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by comparing estimates of ancestral body size in fishes (non-tetrapod craniates) from two large and previously unpublished datasets; a palaeontological dataset representing all principal clades from throughout the Phanerozoic, and a macroecological dataset for all 515 families of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 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: $g = 0.0217 \text{ TL}^{2.861}$ (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 nonteleost actinopterygian genera known only as fossils. Fossil

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



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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 (10⁷-10⁸ MY) and taxonomic (10²-10⁴ 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.

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.

A



Continuous 2

(minimum)

Linear parsimony

1.12–1.68

1.68-2.23

2.23-2.79

3.91-4.46

4.46-5.02

5.02-5.58

5.58-6.13

6.13-6.69

equivocal

2.79-3.35

3.35-3.91

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.

Actinopterygii

Continuous 3

1.3–1.7

22-26

1.7-2.2

2.6-3.1

3.1–3.6

3.6-4.0

4.0-4.5

4.5-4.9

4.9-5.4

5.4-5.9

equivocal

(minimum)

Linear parsimon

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 MESOUITE 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).

Results and discussion

Ancestral size estimates obtained from analysis of the 515 extant fish families are five to eight times larger than estiActa Zoologica (Stockholm) 90 (Suppl. 1): 308–335 (January 2009)



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.

mates 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



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



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 = 69species) 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 actinoptervgians (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 *†Movthomasia 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	(<i>3</i>)
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	(<i>3</i>)
	Paramyxine	R	0	43.0	(<i>3</i>)
	Quadratus	R	0	28.0	(<i>3</i>)
	Myxine	R	0	55.0	(3)
	Nemamyxine	R	0	51.0	(3)
	Neomyxine	R	0	41.0	(<i>3</i>)
	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	М	360	10.0	(11)
	† Mayomyzon pieckoensis	Pn	318	6.0	(10)
	† Pipiscius zangerli	М	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)
	† Trvaonaspis sp.	LD	416	12.0	(10)
	† Tolvpelepis 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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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)
	The seudopetalichthys 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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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 veungae	UD	385	50.0	(22)
	† Diploanathus mirabilis	UD	385	45.0	(10)
	† Pterichthvodes milleri	LD-MD	416	30.0	(10)
	† Asterolepis maxima	MD-UD	398	70.0	(10)
	† Microbrachius dicki	MD	398	6.0	(10)
	† Remiaoleois walkeri	UD	385	40.0	(10)
	† Gemuendia stuertzii	LD	416	100.0	(10)
	+ Jagorina pandora		385	19.0	(10)
Chondricthyes	+ Obtusacanthus corroconis		416	12.0	(23)
ononuneunyes	+ Luponsvroides macracanthus		416	4.0	(23)
	+ Diademodus hydei		385	30.0	(10)
	+ Cladesolacho elarki		305	200.0	(70)
	+ Halicoprian bassanavi		200	100.0	(24)
	+ Eugeneedentidee unnemed		233	80.0	(10)
	L'Eugeneodonitidae unitamed		201	80.0 05.0	(10)
	† Caseodus ealoni	P Dr	299	95.0	(9)
		Pri	318	133.3	(9)
		IVI	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 tergusi	Pn	318	28.0	(25)
	† Damocles serratus	M	360	20.0	(10)
	† Falcatus falcatus	Μ	360	15.0	(10, 24)
	† Symorium reniforme	M-Pn	360	300.0	(10)
	† Cobelodus aculeata	Μ	360	158.3	(<i>9</i>)
	† Helodus simplex	Μ	360	45.0	(15)
	† Chondrenchelys problematica	Μ	360	20.0	(15)
	† Harpagofututor volsellorhinus	Μ	360	10.0	(10)
	† Deltoptychius sp.	M-Pn	360	50.0	(10)
	† Menaspis armata	UP	260	16.0	(10)
	† Cochliodontofomes unnamed 1	Μ	360	14.0	(10)
	† Cochliodontofomes unnamed 2	Μ	360	11.0	(10)
	† Cochliodontofomes unnamed 3	Μ	360	10.0	(10)
	† Cochliodontofomes unnamed 4	Μ	360	9.0	(10)
	† Echinochimaera meltoni	Μ	360	8.0	(10)
	† Delphyodontos dacriformes	Μ	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)
	t Injoptervgijformes unnamed 1	M	360	10.0	(10)
	t Iniopterygijformes unnamed 2	M	360	10.0	(10)
	+ Inioptery rushlaui	Pn	318	24 0	(10)
	+ Iniopera richardeoni	Pn	318	24.0	(10)
	+ Sibirbynchus denisoni	Pn	318	24.U 20 0	(10)
	+ Daliadus problamaticus		416	20.0	(70)
	Dollouus problematicus	LD	410	75.0	(27)

Class	Taxon	Horizon	Min. Age	TL (cm)	Reference
	† Elasmobranchii unnamed	М	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.	М	360	250.0	(15)
	† Onychoselache traquairi	М	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	М	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-PI	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)

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	 I D	416	15.0	(10)
	+ Diplacanthus striatus	MD-UD	398	20.0	(26)
	+ Rhadinacanthus longispinatus	MD	398	16.0	(10)
	+ lechnicanthus aracilis		416	35.0	(10)
Parcontorvaii	+ Pearolonis romori		410	10.0	(70)
sarcopterygi	+ Diabolonia operatua		423	20.0	(32)
	T Diabolepis speralus	LD	410	30.0	(33)
	T Onychoaus sigmolaes		416	200.0	(9)
	T Strunius waiteri	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	М	360	11.0	(10)
	† Allenypterus montanus	М	360	14.0	(10)
	† Coelacanthus granulatus	Р	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	(<i>3</i>)
	† 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	ID	416	30.0	(33)
	+ Holodipterus Ionai		385	45.0	(9)
	+ Dinterus valenciennesi	MD	398	22.0	(15)
	+ Grinbognathus whitei		385	70.0	(10)
	+ Scaumenacia curta	חוו	385	60.0	(26 39)
	+ Phaneronleuron andersoni		385	20.0	(20, 00)
	+ Ptychoceratodus philippei		251	20.0	(41)
	Trivonoceratodus primposi Neoceratodus forstori		1/6	170.0	(41)
	+ Palaodanhus insignia		205	200	(3)
			300	200	(∠0)
	T Neoceratoous tuberculatus	UK	100	200	(42)
	T Kninoaipterus ulrichi	UD	385	28	(43)
	† Protopterus protopteroides	LK	146	/0.0	(42)
	Protopterus spp.	EC	56	93.3	(3)
	Lepidosiren paradoxa	MC	23	125.0	(3)
	† Strepsodus anculonamensis	М	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)
Actinoptervaii	† Andreolepis hedei	US	423	25.0	(9, 46)
. ,0	† Dialipina salgueiroensis	LD	416	25.0	(47)
	† Cheirolepis canadensis	MD	398	30.0	(48, 49)
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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)
	† Sundavichthys elegantulus	UD	374	25.0	(10)
	† Guildayichthys carnegie	Μ	360	8	(51)
	† Aetheretmon valentiacum	М	360	9.0	(10)
	+ Rhadinichthys carinatus	М	360	11.0	(10)
	† Canobius ramsayi	Μ	360	6.0	(10)
	† Coruboniscus budensis	М	360	3.0	(10)
	† Benedenus deneensis	М	360	22.0	(10)
	† Holurus parki	М	360	12.0	(10)
	+ Nematