathaymyrus diadexus* | LC | 530 | 5.0 | (*1*) |
| | † *Pikaea gracilens* | MC | 513 | 3.0 | (*1*) |
| | † *Paleobranchiostoma hamatotergum* | MC | 513 | 4.0 | (*2*) |
| | *Branchiostoma* 16 spp. | R | 0 | 4.0 | (*3*) |
| Yunnanozoa | † *Yunnanozoon lividum* | LC | 530 | 3.0 | (*4*) |
| | † *Haikouella lanceolatum* | LC | 530 | 3.0 | (*5*) (*6*) |
| Hyperotreti | † *Gilpichthys greenei* | Pn | 318 | 8.0 | P. Janvier, pers. comm. |
| | † *Myxinkela siroka* | Pn | 318 | 7.0 | P. Janvier, pers. comm. |
| | † *Myxineides gononorum* | Pn | 318 | 15.0 | P. Janvier, pers. comm. |
| | *Eptatretus* | R | 0 | 53.0 | (*3*) |
| | *Paramyxine* | R | 0 | 43.0 | (*3*) |
| | *Quadratus* | R | 0 | 28.0 | (*3*) |
| | *Myxine* | R | 0 | 55.0 | (*3*) |
| | *Nemamyxine* | R | 0 | 51.0 | (*3*) |
| | *Neomyxine* | R | 0 | 41.0 | (*3*) |
| | *Notomyxine* | R | 0 | 58.0 | (*3*) |
| Myllokunmingiida | † *Myllokunmingia fengjiaoa* | LC | 530 | 2.8 | (*7*) |
| | † *Zhongjianichthys rostratus* | LC | 530 | 2.5 | (*7*) |
| Hyperoartia | † *Haikouichthys ercaicunensis* | LC | 530 | 2.5 | (*8*) |
| | † *Endeiolepis aneri* | UD | 385 | 10.0 | (*9*) |
| | † *Legendrelepis parenti* | UD | 385 | 10.0 | (*10*) |
| | † *Jamoytius kerkwoodi* | LS | 444 | 19.0 | (*10*) |
| | † *Euphanerops longaevus* | UD | 385 | 10.0 | (*9*) |
| | † *Hardistiella montanensis* | M | 360 | 10.0 | (*11*) |
| | † *Mayomyzon pieckoensis* | Pn | 318 | 6.0 | (*10*) |
| | † *Pipiscius zangerli* | M | 360 | 6.2 | P. Janvier, pers. comm. |
| | Geotridae | R | 0 | 36.0 | (*3*) |
| | Petromyzontidae | R | 0 | 30.0 | (*3*) |
| Pteraspidomorphi | † *Andinaspis suarezorum* | LO | 488 | 15.0 | (*12*) |
| | † *Anatolepis sp.* | UC | 501 | 8.0 | (*13*) |
| | † *Arandaspis prionotolepis* | LO | 488 | 14.0 | (*14*) |
| | † *Porophoraspis crenulata* | LO | 488 | 30.0 | P. Janvier, pers. comm. |
| | † *Sacabambaspis janvieri* | UO | 461 | 35.0 | (*10*) |
| | † *Astraspis splendens* | UO | 461 | 40.0 | (*15*) |
| | † *Lepidaspis serrata* | D | 416 | 25.0 | (*10*) |
| | † *Empedaspis inermis* | LD | 416 | 7.0 | (*10*) |
| | † *Athenaegis chattertoni* | LS | 444 | 6.0 | (*10*) |
| | † *Irregulareaspis hoeli* | LD | 416 | 12.0 | (*10*) |
| | † *Pionaspis amplissima* | LD | 416 | 20.0 | (*10*) (*9*) |
| | † *Torpedaspis elongata* | LD | 416 | 25.0 | (*10*) |
| | † *Vernonaspis sp.* | US | 423 | 10.0 | (*10*) |
| | † *Anglaspis insignis* | LD | 416 | 5.0 | (*10*) |
| | † *Canadapteraspis alocostomata* | LD | 416 | 12.0 | (*10*) (*16*) |
| | † *Trygonaspis sp.* | LD | 416 | 12.0 | (*10*) |
| | † *Tolypelepis undulata* | US | 423 | 25.0 | (*17*) |
| | † *Cardipeltis bryanti* | LD | 416 | 19.0 | (*10*) |
| | † *Drepanaspis gemuendensis* | LD | 416 | 53.0 | (*10*) |
| | † *Drepanaspis sp.* | LD | 416 | 100.0 | (*10*) |
| | † *Doryaspis nathorsti* | LD | 416 | 20.0 | (*10*) |
| | † *Larnovaspis goujeti* | LD | 416 | 20.0 | (*10*) |
| | † *Protaspis transversa* | US-LD | 423 | 30.0 | (*10*) |
| | † *Pteraspis rostrata* | LD | 416 | 20.0 | (*10*) |
| | † *Rhinopteraspis sp.* | LD | 416 | 30.0 | (*10*) |
| | † *Psammolepis paradoxa* | UD | 385 | 70.0 | (*9*) |

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**Appendix 1.** *Continued*

| Class | Taxon | Horizon | Min. Age | TL (cm) | Reference |
|---|---|---|---|---|---|
| Thelodonti | † *Loganellia scotica* | LO | 488 | 40.0 | (*18, 19*) |
| | † *Phlebolepis elegans* | US | 423 | 9.0 | (*10*) |
| | † *Shielia taiti* | MS | 428 | 13.3 | (*20*) |
| | † *Loganellia scotia* | US | 423 | 15.0 | (*10*) |
| | † *Lanarkia horrida* | US | 423 | 10.0 | (*10*) |
| | † *Thelodus scotius* | US | 423 | 15.0 | (*10*) |
| | † *Archipelepis turbinata* | LS | 444 | 6.0 | (*19*) |
| | † *Turinia pagei* | LD | 416 | 40.0 | (*10*) |
| Anaspida | † *Birkenia elegans* | US | 423 | 10.0 | (*10*) |
| | † *Lasanius problematicus* | US | 423 | 8.0 | (*10*) |
| | † *Pharyngolepis oblongus* | US | 423 | 20.0 | (*10*) |
| | † *Pterygolepis nitidus* | US | 423 | 10.0 | (*10*) |
| | † *Rhyncholepis parvlus* | LD | 416 | 7.0 | (*10*) |
| | † Birkeniidae unnamed | MS | 428 | 15.0 | (*10*) |
| Galeaspida | † *Hanyangaspis guodinshanensis* | MS | 428 | 30.0 | P. Janvier, pers. comm. |
| | † *Xiushuiaspis sp.* | LS | 444 | 10.0 | (*9*) |
| | † *Sinoszechuanaspis longicornis* | LD | 416 | 8.0 | P. Janvier, pers. comm. |
| | † *Polybranchiaspis sp.* | LD | 416 | 8.5 | (*9*) |
| | † *Bannhuanaspis sp.* | LD | 416 | 20.0 | (*9*) |
| | † *Huananaspis guodinshanensis* | MS | 428 | 25.0 | P, Janvier, pers. comm. |
| | † *Sanqiaspis sp.* | LD | 416 | 12.0 | (*9*) |
| Pituriaspida | † *Pituriaspis doylei* | LD | 416 | 25.0 | (*9*) |
| Osteostraci | † *Atelaspis tessellata* | US | 423 | 20.0 | (*9*) |
| | † *Hemicylclaspis murchisoni* | US | 423 | 18.0 | (*10*) |
| | † *Hirella gracilis* | US | 423 | 7.0 | (*10*) |
| | † *Witaaspis sp.* | US | 423 | 12.0 | (*9*) |
| | † *Dartmuthia sp.* | US | 423 | 18.0 | (*9*) |
| | † *Tyriaspis whitei* | US | 423 | 10.0 | (*10*) |
| | † *Atelaspis robustus* | LD | 416 | 15.0 | (*10*) |
| | † *Boreaspis puella* | LD | 416 | 8.0 | (*10*) |
| | † *Cephalaspis powerei* | LD | 416 | 20.0 | (*10*) |
| | † *Zenaspis pagei* | LD | 416 | 25.0 | (*9*) |
| | † *Parameteoraspis sp.* | LD | 416 | 100.0 | (*16*) |
| | † *Procephalaspis sp.* | US | 423 | 49.0 | (*9*) |
| | † *Norselaspis glacialis* | LD | 416 | 8.0 | (*9*) |
| | † *Escuminaspis laticeps* | UD | 385 | 25.0 | (*9*) |
| | † *Alaspis microtuberculata* | UD | 385 | 31.0 | (*10*) |
| Furcacaudiformes | † *Furcacauda heintzae* | LD | 416 | 9.0 | UALVP 32958 |
| | † *Sphenonectris turnerae* | LD | 416 | 12.0 | UALVP 42212 |
| Placodermi | † *Stensioella heintzi* | LD | 416 | 26.0 | (*10*) |
| | † *Pseudopetalichthys problematicus* | LD | 416 | 18.0 | (*15*) |
| | † *Antarctaspis sp.* | MD | 398 | 30.0 | (*9*) |
| | † *Austrophyllolepis sp.* | MD | 398 | 20.0 | (*9*) |
| | † *Wuttagoonaspis fletsheri* | MD | 398 | 30.0 | (*9*) |
| | † *Sigaspis lepidophora* | LD | 416 | 20.0 | (*9*) |
| | † *Dicksonosteus sp.* | LD-MD | 416 | 20.0 | (*9*) |
| | † *Gemuendenaspis sp.* | LD | 416 | 30.0 | (*9*) |
| | † *Tiaraspis sp.* | LD | 416 | 24.0 | (*9*) |
| | † *Holonema rugosum* | MD-UD | 398 | 70.0 | (*9*) |
| | † *Homosteus milleri* | MD | 398 | 375.0 | (*9*) |
| | † *Antineosteus sp.* | LD | 416 | 40.0 | (*9*) |
| | † *Oxyosteus sp.* | UD | 385 | 100.0 | (*10*) |
| | † *Coccosteus decipiens* | MD | 398 | 60.0 | (*9*) |
| | † *Millerosteus minor* | MD | 398 | 10.0 | (*10*) |
| | † *Watsonosteus fletti* | MD | 398 | 60.0 | (*10*) |
| | † *Plourdosteus canadensis* | UD | 385 | 100.0 | (*9*) |
| | † *Eastmanosteus* | MD-UD | 398 | 300.0 | (*10*) |
| | † *Dunkleosteus terrelli* | UD | 385 | 800.0 | (*10*) |
| | † *Brachyosteus dietrichi* | UD | 385 | 25.0 | (*10*) |


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**Appendix 1.** *Continued*

| Class | Taxon | Horizon | Min. Age | TL (cm) | Reference |
|---|---|---|---|---|---|
| | † *Pholidosteus friedelti* | UD | 385 | 85.0 | (*10*) |
| | † *Phyllolepis sp.* | UD | 385 | 40.0 | (*10*) |
| | † *Lunaspis brolii* | LD | 416 | 30.0 | (*10*) |
| | † *Macropetalichthys sullivani* | MD | 398 | 80.0 | (*10*) |
| | † *Rhamphodopsis threiplandi* | MD | 398 | 7.0 | (*15*) |
| | † *Ctenurella gladbachensis* | UD | 385 | 18.0 | (*10*) |
| | † *Rhamphodopsis trispinatus* | MD | 398 | 12.0 | (*10*) |
| | † *Yunnanolepis spinulosa* | LD | 416 | 5.0 | (*21*) |
| | † *Chuchinolepis spinulosa* | LD | 416 | 7.5 | (*9*) |
| | † *Sinolepis sp.* | LD | 416 | 9.0 | (*9*) |
| | † *Bothrolepis canadensis* | MD-UD | 398 | 50.0 | (*10*) |
| | † *Bothriolepis yeungae* | UD | 385 | 50.0 | (*22*) |
| | † *Diplognathus mirabilis* | UD | 385 | 45.0 | (*10*) |
| | † *Pterichthyodes milleri* | LD-MD | 416 | 30.0 | (*10*) |
| | † *Asterolepis maxima* | MD-UD | 398 | 70.0 | (*10*) |
| | † *Microbrachius dicki* | MD | 398 | 6.0 | (*10*) |
| | † *Remigolepis walkeri* | UD | 385 | 40.0 | (*10*) |
| | † *Gemuendia stuertzii* | LD | 416 | 100.0 | (*10*) |
| | † *Jagorina pandora* | UD | 385 | 19.0 | (*10*) |
| Chondricthyes | † *Obtusacanthus corroconis* | LD | 416 | 12.0 | (*23*) |
| | † *Lupopsyroides macracanthus* | LD | 416 | 4.0 | (*23*) |
| | † *Diademodus hydei* | UD | 385 | 39.0 | (*10*) |
| | † *Cladoselache clarki* | UD-P | 385 | 300.0 | (*24*) |
| | † *Helicoprion bessonovi* | LP | 299 | 100.0 | (*10*) |
| | † Eugeneodontidae unnamed | Tr | 251 | 80.0 | (*10*) |
| | † *Caseodus eatoni* | P | 299 | 95.0 | (*9*) |
| | † *Fadenia crenulata* | Pn | 318 | 133.3 | (*9*) |
| | † *Heteropetalus elegantulus* | M | 360 | 12.0 | (*10*) |
| | † *Belantsea montana* | M | 360 | 27.5 | (*10, 24*) |
| | † *Janassa bituminosa* | M-LP | 360 | 54.0 | (*10*) |
| | † *Stethacanthus tumidus* | UD-Pn | 385 | 150.0 | (*24*) |
| | † *Orestiacanthus fergusi* | Pn | 318 | 28.0 | (*25*) |
| | † *Damocles serratus* | M | 360 | 20.0 | (*10*) |
| | † *Falcatus falcatus* | M | 360 | 15.0 | (*10, 24*) |
| | † *Symorium reniforme* | M-Pn | 360 | 300.0 | (*10*) |
| | † *Cobelodus aculeata* | M | 360 | 158.3 | (*9*) |
| | † *Helodus simplex* | M | 360 | 45.0 | (*15*) |
| | † *Chondrenchelys problematica* | M | 360 | 20.0 | (*15*) |
| | † *Harpagofututor volsellorhinus* | M | 360 | 10.0 | (*10*) |
| | † *Deltoptychius sp.* | M-Pn | 360 | 50.0 | (*10*) |
| | † *Menaspis armata* | UP | 260 | 16.0 | (*10*) |
| | † Cochliodontofomes unnamed 1 | M | 360 | 14.0 | (*10*) |
| | † Cochliodontofomes unnamed 2 | M | 360 | 11.0 | (*10*) |
| | † Cochliodontofomes unnamed 3 | M | 360 | 10.0 | (*10*) |
| | † Cochliodontofomes unnamed 4 | M | 360 | 9.0 | (*10*) |
| | † *Echinochimaera meltoni* | M | 360 | 8.0 | (*10*) |
| | † *Delphyodontos dacriformes* | M | 360 | 11.0 | (*10*) |
| | † *Acanthorhina jaekeli* | LJ | 200 | 50.0 | (*10*) |
| | † *Ischyodus quenstedti* | MJ-PC | 161 | 142.0 | (*10*) |
| | † *Ischyodus avitus* | UJ | 161 | 84.0 | (*26*) |
| | *Chimaera monstrosa* | R | 0 | 150.0 | (*3*) |
| | *Hydrolagus affinis* | R | 0 | 130.0 | (*3*) |
| | *Rhinochimaera pacifica* | R | 0 | 130.0 | (*3*) |
| | † Iniopterygiiformes unnamed 1 | M | 360 | 10.0 | (*10*) |
| | † Iniopterygiiformes unnamed 2 | M | 360 | 10.0 | (*10*) |
| | † *Iniopteryx rushlaui* | Pn | 318 | 24.0 | (*10*) |
| | † *Iniopera richardsoni* | Pn | 318 | 24.0 | (*10*) |
| | † *Sibirhynchus denisoni* | Pn | 318 | 20.0 | (*10*) |
| | † *Doliodus problematicus* | LD | 416 | 75.0 | (*27*) |

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**Appendix 1.** *Continued*

| Class | Taxon | Horizon | Min. Age | TL (cm) | Reference |
|---|---|---|---|---|---|
| | † Elasmobranchii *unnamed* | M | 360 | 18.0 | (*10*) |
| | † *Antarctilamna prisca* | MD | 398 | 60.0 | (*9, 28*) |
| | † *Expleuracanthus gaudryi* | Pn | 318 | 58.0 | (*10*) |
| | † *Orthacanthus senckenbegianus* | LP | 299 | 300.0 | (*26*) |
| | † *Triodus sesselis* | LP | 299 | 50.0 | (*10*) |
| | † *Xenacanthus meisenheimensis* | LP | 299 | 75.0 | (*10, 24*) |
| | † *Ctenacanthus costellatus* | UD | 385 | 150.0 | (*15*) (*24*) |
| | † *Goodrichichthys sp.* | M | 360 | 250.0 | (*15*) |
| | † *Onychoselache traquairi* | M | 360 | 24.0 | (*9*) |
| | † *Hamiltonichthys mapesi* | Pn | 318 | 28.0 | (*10*) |
| | † *Hybodus hauffianis* | UP-UK | 260 | 260.0 | (*10*) |
| | † *Wodnika striaula* | UP | 260 | 48.0 | (*10*) |
| | † *Acronemus tuberculatus* | LTr-UK | 251 | 29.0 | (*10*) |
| | † *Heterodontus falcifer* | UJ-R | 161 | 28.0 | (*10*) |
| | † *Paracestracion zitteli* | UJ | 161 | 15.0 | (*10*) |
| | † *Notidanoides muensteri* | UJ | 161 | 300.0 | (*29*) |
| | † *Hexanchus gracilis* | UK | 86 | 29.0 | (*10*) |
| | † *Chlamydoselachus thompspni* | UK | 100 | 200.0 | (*29*) |
| | † *Chlamydoselachus lawleyi* | PL | 5 | 200.0 | (*29*) |
| | *Chlamydoselachus anguineus* | R | 0 | 200.0 | (*3*) |
| | † Orodontiformes unnamed | M | 360 | 300.0 | (*10*) |
| | † *Macrourogaleus hassei* | UJ | 161 | 12.0 | (*10*) |
| | † *Paleoscyllium formosum* | UJ-UK | 161 | 60.0 | (*10*) |
| | † *Scyliorhinus elongatus* | UK | 100 | 23.0 | (*10*) |
| | † Scyliorhinidae *unammed* | UK | 100 | 87.0 | (*10*) |
| | † *Paratriakis curtirostris* | UK | 100 | 29.0 | (*10*) |
| | † *Carcharodon (=Carcharocles?) megalodon* | ME-Pl | 49 | 1200.0 | (*10*) |
| | † *Eogaleus bolcensis* | ME | 49 | 110.0 | (*10*) |
| | † *Galeorhinus cuvieri* | ME | 49 | 78.0 | (*10*) |
| | † *Squalicorax falcatus* | UK-PC | 100 | 188.0 | (*10*) |
| | † *Scapanorhynchus lewisii* | UK | 100 | 65.0 | (*10*) |
| | † *Orectolobus jurrasicus* | UJ | 161 | 30.0 | (*10*) |
| | † *Paleocarcharius stromeri* | UJ | 161 | 86.0 | (*10*) |
| | † *Phorcynis catulina* | UJ | 161 | 40.0 | (*10*) |
| | † *Mesiteia emiliae* | UK | 100 | 27.0 | (*10*) |
| | † *Aellopus bugesiacus* | UJ | 161 | 110.0 | (*10*) |
| | † *Asterodemus platypterus* | UJ | 161 | 46.0 | (*10*) |
| | † *Belemnobatis sismondae* | UJ | 161 | 40.0 | (*10*) |
| | † *Cyclobatis major* | LK | 146 | 13.0 | (*10*) |
| | † *Pararaja expansa* | UK | 100 | 23.0 | (*10*) |
| | † *Rhinobatos hakelensis* | UK | 100 | 28.0 | (*10*) |
| | † *Rhombopterygia rajoides* | UK | 100 | 42.0 | (*10*) |
| | † *Micropristis solonis* | UK | 100 | 53.0 | (*10*) |
| | † *Sclerorhynchus atavus* | UK | 100 | 100.0 | (*10*) |
| | † *Heliobatis radiens* | EC | 57 | 40.0 | (*10*) |
| | † *Zapteryx bichuti* | EC | 57 | 47.0 | (*10*) |
| | † *Trygon muricata* | ME | 49 | 73.0 | (*10*) |
| | † *Promyliobatis gazoae* | ME | 49 | 45.0 | (*10*) |
| | † *Platyrhina egertoni* | ME | 49 | 55.0 | (*10*) |
| | † *Trigonorhina dezignii* | ME | 49 | 79.0 | (*10*) |
| | † *Urolophus crassicaudatus* | ME | 49 | 80.0 | (*10*) |
| | † *Protospinax annectens* | UJ | 161 | 146.0 | (*10*) |
| | † *Centrophoroides latidens* | UK | 100 | 37.0 | (*10*) |
| | † *Pseudothina alifera* | UJ | 161 | 96.0 | (*10*) |
| | † *Torpdeo sp.* | ME | 49 | 38.0 | (*10*) |
| | † *Narcine molini* | LE | 41 | 90.0 | (*10*) |
| Acanthodii | † *Lupopsyrus pygmaeus* | LD | 416 | 3.3 | (*30*) |
| | † *Climatius reticulatus* | US-LD | 423 | 14.0 | (*10, 17*) |
| | † *Mesacanthus mitchelli* | LD-MD | 416 | 15.0 | (*10, 17*) |


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**Appendix 1.** *Continued*

| Class | Taxon | Horizon | Min. Age | TL (cm) | Reference |
|---|---|---|---|---|---|
| | † *Cheiracanthus latus* | UD | 385 | 30.0 | (*10*) |
| | † *Homalacanthus concinnus* | UD-M | 385 | 15.0 | (*10*) |
| | † *Triazeugacanthus affinis* | UD | 385 | 10.0 | (*10*) |
| | † *Acanthodes bronni* | Pn-LP | 318 | 50.0 | (*10, 17*) |
| | † *Utahacanthus guntheri* | Pn | 318 | 10.0 | (*10*) |
| | † *Traquairichthys pygmaeus* | Pn-LP | 318 | 10.0 | (*10, 17*) |
| | † *Paucicanthus vanelsti* | LD | 416 | 4.0 | (*31*) |
| | † *Poracanthodes menneri* | US-LD | 423 | 3.3 | (*30*) |
| | † *Euthacanthus macnicolli* | LD | 416 | 14.0 | (*10*) |
| | † *Parexus falcatus* | LD | 416 | 14.0 | (*10*) |
| | † *Vernicomacanthus uncinatus* | LD | 416 | 15.0 | (*10*) |
| | † *Diplacanthus striatus* | MD-UD | 398 | 20.0 | (*26*) |
| | † *Rhadinacanthus longispinatus* | MD | 398 | 16.0 | (*10*) |
| | † *Ischnicanthus gracilis* | LD | 416 | 35.0 | (*10*) |
| Sarcopterygii | † *Psarolepis romeri* | US-LD | 423 | 10.0 | (*32*) |
| | † *Diabolepis speratus* | LD | 416 | 30.0 | (*33*) |
| | † *Onychodus sigmoides* | LD | 416 | 200.0 | (*9*) |
| | † *Strunius walteri* | MD | 398 | 10.0 | (*15*) |
| | † *Miguashaia bureaui* | MD | 398 | 50.0 | (*9*) (*34*) |
| | † *Diplurus macropterus* | LP | 299 | 25.0 | (*10*) |
| | † *Diplurus newarki* | UD | 385 | 25.0 | (*15*) |
| | † *Lochmocerus aciculiodontus* | M | 360 | 11.0 | (*10*) |
| | † *Allenypterus montanus* | M | 360 | 14.0 | (*10*) |
| | † *Coelacanthus granulatus* | P | 299 | 56.5 | (*15*) |
| | † *Whiteia woodwardi* | LTr | 251 | 75.0 | (*35*) |
| | † *Rhabdoderma elegans* | UTr | 228 | 15.0 | (*26*) |
| | † *Axelrodichthys araripensis* | LK | 146 | 70.0 | (*26*) |
| | † *Macropoma lewesiensis* | UK | 85 | 60.0 | (*35–37*) |
| | *Latimeria spp.* | R | 0 | 180.0 | (*3*) |
| | † *Uranolophus wyomingensis* | LD | 416 | 100.0 | (*38*) |
| | † *Holoptychius quebecensis* | UD | 385 | 43.0 | (*26*) |
| | † *Porolepis elongata* | LD | 416 | 100.0 | (*9, 24*) |
| | † *Porolepis brevis* | MD | 398 | 20.0 | (*10*) |
| | † *Laccognathus panderi* | UD | 385 | 100.0 | (*9*) |
| | † *Youngolepis preacursor* | LD | 416 | 30.0 | (*33*) |
| | † *Holodipterus longi* | UD | 385 | 45.0 | (*9*) |
| | † *Dipterus valenciennesi* | MD | 398 | 22.0 | (*15*) |
| | † *Griphognathus whitei* | UD | 385 | 70.0 | (*9*) |
| | † *Scaumenacia curta* | UD | 385 | 60.0 | (*26, 39*) |
| | † *Phaneropleuron andersoni* | UD | 385 | 20.0 | (*40*) |
| | † *Ptychoceratodus philippsi* | LTr | 251 | 60.0 | (*41*) |
| | *Neoceratodus forsteri* | UK | 146 | 170.0 | (*3*) |
| | † *Palaedaphus insignis* | UD | 385 | 200 | (*28*) |
| | † *Neoceratodus tuberculatus* | UK | 100 | 200 | (*42*) |
| | † *Rhinodipterus ulrichi* | UD | 385 | 28 | (*43*) |
| | † *Protopterus protopteroides* | LK | 146 | 70.0 | (*42*) |
| | *Protopterus spp.* | EC | 56 | 93.3 | (*3*) |
| | *Lepidosiren paradoxa* | MC | 23 | 125.0 | (*3*) |
| | † *Strepsodus anculonamensis* | M | 360 | 30.0 | (*9*) |
| | † *Osteolepis macrolepidotus* | MD | 398 | 21.0 | (*15*) |
| | † *Eusthenopteron foordi* | UD | 385 | 25.0 | (*26*) |
| | † *Elpistostege watsoni* | UD | 385 | 50.0 | (*9*) |
| | † *Panderichthys rhombolepis* | UD | 385 | 145.0 | (*44*) |
| | † *Sauripteris taylori* | UD | 385 | 200.0 | (*26*) |
| | † *Acanthostega gunnari* | UD | 385 | 63.0 | (*26*) |
| | † *Ichthyostega sp.* | UD | 385 | 100.0 | (*45*) |
| Actinopterygii | † *Andreolepis hedei* | US | 423 | 25.0 | (*9, 46*) |
| | † *Dialipina salgueiroensis* | LD | 416 | 25.0 | (*47*) |
| | † *Cheirolepis canadensis* | MD | 398 | 30.0 | (*48, 49*) |

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**Appendix 1.** *Continued*

| Class | Taxon | Horizon | Min. Age | TL (cm) | Reference |
|---|---|---|---|---|---|
| | † *Cheirolepis tralii* | MD | 398 | 25.0 | (*10*) |
| | † *Cheirolepis schultzi* | MD | 398 | 10.0 | (*48*) |
| | † *Stegotrachelys finlayi* | MD | 398 | 9.0 | (*10*) |
| | † *Moythomasia nitida* | MD | 398 | 10.0 | (*10, 14, 50*) |
| | † *Howqualepis rostridens* | UD | 385 | 95.0 | (*28, 50*) |
| | † *Mimia paravertebra* | UD | 385 | 20.0 | (*9, 28, 50*) |
| | † *Mentzichthys walsjhi* | UD | 374 | 9.0 | (*10*) |
| | † *Sundayichthys elegantulus* | UD | 374 | 25.0 | (*10*) |
| | † *Guildayichthys carnegie* | M | 360 | 8 | (*51*) |
| | † *Aetheretmon valentiacum* | M | 360 | 9.0 | (*10*) |
| | † *Rhadinichthys carinatus* | M | 360 | 11.0 | (*10*) |
| | † *Canobius ramsayi* | M | 360 | 6.0 | (*10*) |
| | † *Coruboniscus budensis* | M | 360 | 3.0 | (*10*) |
| | † *Benedenus deneensis* | M | 360 | 22.0 | (*10*) |
| | † *Holurus parki* | M | 360 | 12.0 | (*10*) |
| | † *Nematoptychius greenocki* | M | 360 | 45.0 | (*10*) |
| | † *Drydenius insignis* | M | 360 | 10.0 | (*10*) |
| | † *Gonatodus punctatus* | M | 360 | 17.0 | (*10*) |
| | † *Acrolepis ortholepis* | M | 360 | 30.0 | (*10*) |
| | † *Acrolepis sedgwickii* | M | 360 | 60.0 | (*52*) |
| | † *Paramblypterus gelberti* | P | 299 | 25.0 | (*53*) |
| | † *Ganolepis gracilis* | P | 299 | 7.0 | (*10*) |
| | † *Acrolophis stensioei* | P | 299 | 65.0 | (*10*) |
| | † *Pygopterus humboldti* | UP | 260 | 60.0 | (*52*) |
| | † *Elonichthys punctatus* | LP | 260 | 8.0 | (*10*) |
| | † *Reticulepis exsculpta* | UP | 260 | 57.0 | (*10*) |
| | † *Bobasatriana canadensis* | Tr | 251 | 67.0 | (*26*) |
| | † *Apatolepis australis* | MTr | 228 | 14.0 | (*10*) |
| | † *Mesembroniscus longisquamosus* | MTr | 228 | 8.0 | (*10*) |
| | † *Polypterus dageti* | UK | 98.6 | 54.1 | (*54*) |
| | † *Mesopoma politum* | M | 360 | 7.0 | (*10*) |
| | † *Mesopoma planti* | Pn | 318 | 7.0 | (*55*) |
| | † *Dorypterus hoffmanni* | P | 299 | 12.0 | (*52*) |
| | † *Paleoniscum freislebeni* | UP | 260 | 19.0 | (*26*) |
| | † *Birgeria groenlandica* | LTr | 251 | 84.0 | (*56*) |
| | † *Saurichthys seefeldensis* | MTr | 228 | 180.0 | (*9*) |
| | † *Boreosomus gillioti* | LTr | 251 | 13.0 | (*10*) |
| | † *Perleidus madagascarensis* | LTr | 251 | 12.0 | (*26*) |
| | † *Redfieldius gracilis* | UTr | 228 | 19.0 | (*26*) |
| | † *Chondrosteus hindenburgi* | LJ | 200 | 300.0 | (*10*) |
| | † *Dapedium pholidotum* | LJ | 200 | 26.0 | (*26*) |
| | † *Peipiaosteus pani* | UJ | 161 | 60.0 | (*56*) |
| | † *Protopsephurus liui* | UJ | 161 | 23.3 | (*52*) |
| | † *Protoscaphirhynchus squamosus* | LK | 146 | 56.0 | (*10*) |
| | † *Polyodon tuberculata* | EC | 55 | 260.5 | (*3*) |
| | † *Crossopholis magnicaudata* | EC | 55 | 39.0 | (*10*) |
| | *Huso spp.* | R | 0 | 530.0 | (*3*) |
| | *Acipenser sinensis* | R | 0 | 130.0 | (*3*) |
| | *Scaphirhynchus spp.* | R | 0 | 140.0 | (*3*) |
| | *Pseudoscaphirhynchus* | R | 0 | 56.0 | (*3*) |
| | *Psephurus gladius* | R | 0 | 300.0 | (*3*) |
| | † *Paralepidotus ornatus* | UTr | 228 | 30.0 | (*57*) |
| | † *Semionotus agassizii* | UTr | 228 | 29.0 | (*26*) |
| | † *Pachchormus eoconus* | LJ | 200 | 94.0 | (*26*) |
| | † *Caturus velifer* | UJ | 161 | 57.0 | (*26*) |
| | † *Strobilodus giganteus* | UJ | 161 | 177.0 | (*10*) |
| | † *Amiopsis dolloi* | LK | 146 | 14.0 | (*10*) |
| | † *Calamopleurus cylindricus* | LK | 146 | 91.0 | (*26*) |
| | † *Lepisosteus simplex* | LK | 146 | 73.0 | (*26*) |

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**Appendix 1.** *Continued*

| Class | Taxon | Horizon | Min. Age | TL (cm) | Reference |
|---|---|---|---|---|---|
| | † *Obaichthys decoratus* | LK | 146 | 65.0 | (*26*) |
| | † *Teoichthys kallistos* | LK | 146 | 25.0 | (*26*) |
| | † *Neoproscinetes penalvi* | LK | 146 | 30.0 | (*26*) |
| | *Amia calva* | EC | 50 | 109.0 | (*3*) |
| | † *Amia scutata* | EC | 50 | 70.0 | (*58*) |
| | † *Pholidophorus bechei* | LJ | 200 | 20.0 | (*26*) |
| | † *Parapholidophorus caffi* | UTr | 228 | 8.0 | (*10*) |
| | † *Pholidophorus macrocephalus* | LJ | 200 | 33.0 | (*10*) |
| | † *Aspidorhynchus acutirostris* | UJ | 161 | 57.0 | (*26*) |
| | † *Vinctifer comptoni* | LK | 146 | 75.0 | (*26*) |
| | † *Longileptolepis weidenothi* | LJ | 183 | 37.4 | (*49*) |
| | † *Humbertia operta* | UK | 100 | 10.0 | (*10*) |
| | † *Leptolepides haertesi* | UJ | 150 | 5.4 | (*59*) |
| | † *Leptolepides spratiformis* | UJ | 150 | 9.1 | (*59*) |
| | † *Longileptolepis wiedenrothi* | UJ | 161 | 36.0 | (*49*) |
| | † *Orthogonikleithrus hoelli* | UJ | 161 | 4.5 | (*59*) |
| | † *Orthogonikleithrus leichi* | UJ | 161 | 10.1 | (*59*) |
| | † *Cavenderichthys talbragarensis* | LJ | 183 | 12.0 | (*10*) |
| | † *Cladocyclus gardneri* | LK | 146 | 111.0 | (*26*) |
| | † *Gillicus arcuatus* | LK | 146 | 157.0 | (*10*) |
| | † *Ichthyodectes ctenodon* | LK | 146 | 220.0 | (*10*) |
| | † *Pachythrissops propterus* | UJ | 150 | 38.0 | (*10*) |
| | † *Thrissops formosus* | UJ | 150 | 28.0 | (*10*) |
| | † *Antarctithrissops australis* | UJ | 150 | 30.0 | (*60*) |
| | † *Xiphactinus audax* | UK | 100 | 430.0 | (*10*) |
| | † *Eohiodon falcatus* | EC | 50 | 17.0 | (*10*) |
| | *Hiodon tergisus* | EC | 50 | 50.0 | (*59*) |
| | † *Lycoptera davidi* | LK | 146 | 8.0 | (*10*) |
| | *Arapiama gigas* | MM | 15 | 450.0 | (*61*) |
| | *Heterotis niloticus* | R | 0 | 100.0 | (*3*) |
| | *Osteoglossum bicirrhosum* | R | 0 | 120.0 | (*3*) |
| | *Pantodon buchholzi* | R | 0 | 10.0 | (*3*) |
| | † *Phareodus testis* | EC | 54 | 31.0 | (*10*) |
| | † *Singida jacksonoides* | EC | 54 | 18.0 | (*62*) |
| | † *Chauliopareion mahengeense* | EC | 45 | 9.0 | (*62*) |
| | † *Lebonichthys lewisi* | UK | 100 | 30.0 | (*10*) |
| | † *Mylomyrus frangens* | EC | 54 | 31.0 | (*10*) |
| | † *Notelops brama* | LK | 146 | 73.0 | (*10*) |
| | † *Rhacolepis buccalis* | LK | 146 | 14.0 | (*10*) |
| | † *Spaniodon elongatus* | UK | 100 | 18.0 | (*10*) |
| | † *Brannerion sp.* | LK | 146 | 45.0 | (*26*) |
| | † *Elops sp.* | UJ | 150 | 20.0 | (*59*) |
| | † *Eomyrophis latispinus* | EC | 57 | 24.0 | (*26*) |
| | † *Paraelops cearensis* | LK | 146 | 70.0 | (*10*) |
| | † *Anaethalion knorri* | UJ | 150 | 17.2 | (*59*) |
| | † *Daitingichtys tischlingeri* | UJ | 150 | 30.0 | (*10*) |
| | † *Araripicthys castilhoi* | LK | 146 | 42.0 | (*10*) |
| | *Denticeps clupeoides* | R | 0 | 15.0 | (*3*) |
| | † *Clupea humilis* | EC | 56 | 36.0 | (*3*) |
| | † *Ellimma branneri* | LK | 146 | 10.2 | (*63*) |
| | † *Ellimmichthys longicostatus* | LK | 146 | 10.4 | (*64*) |
| | † *Ellimmichthys goodi* | LK | 146 | 13.4 | (*64*) |
| | † *Diplomystus dentatus* | UK | 100 | 28.0 | (*10*) |
| | † *Diplomystus shengliensis* | LK | 146 | 5.5 | (*63*) |
| | † *Paraclupea chetungensis* | LK | 146 | 9.0 | (*64*) |
| | † *Palaeodenticeps tanganyikae* | OC | 34 | 3.0 | (*10*) |
| | † *Engraulis eurystole* | EC | 54 | 15.5 | (*59*) |
| | † *Knightia eocaena* | EC | 57 | 9.0 | (*26*) |
| | † *Santanaclupea silvasantosi* | LK | 125 | 12.0 | (*65*) |

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**Appendix 1.** *Continued*

| Class | Taxon | Horizon | Min. Age | TL (cm) | Reference |
|---|---|---|---|---|---|
| | † *Protoclupea chilensis* | UJ | 150 | 9.7 | (*59*) |
| | † *Aethalionopsis robusta* | UK | 100 | 17.0 | (*10*) |
| | † *Chanoides macropoma* | EC | 50 | 12.0 | (*10*) |
| | *Chanos chanos* | EC | 54 | 170.0 | (*3*) |
| | † *Chanos zignii* | UK | 100 | 39.0 | (*10*) |
| | † *Charitosomus hekelensis* | UK | 100 | 14.0 | (*10*) |
| | † *Notogoneus osculus* | EC | 54 | 58.0 | (*10*) |
| | † *Parachanos aethiopicus* | UK | 100 | 22.0 | (*10*) |
| | † *Tischlingerichthys viohli* | UJ | 150 | 12.8 | (*59*) |
| | † *Santanichthys diasii* | UK | 100 | 6.8 | (*65, 66*) |
| | † *Amyzon aggregatus* | EC | 54 | 22.0 | (*10*) |
| | † *Esox lepidotus* | PC | 61 | 70.0 | (*10*) |
| | † *Umbra krameri* | EC | 54 | 17.0 | (*3*) |
| | † *Umbra perpusilla* | EC | 54 | 3.0 | (*10*) |
| | *Dallia pectoralis* | R | 0 | 33.0 | (*3*) |
| | † *Estesesox tiemani* | PC | 61 | 30.0 | (*67*) |
| | † *Beurlenichthys ouricuriensis* | LK | 125 | 6.0 | (*65, 68*) |
| | † *Boltyshia brevicauda* | PC | 61 | 8.0 | (*10*) |
| | † *Prostomias maroccanus* | LK | 125 | 17.0 | (*10*) |
| | † *Dactylopogon grandis* | UK | 95 | 44.0 | (*10*) |
| | † *Hakelia laticauda* | UK | 95 | 9.0 | (*10*) |
| | † *Leptosoma elongatus* | UK | 95 | 8.0 | (*10*) |
| | † *Nematonotus longispinnus* | UK | 95 | 14.0 | (*10*) |
| | † *Tachynectes longipes* | UK | 95 | 27.0 | (*10*) |
| | † *Sardinoides monasterii* | UK | 95 | 18.0 | (*10*) |
| | † *Digoria ambigua* | UK | 95 | 7.0 | (*10*) |
| | † *Dinopteryx spinosus* | UK | 95 | 14.0 | (*10*) |
| | † *Aipichthys vilifer* | UK | 95 | 8.0 | (*10*) |
| | † *Pycnosteroides* | UK | 95 | 7.0 | (*10*) |
| | † *Stichocentrus livatus* | UK | 95 | 6.0 | (*10*) |
| | † *Enchodus macropterus* | UK | 95 | 23.0 | (*10*) |
| | † *Leptecodon rectus* | UK | 95 | 23.0 | (*10*) |
| | † *Palaeolycus dregensis* | UK | 95 | 40.0 | (*10*) |
| | † *Halec microlepis* | UK | 95 | 18.0 | (*10*) |
| | † *Phylactocephalus microlepis* | UK | 95 | 15.0 | (*10*) |
| | † *Apateopholis laniatus* | UK | 95 | 31.0 | (*10*) |
| | † *Ichthyotringa furcata* | UK | 95 | 15.0 | (*10*) |
| | † *Sardinius cordieri* | UK | 95 | 14.0 | (*10*) |
| | † *Ctenocephalichtys loreti* | UK | 95 | 5.0 | (*10*) |
| | † *Myripristis homopterygius* | ME | 49 | 11.0 | (*10*) |
| | † *Paraspinus cupulus* | UK | 95 | 16.0 | (*10*) |
| | † *Stichoberyx polydesmus* | LK | 125 | 8.0 | (*10*) |
| | † *Acrogaster heckeli* | UK | 95 | 7.0 | (*10*) |
| | † *Hoplopteryx antiquus* | UK | 95 | 13.0 | (*10*) |
| | † *Libanoberyx spinosus* | UK | 95 | 5.5 | (*10*) |
| | † *Lissoberyx arambourgi* | UK | 95 | 6.0 | (*10*) |
| | † *Stichopteryx lewisi* | UK | 95 | 7.0 | (*10*) |
| | † *Tubantia cataphractus* | UK | 95 | 16.0 | (*10*) |
| | † *Sphenocephalus fissicaudus* | UK | 95 | 11.0 | (*10*) |
| | † *Ctenothrissa vexillifer* | UK | 95 | 9.0 | (*10*) |
| | † *Mcconichthys longipinnis* | UK | 95 | 33.0 | (*10*) |
| | † *Humilichthys orientalis* | UK | 95 | 4.5 | (*10*) |
| | † *Pattersonichthys delicatus* | UK | 95 | 4.0 | (*10*) |
| | † *Phonicolepis arcuatus* | UK | 95 | 5.0 | (*10*) |
| | † *Omosoma sahelalmae* | UK | 95 | 8.0 | (*10*) |
| | † *Platycornus germanus* | UK | 95 | 20.0 | (*10*) |
| | † *Pycnosterinx russeggeri* | UK | 95 | 5.0 | (*10*) |


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**Appendix 2. The extant fish dataset.** Size (average standard length in cm and ln cm), size variation (standard deviation, skew, kurtosis) and species richness (N) for all 515 recognized extant fish families. Data summaries of maximum recorded standard lengths for 24,259 species from (Froese and Pauly 2005). NA, not applicable. Taxa sorted alphabetically by species.

| Family | N | Avg. (cm) | Avg. (ln cm) | Stdev | Skew | Kurt |
|---|---|---|---|---|---|---|
| Abyssocottidae | 13 | 15.0 | 2.6 | 0.4 | –0.2 | 0.7 |
| Acanthuridae | 79 | 38.1 | 3.5 | 0.5 | 0.0 | –0.6 |
| Acestrorhynchidae | 15 | 19.1 | 2.8 | 0.6 | –0.3 | –1.6 |
| Achiridae | 31 | 14.5 | 2.6 | 0.5 | –0.8 | –0.1 |
| Achiropsettidae | 6 | 33.1 | 3.2 | 0.9 | –1.0 | –0.9 |
| Acipenseridae | 25 | 239.3 | 5.3 | 0.7 | –0.6 | 1.0 |
| Adrianichthyidae | 25 | 5.1 | 1.4 | 0.6 | 0.8 | 0.8 |
| Agonidae | 37 | 18.3 | 2.8 | 0.4 | 0.0 | –0.4 |
| Akysidae | 35 | 6.9 | 1.8 | 0.5 | 0.4 | –0.7 |
| Albulidae | 6 | 75.8 | 4.3 | 0.4 | –0.7 | –1.3 |
| Alepisauridae | 2 | 155.5 | 5.0 | 0.6 | – | – |
| Alepocephalidae | 78 | 32.7 | 3.4 | 0.4 | 0.3 | 0.3 |
| Alestiidae | 107 | 16.2 | 2.4 | 0.8 | 0.9 | 0.9 |
| Alopiidae | 3 | 543.7 | 6.3 | 0.3 | 0.8 | – |
| Amarsipidae | 1 | 12.0 | 2.5 | – | – | – |
| Ambassidae | 45 | 9.4 | 2.1 | 0.5 | –0.8 | 0.9 |
| Amblycipitidae | 14 | 8.5 | 2.1 | 0.4 | 0.2 | –1.5 |
| Amblyopsidae | 6 | 8.2 | 2.1 | 0.2 | 0.3 | –1.2 |
| Amiidae | 1 | 109.0 | 4.7 | – | – | – |
| Ammodytidae | 23 | 18.5 | 2.8 | 0.4 | 0.2 | –0.3 |
| Amphiliidae | 65 | 8.9 | 2.0 | 0.6 | 0.0 | 0.4 |
| Anabantidae | 35 | 11.7 | 2.3 | 0.6 | 0.2 | –0.8 |
| Anablepidae | 11 | 14.2 | 2.3 | 0.8 | 0.4 | –1.2 |
| Anacanthobatidae | 5 | 34.0 | 3.5 | 0.3 | –0.7 | –2.3 |
| Anarhichadidae | 5 | 170.0 | 5.1 | 0.3 | –0.8 | 1.3 |
| Anguillidae | 18 | 137.6 | 4.9 | 0.3 | –0.4 | 0.3 |
| Anomalopidae | 6 | 13.9 | 2.4 | 0.7 | 0.8 | 2.0 |
| Anoplogasteridae | 2 | 10.6 | 2.3 | 0.7 | – | – |
| Anoplopomatidae | 2 | 151.5 | 5.0 | 0.3 | – | – |
| Anostomidae | 72 | 21.4 | 2.9 | 0.5 | –0.1 | –0.4 |
| Anotopteridae | 3 | 115.7 | 4.7 | 0.2 | 1.4 | – |
| Antennariidae | 44 | 15.0 | 2.5 | 0.6 | 0.1 | –0.7 |
| Aphredoderidae | 1 | 14.0 | 2.6 | – | – | – |
| Aphyonidae | 11 | 9.4 | 2.2 | 0.4 | 0.4 | 0.4 |
| Apistidae | 2 | 19.5 | 3.0 | 0.0 | – | – |
| Aploactinidae | 2 | 6.0 | 1.5 | 1.1 | – | – |
| Aplocheilidae | 225 | 5.8 | 1.7 | 0.2 | 0.3 | 0.7 |
| Aplodactylidae | 5 | 41.1 | 3.6 | 0.5 | –1.3 | 2.2 |
| Apogonidae | 281 | 8.8 | 2.1 | 0.5 | –0.1 | –0.4 |
| Apteronotidae | 46 | 33.5 | 3.4 | 0.4 | 1.3 | 2.9 |
| Arapaimidae | 2 | 275.0 | 5.4 | 1.1 | – | – |
| Argentinidae | 20 | 19.2 | 2.8 | 0.5 | 1.0 | 2.5 |


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**Appendix 2.** *Continued*

| Family | N | Avg. (cm) | Avg. (ln cm) | Stdev | Skew | Kurt |
|---|---|---|---|---|---|---|
| Ariidae | 122 | 48.1 | 3.7 | 0.5 | 0.5 | 0.5 |
| Ariommatidae | 8 | 38.0 | 3.5 | 0.5 | 0.9 | 0.1 |
| Arripidae | 4 | 77.8 | 4.3 | 0.4 | –1.9 | 3.7 |
| Artedidraconidae | 27 | 19.2 | 2.9 | 0.5 | –1.3 | 1.8 |
| Aspredinidae | 36 | 9.5 | 1.9 | 0.8 | 0.0 | –0.4 |
| Astroblepidae | 53 | 8.8 | 2.1 | 0.4 | 0.1 | 2.9 |
| Ateleopodidae | 6 | 127.0 | 4.7 | 0.7 | –0.6 | –1.3 |
| Atherinidae | 54 | 9.7 | 2.2 | 0.4 | 0.1 | 0.4 |
| Atherinopsidae | 41 | 15.9 | 2.6 | 0.6 | 0.6 | 0.1 |
| Auchenipteridae | 76 | 14.2 | 2.4 | 0.7 | –0.2 | –0.2 |
| Aulopidae | 8 | 32.3 | 3.4 | 0.4 | 0.8 | –0.8 |
| Aulorhynchidae | 2 | 15.4 | 2.7 | 0.2 | – | – |
| Aulostomidae | 3 | 85.0 | 4.4 | 0.2 | 1.4 | – |
| Badidae | 16 | 4.0 | 1.3 | 0.4 | –0.1 | 0.4 |
| Bagridae | 219 | 30.3 | 3.0 | 0.8 | 0.2 | 0.0 |
| Balistidae | 39 | 41.4 | 3.6 | 0.5 | –0.4 | 0.0 |
| Balitoridae | 416 | 7.5 | 1.9 | 0.5 | 0.6 | 1.8 |
| Barbourisiidae | 1 | 34.5 | 3.5 | – | – | – |
| Bathyclupeidae | 2 | 19.5 | 3.0 | 0.1 | – | – |
| Bathydraconidae | 15 | 26.9 | 3.2 | 0.4 | 0.6 | 0.2 |
| Bathylagidae | 19 | 16.4 | 2.8 | 0.3 | 0.1 | –0.5 |
| Bathylutichthyidae | 1 | 10.0 | 2.3 | – | – | – |
| Bathymasteridae | 6 | 23.3 | 3.1 | 0.4 | 0.6 | –1.0 |
| Bathysauroididae | 1 | 29.0 | 3.4 | – | – | – |
| Batrachoididae | 62 | 25.1 | 3.1 | 0.6 | –0.8 | 0.3 |
| Bedotiidae | 11 | 8.1 | 2.0 | 0.4 | –0.2 | –0.6 |
| Belonidae | 43 | 68.7 | 4.0 | 0.8 | –1.0 | 1.7 |
| Bembridae | 6 | 22.7 | 3.1 | 0.4 | –1.7 | 3.1 |
| Berycidae | 9 | 50.8 | 3.8 | 0.5 | –0.3 | –0.9 |
| Blenniidae | 325 | 8.7 | 2.0 | 0.5 | 0.2 | 0.0 |
| Bothidae | 117 | 16.2 | 2.7 | 0.5 | –0.2 | 0.3 |
| Bovichtidae | 4 | 33.6 | 3.2 | 0.9 | 0.7 | 0.4 |
| Brachaeluridae | 2 | 99.0 | 4.6 | 0.3 | – | – |
| Brachionichthyidae | 2 | 11.5 | 2.4 | 0.4 | – | – |
| Bramidae | 19 | 51.4 | 3.8 | 0.6 | –1.5 | 3.6 |
| Bregmacerotidae | 12 | 6.4 | 1.7 | 0.7 | –1.2 | 0.7 |
| Bythitidae | 61 | 16.5 | 2.5 | 0.8 | 0.8 | 0.1 |
| Caesionidae | 20 | 29.4 | 3.3 | 0.4 | –0.1 | –0.3 |
| Callanthiidae | 9 | 26.1 | 3.1 | 0.7 | 0.2 | –0.7 |
| Callichthyidae | 173 | 5.2 | 1.6 | 0.4 | 0.9 | 3.4 |
| Callionymidae | 123 | 10.7 | 2.1 | 0.7 | –0.5 | –0.7 |
| Callorhinchidae | 3 | 112.1 | 4.7 | 0.2 | –1.7 | – |
| Caproidae | 8 | 15.7 | 2.6 | 0.6 | 0.0 | –0.9 |
| Caracanthidae | 4 | 4.5 | 1.5 | 0.3 | –2.0 | 4.0 |
| Carangidae | 141 | 68.9 | 4.1 | 0.5 | 0.2 | –0.3 |
| Carapidae | 33 | 19.8 | 2.9 | 0.4 | –0.1 | –0.7 |
| Carcharhinidae | 49 | 220.3 | 5.2 | 0.6 | 0.0 | –0.6 |
| Caristiidae | 4 | 27.6 | 3.3 | 0.3 | –1.9 | 3.7 |
| Catostomidae | 61 | 53.8 | 3.9 | 0.5 | –0.5 | –0.4 |
| Caulophrynidae | 3 | 16.4 | 2.8 | 0.2 | 1.6 | – |
| Centracanthidae | 8 | 28.4 | 3.3 | 0.2 | –0.4 | –1.0 |
| Centrarchidae | 30 | 37.1 | 3.4 | 0.7 | –0.5 | –0.5 |
| Centriscidae | 12 | 22.0 | 3.0 | 0.3 | 0.4 | –1.7 |
| Centrogeniidae | 1 | 25.0 | 3.2 | – | – | – |
| Centrolophidae | 25 | 63.7 | 4.0 | 0.7 | –0.6 | –0.5 |
| Centrophoridae | 14 | 117.3 | 4.7 | 0.3 | 0.2 | –1.3 |
| Centrophrynidae | 1 | 23.0 | 3.1 | – | – | – |
| Centropomidae | 22 | 85.9 | 4.3 | 0.6 | 0.2 | –1.2 |
| Cepolidae | 15 | 41.3 | 3.6 | 0.5 | –1.0 | 2.0 |

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**Appendix 2.** *Continued*

| Family | N | Avg. (cm) | Avg. (ln cm) | Stdev | Skew | Kurt |
|---|---|---|---|---|---|---|
| Ceratiidae | 4 | 69.0 | 4.1 | 0.7 | –0.4 | –2.1 |
| Ceratodontidae | 1 | 170.0 | 5.1 | – | – | – |
| Cetomimidae | 13 | 13.9 | 2.5 | 0.6 | 0.2 | –1.0 |
| Cetopsidae | 23 | 10.8 | 2.1 | 0.8 | –0.2 | –0.8 |
| Cetorhinidae | 1 | 900.0 | 6.8 | – | – | – |
| Chacidae | 3 | 20.0 | 3.0 | 0.0 | – | – |
| Chaenopsidae | 69 | 6.3 | 1.7 | 0.5 | 0.8 | 1.6 |
| Chaetodontidae | 125 | 17.1 | 2.8 | 0.2 | 0.0 | 0.2 |
| Champsodontidae | 12 | 11.2 | 2.4 | 0.2 | –0.2 | –0.5 |
| Chanidae | 1 | 124.0 | 4.8 | – | – | – |
| Channichthyidae | 19 | 45.4 | 3.8 | 0.3 | –0.1 | –1.2 |
| Channidae | 28 | 48.6 | 3.6 | 0.7 | 0.6 | –0.7 |
| Characidae | 842 | 9.7 | 1.9 | 0.8 | 0.7 | 0.3 |
| Chaudhuriidae | 9 | 5.5 | 1.7 | 0.3 | –0.8 | –0.3 |
| Chaunacidae | 14 | 21.6 | 3.0 | 0.4 | –0.1 | –1.2 |
| Cheilodactylidae | 23 | 56.2 | 3.9 | 0.6 | 0.5 | 0.2 |
| Cheimarrhichthyidae | 1 | 15.0 | 2.7 | – | – | – |
| Chiasmodontidae | 13 | 18.7 | 2.8 | 0.7 | –1.8 | 2.2 |
| Chilodontidae | 7 | 10.2 | 2.3 | 0.4 | 0.6 | –1.5 |
| Chimaeridae | 17 | 93.3 | 4.5 | 0.4 | –0.3 | –0.8 |
| Chirocentridae | 2 | 100.0 | 4.6 | 0.0 | – | – |
| Chironemidae | 3 | 31.7 | 3.4 | 0.4 | –1.5 | – |
| Chlamydoselachidae | 1 | 200.0 | 5.3 | – | – | – |
| Chlopsidae | 21 | 21.1 | 3.0 | 0.3 | 0.3 | –0.4 |
| Chlorophthalmidae | 9 | 24.3 | 3.1 | 0.3 | 0.0 | 0.0 |
| Cichlidae | 1456 | 15.2 | 2.6 | 0.6 | 0.2 | 0.3 |
| Cirrhitidae | 28 | 15.5 | 2.6 | 0.5 | 1.0 | 1.2 |
| Citharidae | 6 | 25.6 | 3.2 | 0.3 | –0.9 | 0.1 |
| Citharinidae | 102 | 19.9 | 2.3 | 1.1 | 0.4 | –1.1 |
| Clariidae | 102 | 40.8 | 3.4 | 0.8 | 0.1 | –0.2 |
| Clinidae | 79 | 14.5 | 2.5 | 0.6 | 0.5 | 0.3 |
| Clupeidae | 202 | 20.0 | 2.7 | 0.7 | –0.2 | –0.3 |
| Cobitidae | 137 | 11.5 | 2.2 | 0.6 | 0.5 | 0.1 |
| Coiidae | 5 | 37.4 | 3.6 | 0.2 | –0.3 | –2.1 |
| Colocongridae | 5 | 56.9 | 4.0 | 0.3 | 1.0 | 2.2 |
| Comephoridae | 2 | 18.5 | 2.9 | 0.2 | – | – |
| Congiopodidae | 6 | 39.9 | 3.6 | 0.5 | –0.2 | 0.9 |
| Congridae | 121 | 57.9 | 3.9 | 0.6 | –0.1 | 2.7 |
| Coryphaenidae | 2 | 168.5 | 5.1 | 0.4 | – | – |
| Cottidae | 190 | 16.3 | 2.6 | 0.7 | 0.3 | 0.2 |
| Cottocomephoridae | 6 | 19.8 | 3.0 | 0.2 | –1.1 | 1.8 |
| Cranoglanididae | 2 | 36.0 | 3.6 | 0.3 | – | – |
| Creediidae | 16 | 5.1 | 1.6 | 0.4 | –0.3 | –0.6 |
| Crenuchidae | 75 | 4.7 | 1.5 | 0.5 | –0.3 | –0.2 |
| Cryptacanthodidae | 3 | 79.3 | 4.2 | 0.7 | –1.5 | – |
| Ctenoluciidae | 7 | 7.0 | 3.6 | 3.6 | 0.4 | 1.5 |
| Curimatidae | 98 | 12.6 | 2.4 | 0.5 | –0.6 | –0.1 |
| Cyclopteridae | 19 | 13.3 | 2.2 | 0.8 | 0.8 | 1.4 |
| Cyematidae | 2 | 15.5 | 2.7 | 0.0 | – | – |
| Cynodontidae | 14 | 36.2 | 3.3 | 0.7 | 0.4 | –0.6 |
| Cynoglossidae | 113 | 21.0 | 2.9 | 0.6 | 0.1 | –0.1 |
| Cyprinidae | 1895 | 21.2 | 2.6 | 0.9 | 0.4 | –0.1 |
| Cyprinodontidae | 120 | 7.0 | 1.8 | 0.4 | 1.2 | 1.5 |
| Cyttidae | 3 | 45.0 | 3.8 | 0.2 | 1.7 | – |
| Dactylopteridae | 7 | 35.2 | 3.4 | 0.7 | 0.1 | 1.8 |
| Dactyloscopidae | 36 | 5.9 | 1.7 | 0.4 | 0.1 | 0.4 |
| Dalatiidae | 64 | 78.2 | 4.0 | 0.7 | 1.2 | 2.3 |
| Dasyatidae | 60 | 136.4 | 4.6 | 0.8 | –0.3 | –0.4 |
| Dentatherinidae | 1 | 5.0 | 1.6 | – | – | – |


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**Appendix 2.** *Continued*

| Family | N | Avg. (cm) | Avg. (ln cm) | Stdev | Skew | Kurt |
|---|---|---|---|---|---|---|
| Denticipitidae | 1 | 15.0 | 2.7 | – | – | – |
| Derichthyidae | 3 | 43.3 | 3.7 | 0.3 | 0.5 | – |
| Diceratiidae | 5 | 17.2 | 2.8 | 0.4 | 0.0 | –2.8 |
| Dichistiidae | 2 | 57.5 | 4.0 | 0.6 | – | – |
| Dinolestidae | 1 | 84.0 | 4.4 | – | – | – |
| Dinopercidae | 2 | 52.9 | 3.9 | 0.6 | – | – |
| Diodontidae | 20 | 41.4 | 3.7 | 0.4 | 0.7 | –0.4 |
| Diplomystidae | 6 | 24.2 | 3.2 | 0.2 | –0.3 | 1.2 |
| Diretmidae | 4 | 31.6 | 3.4 | 0.3 | –0.1 | –4.6 |
| Doradidae | 73 | 22.8 | 2.8 | 0.7 | 0.7 | 0.1 |
| Draconettidae | 10 | 9.8 | 2.3 | 0.2 | –1.4 | 3.5 |
| Drepaneidae | 3 | 48.3 | 3.9 | 0.1 | –1.7 | – |
| Echeneidae | 8 | 66.7 | 4.1 | 0.5 | –0.5 | –1.3 |
| Echinorhinidae | 2 | 218.0 | 5.3 | 0.6 | – | – |
| Elassomatidae | 5 | 3.6 | 1.3 | 0.2 | 2.1 | 4.5 |
| Eleginopidae | 1 | 60.0 | 4.1 | – | – | – |
| Eleotridae | 131 | 15.4 | 2.5 | 0.7 | 0.1 | –0.3 |
| Elopidae | 6 | 99.8 | 4.6 | 0.1 | 1.1 | 1.8 |
| Embiotocidae | 22 | 28.1 | 3.3 | 0.4 | –0.1 | –1.1 |
| Emmelichthyidae | 16 | 35.0 | 3.4 | 0.6 | –0.4 | 0.1 |
| Engraulidae | 139 | 13.8 | 2.5 | 0.6 | –0.3 | 0.2 |
| Enoplosidae | 1 | 50.0 | 3.9 | – | – | – |
| Ephippidae | 15 | 46.3 | 3.7 | 0.5 | –0.3 | 0.1 |
| Epigonidae | 20 | 19.4 | 2.7 | 0.7 | –0.2 | 1.5 |
| Erethistidae | 10 | 7.2 | 1.6 | 0.8 | 1.5 | 2.3 |
| Ereuniidae | 3 | 25.8 | 3.2 | 0.2 | –1.4 | – |
| Erythrinidae | 11 | 46.5 | 3.6 | 0.7 | 0.3 | –1.3 |
| Eschmeyeridae | 1 | 4.1 | 1.4 | – | – | – |
| Esocidae | 6 | 101.5 | 4.5 | 0.7 | –0.4 | –1.8 |
| Euclichthyidae | 1 | 35.0 | 3.6 | – | – | – |
| Eurypharyngidae | 1 | 100.0 | 4.6 | – | – | – |
| Evermannellidae | 5 | 15.0 | 2.7 | 0.2 | 0.1 | –4.6 |
| Exocoetidae | 57 | 26.7 | 3.2 | 0.3 | –0.1 | –0.3 |
| Fistulariidae | 4 | 157.5 | 5.0 | 0.5 | –1.8 | 3.0 |
| Fundulidae | 45 | 9.4 | 2.2 | 0.4 | 0.1 | 0.1 |
| Gadidae | 24 | 65.8 | 4.0 | 0.7 | 0.0 | –0.2 |
| Galaxiidae | 45 | 13.0 | 2.4 | 0.6 | 0.5 | –0.4 |
| Gasteropelecidae | 9 | 4.4 | 1.4 | 0.5 | 0.4 | –1.3 |
| Gasterosteidae | 10 | 9.3 | 2.2 | 0.4 | 1.7 | 3.9 |
| Gempylidae | 24 | 78.9 | 4.1 | 0.8 | 0.4 | –1.3 |
| Geotriidae | 4 | 35.8 | 3.4 | 0.7 | 0.1 | –5.6 |
| Gerreidae | 50 | 21.9 | 3.0 | 0.4 | –0.4 | 0.3 |
| Gibberichthyidae | 2 | 12.5 | 2.5 | 0.1 | – | – |
| Gigantactinidae | 19 | 18.2 | 2.7 | 0.7 | –0.5 | 0.1 |
| Giganturidae | 2 | 18.0 | 2.9 | 0.2 | – | – |
| Ginglymostomatidae | 3 | 275.0 | 5.4 | 0.9 | –1.5 | – |
| Glaucosomatidae | 4 | 67.3 | 4.1 | 0.6 | 0.4 | –0.9 |
| Gnathanacanthidae | 1 | 30.0 | 3.4 | – | – | – |
| Gobiesocidae | 114 | 5.4 | 1.5 | 0.6 | 0.3 | 0.2 |
| Gobiidae | 1070 | 7.6 | 1.8 | 0.7 | 0.3 | 0.0 |
| Gonorynchidae | 5 | 43.9 | 3.7 | 0.3 | –0.3 | –2.7 |
| Gonostomatidae | 28 | 12.5 | 2.2 | 0.8 | 0.3 | –1.0 |
| Goodeidae | 48 | 6.8 | 1.9 | 0.3 | 0.4 | 0.1 |
| Grammatidae | 12 | 4.7 | 1.4 | 0.6 | –0.2 | –0.8 |
| Grammicolepididae | 2 | 39.5 | 3.4 | 1.0 | – | – |
| Gymnarchidae | 1 | 167.0 | 5.1 | – | – | – |
| Gymnotidae | 25 | 34.0 | 3.2 | 0.7 | 1.4 | 4.1 |
| Gymnuridae | 9 | 167.6 | 4.9 | 0.8 | –0.5 | 0.4 |
| Gyrinocheilidae | 3 | 30.5 | 3.4 | 0.1 | 1.7 | – |

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**Appendix 2.** *Continued*

| Family | N | Avg. (cm) | Avg. (ln cm) | Stdev | Skew | Kurt |
|---|---|---|---|---|---|---|
| Haemulidae | 135 | 45.1 | 3.7 | 0.5 | –0.2 | –0.1 |
| Halosauridae | 13 | 54.5 | 4.0 | 0.2 | 0.4 | 1.3 |
| Harpagiferidae | 6 | 8.2 | 2.1 | 0.1 | 0.0 | –1.9 |
| Hemigaleidae | 7 | 117.5 | 4.7 | 0.5 | 0.1 | 1.6 |
| Hemiodontidae | 28 | 16.7 | 2.7 | 0.4 | –0.1 | –1.0 |
| Hemiramphidae | 101 | 19.8 | 2.8 | 0.7 | –0.3 | –0.7 |
| Hemiscylliidae | 13 | 74.5 | 4.3 | 0.2 | 0.1 | –0.1 |
| Hemitripteridae | 8 | 31.5 | 3.2 | 0.9 | –0.1 | –1.0 |
| Hepsetidae | 1 | 70.0 | 4.2 | – | – | – |
| Heptapteridae | 70 | 12.1 | 2.3 | 0.6 | 0.1 | –0.1 |
| Heterenchelyidae | 7 | 69.3 | 4.1 | 0.5 | 0.7 | –0.1 |
| Heterodontidae | 8 | 118.0 | 4.7 | 0.3 | –0.6 | –0.3 |
| Heteropneustidae | 3 | 24.0 | 3.1 | 0.4 | –1.6 | – |
| Hexagrammidae | 12 | 52.4 | 3.8 | 0.5 | 0.9 | 1.2 |
| Hexanchidae | 4 | 275.5 | 5.5 | 0.5 | 0.4 | –1.9 |
| Hexatrygonidae | 4 | 103.8 | 4.6 | 0.4 | –1.2 | 2.2 |
| Himantolophidae | 7 | 22.6 | 2.7 | 1.0 | 0.0 | –1.4 |
| Hiodontidae | 2 | 49.5 | 3.9 | 0.1 | – | – |
| Hispidoberycidae | 1 | 18.1 | 2.9 | – | – | – |
| Holocentridae | 81 | 23.2 | 3.1 | 0.4 | –0.1 | 0.6 |
| Hoplichthyidae | 8 | 21.9 | 3.0 | 0.5 | –0.8 | 2.3 |
| Hypopomidae | 14 | 18.7 | 2.8 | 0.4 | 0.0 | –0.6 |
| Hypoptychidae | 1 | 6.7 | 1.9 | – | – | – |
| Icosteidae | 1 | 213.0 | 5.4 | – | – | – |
| Ictaluridae | 40 | 31.0 | 2.9 | 0.9 | 0.9 | 0.0 |
| Indostomidae | 3 | 2.8 | 1.0 | 0.1 | –1.7 | – |
| Inermiidae | 2 | 18.0 | 2.9 | 0.4 | – | – |
| Ipnopidae | 20 | 22.5 | 3.1 | 0.4 | 0.1 | –1.1 |
| Istiophoridae | 11 | 341.5 | 5.8 | 0.3 | –0.1 | –1.2 |
| Kneriidae | 30 | 6.6 | 1.8 | 0.4 | –0.8 | 1.7 |
| Kraemeriidae | 4 | 4.1 | 1.4 | 0.1 | –1.0 | –0.7 |
| Kuhliidae | 12 | 22.9 | 3.0 | 0.4 | 0.5 | 0.0 |
| Kurtidae | 2 | 37.8 | 3.3 | 1.1 | – | – |
| Kyphosidae | 41 | 43.5 | 3.7 | 0.5 | –0.2 | –1.0 |
| Labridae | 536 | 26.8 | 3.0 | 0.7 | 0.4 | –0.4 |
| Labrisomidae | 79 | 7.1 | 1.8 | 0.6 | 0.1 | –0.6 |
| Lactariidae | 1 | 40.0 | 3.7 | – | – | – |
| Lamnidae | 5 | 438.4 | 6.0 | 0.3 | 1.5 | 2.7 |
| Lampridae | 2 | 155.0 | 5.0 | 0.4 | – | – |
| Lateolabracidae | 2 | 98.0 | 4.6 | 0.1 | – | – |
| Latimeriidae | 2 | 154.0 | 5.0 | 0.1 | – | – |
| Latridae | 4 | 76.3 | 4.3 | 0.5 | –0.2 | 0.5 |
| Lebiasinidae | 60 | 7.3 | 1.8 | 0.6 | 0.2 | –1.0 |
| Leiognathidae | 34 | 12.8 | 2.5 | 0.4 | 0.1 | –0.1 |
| Lepidogalaxiidae | 1 | 6.7 | 1.9 | – | – | – |
| Lepidosirenidae | 1 | 125.0 | 4.8 | – | – | – |
| Lepisosteidae | 6 | 142.8 | 4.9 | 0.3 | 0.1 | –1.2 |
| Leptobramidae | 1 | 37.5 | 3.6 | – | – | – |
| Leptochariidae | 1 | 82.0 | 4.4 | – | – | – |
| Leptochilichthyidae | 3 | 28.5 | 3.3 | 0.1 | –1.7 | – |
| Leptoscopidae | 3 | 13.3 | 2.6 | 0.2 | 1.5 | – |
| Lethrinidae | 37 | 53.4 | 3.9 | 0.4 | –0.4 | –0.1 |
| Linophrynidae | 18 | 7.6 | 1.9 | 0.5 | 1.0 | 0.8 |
| Liparidae | 218 | 15.6 | 2.5 | 0.7 | 0.0 | –0.1 |
| Lobotidae | 2 | 105.0 | 4.7 | 0.1 | – | – |
| Lophichthyidae | 1 | 5.1 | 1.6 | – | – | – |
| Lophiidae | 23 | 52.9 | 3.6 | 0.8 | 0.3 | –0.2 |
| Lophotidae | 3 | 183.3 | 5.2 | 0.2 | –1.7 | – |
| Loricariidae | 670 | 16.2 | 2.6 | 0.7 | –0.1 | –0.1 |
| Lotidae | 20 | 62.0 | 3.8 | 0.7 | 0.8 | –0.6 |


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**Appendix 2.** *Continued*

| Family | N | Avg. (cm) | Avg. (ln cm) | Stdev | Skew | Kurt |
|---|---|---|---|---|---|---|
| Lutjanidae | 108 | 66.2 | 4.1 | 0.5 | –0.2 | –0.3 |
| Macrouridae | 300 | 39.8 | 3.6 | 0.4 | –0.1 | 0.3 |
| Malacanthidae | 41 | 39.6 | 3.5 | 0.6 | 0.0 | –0.7 |
| Malapteruridae | 11 | 47.4 | 3.6 | 0.8 | 0.2 | –1.3 |
| Mastacembelidae | 71 | 30.3 | 3.3 | 0.5 | 0.2 | 0.5 |
| Megachasmidae | 1 | 549.0 | 6.3 | – | – | – |
| Megalomycteridae | 3 | 4.1 | 1.4 | 0.1 | 0.1 | – |
| Megalopidae | 2 | 200.0 | 5.3 | 0.4 | – | – |
| Melamphaidae | 25 | 7.9 | 1.9 | 0.6 | –0.7 | –0.4 |
| Melanocetidae | 4 | 13.2 | 2.6 | 0.2 | 1.8 | 3.5 |
| Melanonidae | 2 | 23.4 | 3.1 | 0.3 | – | – |
| Melanotaeniidae | 67 | 8.7 | 2.1 | 0.3 | –0.1 | 0.4 |
| Menidae | 1 | 30.0 | 3.4 | – | – | – |
| Merlucciidae | 20 | 87.3 | 4.4 | 0.5 | –1.0 | 0.1 |
| Microdesmidae | 40 | 9.1 | 2.1 | 0.5 | –0.3 | 0.0 |
| Microstomatidae | 19 | 16.8 | 2.8 | 0.4 | –0.2 | –1.4 |
| Mirapinnidae | 4 | 4.7 | 1.5 | 0.2 | –1.3 | 1.0 |
| Mochokidae | 188 | 19.3 | 2.6 | 0.8 | –0.1 | –0.9 |
| Molidae | 5 | 256.0 | 5.5 | 0.5 | –1.6 | 2.1 |
| Monacanthidae | 100 | 24.0 | 2.9 | 0.7 | –0.1 | –0.1 |
| Monocentridae | 3 | 16.3 | 2.7 | 0.4 | –1.0 | – |
| Monodactylidae | 6 | 22.1 | 3.0 | 0.5 | –2.0 | 4.4 |
| Monognathidae | 15 | 7.1 | 1.9 | 0.3 | 0.7 | –0.5 |
| Moridae | 86 | 29.9 | 3.2 | 0.6 | –0.5 | 2.1 |
| Moringuidae | 8 | 64.0 | 4.0 | 0.6 | 0.7 | –1.0 |
| Mormyridae | 200 | 23.7 | 2.9 | 0.7 | 0.2 | –0.4 |
| Moronidae | 6 | 85.6 | 4.3 | 0.6 | 1.2 | 0.6 |
| Mugilidae | 72 | 44.3 | 3.6 | 0.6 | –0.8 | 1.0 |
| Mullidae | 65 | 29.9 | 3.3 | 0.4 | –0.8 | 0.7 |
| Muraenesocidae | 13 | 135.3 | 4.8 | 0.5 | 0.2 | –1.9 |
| Muraenidae | 171 | 79.2 | 4.1 | 0.7 | –0.3 | 0.4 |
| Muraenolepididae | 4 | 33.8 | 3.5 | 0.1 | 0.7 | –1.9 |
| Myctophidae | 203 | 9.3 | 2.1 | 0.5 | 0.0 | –0.3 |
| Myliobatidae | 33 | 183.2 | 5.0 | 0.6 | 0.7 | 0.8 |
| Myrocongridae | 4 | 44.1 | 3.8 | 0.2 | 0.3 | –3.7 |
| Myxinidae | 69 | 51.2 | 3.9 | 0.4 | –0.3 | 0.1 |
| Nandidae | 8 | 13.1 | 2.5 | 0.5 | –0.6 | –1.2 |
| Narcinidae | 27 | 36.2 | 3.5 | 0.4 | –0.3 | 0.2 |
| Nematistiidae | 1 | 163.0 | 5.1 | – | – | – |
| Nemichthyidae | 7 | 102.9 | 4.6 | 0.4 | 0.1 | –1.7 |
| Nemipteridae | 63 | 22.5 | 3.1 | 0.3 | –0.7 | 0.7 |
| Neoceratiidae | 1 | 6.0 | 1.8 | – | – | – |
| Neoscopelidae | 3 | 25.2 | 3.2 | 0.2 | –0.2 | – |
| Neosebastidae | 8 | 29.9 | 3.2 | 0.7 | –1.1 | –0.1 |
| Nettastomatidae | 29 | 57.4 | 4.0 | 0.4 | –0.3 | 0.1 |
| Nomeidae | 17 | 42.4 | 3.5 | 0.8 | 0.6 | –1.2 |
| Normanichthyidae | 1 | 11.0 | 2.4 | – | – | – |
| Notacanthidae | 8 | 49.4 | 3.7 | 0.8 | –0.6 | 0.3 |
| Notocheiridae | 5 | 5.9 | 1.7 | 0.3 | 0.2 | –2.2 |
| Notograptidae | 2 | 10.3 | 2.3 | 0.0 | – | – |
| Notopteridae | 8 | 85.4 | 4.3 | 0.7 | –0.9 | –0.5 |
| Notosudidae | 14 | 25.8 | 3.2 | 0.4 | –0.2 | –0.1 |
| Nototheniidae | 42 | 41.8 | 3.5 | 0.7 | 0.9 | 1.1 |
| Odacidae | 12 | 22.7 | 3.0 | 0.5 | 0.0 | –1.8 |
| Odontaspididae | 4 | 354.3 | 5.9 | 0.1 | –1.8 | 3.4 |
| Odontobutidae | 10 | 10.8 | 2.2 | 0.5 | 0.4 | –0.7 |
| Ogcocephalidae | 62 | 13.9 | 2.5 | 0.6 | 0.3 | –0.4 |
| Olyridae | 4 | 10.9 | 2.4 | 0.3 | –0.8 | 1.9 |
| Omosudidae | 1 | 23.0 | 3.1 | – | – | – |
| Oneirodidae | 46 | 10.6 | 2.2 | 0.6 | –0.7 | –0.3 |

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**Appendix 2.** *Continued*

| Family | N | Avg. (cm) | Avg. (ln cm) | Stdev | Skew | Kurt |
|---|---|---|---|---|---|---|
| Ophichthidae | 207 | 61.6 | 3.9 | 0.6 | –0.3 | 0.5 |
| Ophidiidae | 156 | 36.6 | 3.3 | 0.7 | 0.6 | 0.3 |
| Opisthoproctidae | 10 | 18.5 | 2.7 | 0.7 | –0.2 | 1.1 |
| Opistognathidae | 43 | 20.2 | 2.6 | 0.9 | 0.3 | –0.5 |
| Oplegnathidae | 7 | 71.0 | 4.2 | 0.2 | –0.8 | 0.0 |
| Orectolobidae | 6 | 165.0 | 4.9 | 0.7 | 0.5 | –1.6 |
| Oreosomatidae | 10 | 34.1 | 3.4 | 0.4 | –0.2 | –0.9 |
| Osmeridae | 15 | 27.7 | 3.2 | 0.5 | 0.6 | 0.6 |
| Osphronemidae | 88 | 9.2 | 1.9 | 0.7 | 1.1 | 1.8 |
| Osteoglossidae | 5 | 98.0 | 4.6 | 0.1 | 1.6 | 2.2 |
| Ostraciidae | 34 | 28.2 | 3.2 | 0.5 | –0.1 | –1.3 |
| Ostracoberycidae | 3 | 15.6 | 2.7 | 0.5 | –0.8 | – |
| Pangasiidae | 27 | 92.8 | 4.2 | 0.8 | 0.3 | –0.6 |
| Pantodontidae | 1 | 11.9 | 2.5 | – | – | – |
| Parabembridae | 2 | 19.6 | 2.9 | 0.3 | – | – |
| Parabrotulidae | 3 | 5.0 | 1.6 | 0.1 | –0.1 | – |
| Parakysidae | 5 | 4.2 | 1.4 | 0.4 | –1.0 | 1.0 |
| Paralepididae | 39 | 25.5 | 3.0 | 0.8 | –0.6 | 1.3 |
| Paralichthyidae | 83 | 32.8 | 3.3 | 0.6 | 0.4 | 0.2 |
| Parascorpididae | 1 | 60.0 | 4.1 | – | – | – |
| Parascylliidae | 7 | 65.4 | 4.1 | 0.4 | –0.5 | –2.0 |
| Paraulopidae | 8 | 13.3 | 2.6 | 0.3 | 0.2 | 1.1 |
| Parazenidae | 3 | 17.6 | 2.7 | 0.7 | 0.5 | – |
| Parodontidae | 26 | 10.2 | 2.3 | 0.3 | –0.9 | 0.3 |
| Pataecidae | 3 | 18.0 | 2.7 | 0.8 | –1.5 | – |
| Pegasidae | 5 | 10.5 | 2.3 | 0.3 | 1.7 | 3.1 |
| Pempheridae | 23 | 16.1 | 2.7 | 0.3 | –0.6 | 1.8 |
| Pentacerotidae | 12 | 53.5 | 3.9 | 0.5 | 0.3 | –1.1 |
| Percichthyidae | 30 | 31.9 | 3.0 | 1.0 | 0.6 | –0.9 |
| Percidae | 173 | 11.5 | 2.2 | 0.6 | 2.2 | 6.4 |
| Perciliidae | 2 | 9.3 | 2.2 | 0.0 | – | – |
| Percophidae | 33 | 17.0 | 2.6 | 0.7 | –0.5 | –0.5 |
| Percopsidae | 2 | 14.8 | 2.6 | 0.5 | – | – |
| Peristediidae | 31 | 26.3 | 3.1 | 0.5 | –0.1 | 0.3 |
| Petromyzontidae | 36 | 29.9 | 3.2 | 0.5 | 1.2 | 1.4 |
| Phallostethidae | 19 | 2.4 | 0.9 | 0.3 | 0.3 | 0.1 |
| Pholidae | 14 | 24.4 | 3.1 | 0.4 | –1.0 | 1.4 |
| Pholidichthyidae | 2 | 29.3 | 3.4 | 0.2 | – | – |
| Photichthyidae | 21 | 13.1 | 2.4 | 0.7 | 0.1 | –1.2 |
| Phractolaemidae | 1 | 19.0 | 2.9 | – | – | – |
| Phycidae | 11 | 63.5 | 4.1 | 0.4 | 0.9 | –0.1 |
| Pimelodidae | 56 | 60.5 | 3.7 | 0.9 | 0.0 | –0.1 |
| Pinguipedidae | 50 | 24.4 | 3.0 | 0.6 | 1.3 | 2.2 |
| Platycephalidae | 61 | 35.0 | 3.4 | 0.6 | 0.0 | 0.0 |
| Platytroctidae | 37 | 19.3 | 2.9 | 0.3 | –0.3 | –0.6 |
| Plecoglossidae | 2 | 40.7 | 3.3 | 1.3 | – | – |
| Plectrogenidae | 2 | 9.5 | 2.2 | 0.4 | – | – |
| Plesiobatidae | 1 | 270.0 | 5.6 | – | – | – |
| Plesiopidae | 40 | 10.8 | 2.2 | 0.7 | –0.2 | –0.5 |
| Pleuronectidae | 89 | 46.8 | 3.6 | 0.7 | 0.1 | 0.2 |
| Plotosidae | 32 | 42.0 | 3.5 | 0.6 | 0.3 | 0.6 |
| Poeciliidae | 285 | 5.2 | 1.6 | 0.4 | 0.2 | 1.0 |
| Polycentridae | 2 | 9.0 | 2.2 | 0.2 | – | – |
| Polymixiidae | 10 | 26.7 | 3.2 | 0.4 | 0.8 | –0.1 |
| Polynemidae | 40 | 41.7 | 3.3 | 0.8 | 1.1 | 0.8 |
| Polyodontidae | 2 | 260.5 | 5.6 | 0.2 | – | – |
| Polyprionidae | 5 | 202.0 | 5.3 | 0.2 | –0.8 | 2.1 |
| Polypteridae | 18 | 52.4 | 3.9 | 0.4 | 0.0 | –1.1 |
| Pomacanthidae | 84 | 21.9 | 2.9 | 0.6 | 0.0 | –1.0 |
| Pomacentridae | 349 | 11.4 | 2.4 | 0.4 | 0.1 | 0.0 |

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**Appendix 2.** *Continued*

| Family | N | Avg. (cm) | Avg. (ln cm) | Stdev | Skew | Kurt |
|---|---|---|---|---|---|---|
| Pomatomidae | 1 | 130.0 | 4.9 | – | – | – |
| Potamotrygonidae | 18 | 50.9 | 3.8 | 0.4 | 0.0 | –0.2 |
| Priacanthidae | 18 | 34.3 | 3.5 | 0.3 | 0.6 | 0.4 |
| Pristidae | 7 | 558.0 | 6.2 | 0.6 | –2.2 | 5.0 |
| Pristigasteridae | 22 | 25.6 | 3.0 | 0.7 | –0.3 | 1.7 |
| Pristiophoridae | 5 | 129.0 | 4.8 | 0.3 | –1.2 | 2.3 |
| Prochilodontidae | 21 | 32.8 | 3.5 | 0.2 | 0.3 | –1.1 |
| Profundulidae | 5 | 9.0 | 2.2 | 0.2 | 0.8 | –1.4 |
| Proscylliidae | 6 | 78.9 | 4.1 | 0.8 | 0.6 | –0.4 |
| Protopteridae | 6 | 93.3 | 4.5 | 0.4 | –1.7 | 4.0 |
| Psettodidae | 3 | 66.3 | 4.2 | 0.2 | 0.6 | – |
| Pseudaphritidae | 1 | 36.0 | 3.6 | – | – | – |
| Pseudocarchariidae | 1 | 110.0 | 4.7 | – | – | – |
| Pseudochromidae | 104 | 8.4 | 2.0 | 0.5 | 0.3 | 0.4 |
| Pseudomugilidae | 15 | 3.6 | 1.3 | 0.2 | 0.5 | –1.1 |
| Pseudopimelodidae | 26 | 19.4 | 2.5 | 0.9 | 0.2 | –0.7 |
| Pseudotriakidae | 1 | 295.0 | 5.7 | – | – | – |
| Pseudotrichonotidae | 2 | 7.5 | 2.0 | 0.3 | – | – |
| Psilorhynchidae | 6 | 7.2 | 1.9 | 0.2 | 0.4 | –1.6 |
| Psychrolutidae | 30 | 24.3 | 3.0 | 0.6 | –0.7 | 0.1 |
| Ptilichthyidae | 1 | 34.0 | 3.5 | – | – | – |
| Rachycentridae | 1 | 200.0 | 5.3 | – | – | – |
| Radiicephalidae | 1 | 76.0 | 4.3 | – | – | – |
| Rajidae | 154 | 78.0 | 4.2 | 0.6 | 0.1 | –0.2 |
| Regalecidae | 3 | 468.5 | 4.8 | 2.8 | –1.3 | – |
| Retropinnidae | 6 | 14.7 | 2.5 | 0.6 | 1.0 | –0.9 |
| Rhamphichthyidae | 7 | 50.8 | 3.7 | 0.7 | –0.2 | –1.7 |
| Rhamphocottidae | 1 | 8.9 | 2.2 | – | – | – |
| Rhincodontidae | 1 | 2000.0 | 7.6 | – | – | – |
| Rhinobatidae | 43 | 121.9 | 4.7 | 0.5 | 0.6 | 0.0 |
| Rhinochimaeridae | 7 | 104.6 | 4.6 | 0.3 | –0.4 | –2.5 |
| Rhyacichthyidae | 2 | 21.5 | 3.1 | 0.2 | – | – |
| Rivulidae | 225 | 6.1 | 1.7 | 0.4 | 0.3 | 0.2 |
| Rondeletiidae | 2 | 11.1 | 2.4 | 0.0 | – | – |
| Saccopharyngidae | 4 | 104.9 | 4.6 | 0.4 | 0.1 | 0.5 |
| Salangidae | 13 | 10.7 | 2.3 | 0.4 | 0.1 | –1.7 |
| Salmonidae | 104 | 65.8 | 4.0 | 0.6 | 0.0 | –0.4 |
| Samaridae | 17 | 10.8 | 2.3 | 0.4 | 0.0 | –0.4 |
| Scatophagidae | 4 | 27.3 | 3.2 | 0.7 | –1.9 | 3.6 |
| Schilbeidae | 56 | 28.9 | 3.1 | 0.7 | 0.4 | –0.1 |
| Schindleriidae | 2 | 1.7 | 0.4 | 0.8 | – | – |
| Sciaenidae | 257 | 47.8 | 3.6 | 0.7 | 0.4 | 0.0 |
| Scoloplacidae | 4 | 1.6 | 0.4 | 0.2 | –0.1 | –3.4 |
| Scomberesocidae | 5 | 31.6 | 3.1 | 1.0 | –1.0 | –0.7 |
| Scombridae | 53 | 126.1 | 4.6 | 0.6 | –0.2 | 0.1 |
| Scombrolabracidae | 1 | 30.0 | 3.4 | – | – | – |
| Scombropidae | 3 | 124.7 | 4.8 | 0.2 | 0.6 | – |
| Scopelarchidae | 15 | 13.6 | 2.5 | 0.6 | 0.1 | 0.6 |
| Scophthalmidae | 9 | 46.9 | 3.7 | 0.7 | –0.5 | –0.3 |
| Scorpaenidae | 172 | 18.7 | 2.7 | 0.7 | 0.0 | –0.7 |
| Scyliorhinidae | 108 | 63.2 | 4.0 | 0.5 | 0.8 | 2.8 |
| Scytalinidae | 1 | 15.0 | 2.7 | – | – | – |
| Sebastidae | 116 | 44.7 | 3.7 | 0.5 | –0.2 | –0.2 |
| Serranidae | 511 | 38.7 | 3.2 | 1.0 | 0.1 | –0.6 |
| Serrivomeridae | 8 | 59.2 | 4.1 | 0.3 | –0.6 | –1.0 |
| Setarchidae | 4 | 18.5 | 2.9 | 0.3 | 0.0 | 1.5 |
| Siganidae | 27 | 32.5 | 3.4 | 0.3 | 0.2 | –1.0 |
| Sillaginidae | 30 | 29.0 | 3.3 | 0.4 | 0.3 | –0.3 |
| Siluridae | 84 | 45.8 | 3.2 | 1.0 | 0.8 | 0.8 |
| Sisoridae | 95 | 18.2 | 2.5 | 0.7 | 1.8 | 4.5 |

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**Appendix 2.** *Continued*

| Family | N | Avg. (cm) | Avg. (ln cm) | Stdev | Skew | Kurt |
|---|---|---|---|---|---|---|
| Soleidae | 105 | 21.9 | 2.9 | 0.7 | –0.2 | 0.9 |
| Solenostomidae | 4 | 11.2 | 2.3 | 0.5 | –0.7 | 1.0 |
| Sparidae | 120 | 56.2 | 3.9 | 0.5 | 0.3 | 0.4 |
| Sphyraenidae | 25 | 98.8 | 4.4 | 0.6 | –0.2 | –1.1 |
| Sphyrnidae | 9 | 285.1 | 5.5 | 0.7 | 0.2 | –1.4 |
| Squalidae | 10 | 97.5 | 4.5 | 0.3 | 0.3 | –0.3 |
| Squatinidae | 13 | 136.5 | 4.8 | 0.4 | –1.4 | 1.4 |
| Stegostomatidae | 1 | 235.0 | 5.5 | – | – | – |
| Stephanoberycidae | 2 | 10.6 | 2.3 | 0.3 | – | – |
| Sternoptychidae | 62 | 5.9 | 1.7 | 0.4 | –0.2 | 0.5 |
| Sternopygidae | 28 | 40.8 | 3.6 | 0.5 | 0.2 | 1.3 |
| Stichaeidae | 68 | 21.8 | 2.9 | 0.6 | 0.3 | –0.5 |
| Stomiidae | 225 | 18.6 | 2.8 | 0.5 | –0.3 | 1.4 |
| Stromateidae | 17 | 32.6 | 3.4 | 0.4 | 0.2 | 0.5 |
| Stylephoridae | 1 | 28.0 | 3.3 | – | – | – |
| Sundasalangidae | 4 | 2.6 | 0.9 | 0.1 | 0.2 | –4.5 |
| Symphysanodontidae | 4 | 16.5 | 2.8 | 0.2 | –0.4 | 1.0 |
| Synanceiidae | 28 | 18.5 | 2.8 | 0.5 | 0.8 | 0.7 |
| Synaphobranchidae | 25 | 66.1 | 4.0 | 0.6 | –0.1 | –0.8 |
| Synbranchidae | 13 | 56.6 | 3.8 | 0.8 | –0.3 | –0.5 |
| Syngnathidae | 258 | 16.3 | 2.6 | 0.7 | –0.1 | 0.1 |
| Synodontidae | 57 | 31.7 | 3.3 | 0.6 | –0.1 | –0.5 |
| Telmatherinidae | 17 | 8.4 | 2.0 | 0.4 | 1.0 | 0.3 |
| Terapontidae | 43 | 22.9 | 3.0 | 0.4 | 0.1 | –1.0 |
| Tetrabrachiidae | 1 | 7.0 | 1.9 | – | – | – |
| Tetragonuridae | 2 | 60.0 | 4.1 | 0.2 | – | – |
| Tetraodontidae | 155 | 24.2 | 2.9 | 0.7 | 0.1 | –0.3 |
| Tetrarogidae | 33 | 13.9 | 2.4 | 0.6 | 0.8 | 1.9 |
| Thaumatichthyidae | 5 | 9.9 | 2.3 | 0.2 | 0.4 | –1.4 |
| Torpedinidae | 14 | 86.6 | 4.3 | 0.6 | –1.2 | 2.3 |
| Toxotidae | 5 | 23.0 | 3.0 | 0.5 | 0.8 | –2.1 |
| Trachichthyidae | 31 | 23.4 | 2.9 | 0.7 | 0.6 | –0.4 |
| Trachinidae | 8 | 31.0 | 3.3 | 0.6 | 0.1 | –2.4 |
| Trachipteridae | 10 | 187.8 | 5.2 | 0.4 | 0.3 | –1.9 |
| Triacanthidae | 7 | 24.0 | 3.2 | 0.3 | –0.7 | –0.5 |
| Triacanthodidae | 16 | 12.1 | 2.4 | 0.4 | –0.5 | 0.7 |
| Triakidae | 36 | 130.1 | 4.8 | 0.4 | –0.5 | –0.8 |
| Trichiuridae | 39 | 97.7 | 4.4 | 0.6 | –0.1 | 0.1 |
| Trichodontidae | 9 | 18.6 | 2.9 | 0.3 | 0.4 | 0.2 |
| Trichomycteridae | 165 | 7.8 | 1.9 | 0.6 | 0.2 | 0.1 |
| Triglidae | 94 | 23.9 | 3.0 | 0.5 | 0.5 | –0.1 |
| Triodontidae | 1 | 54.0 | 4.0 | – | – | – |
| Tripterygiidae | 138 | 4.9 | 1.5 | 0.5 | 0.8 | 0.4 |
| Umbridae | 5 | 17.4 | 2.8 | 0.5 | 0.4 | 1.7 |
| Uranoscopidae | 39 | 45.5 | 3.3 | 1.1 | –0.5 | 1.4 |
| Urolophidae | 38 | 42.3 | 3.7 | 0.4 | –0.7 | 1.1 |
| Valenciidae | 2 | 8.0 | 2.1 | 0.0 | – | – |
| Veliferidae | 1 | 28.0 | 3.3 | – | – | – |
| Xenisthmidae | 5 | 3.0 | 1.1 | 0.2 | 1.1 | 1.1 |
| Xiphiidae | 1 | 455.0 | 6.1 | – | – | – |
| Zanclidae | 1 | 23.0 | 3.1 | – | – | – |
| Zaproridae | 1 | 88.0 | 4.5 | – | – | – |
| Zeidae | 4 | 82.5 | 4.4 | 0.1 | –1.0 | –0.7 |
| Zenionidae | 6 | 11.0 | 2.4 | 0.3 | –0.1 | 1.5 |
| Zoarcidae | 210 | 25.6 | 3.1 | 0.5 | 0.2 | –0.3 |
| **Count** | 24259 | | | | | |
| **Min** | 1 | 1.6 | 0.4 | 0.0 | –2.2 | –5.6 |
| **Max** | 1895 | 2000 | 7.6 | 3.6 | 2.2 | 6.4 |
| **Average** | 47.2 | 57.8 | 3.3 | 0.5 | 0.0 | 0.1 |

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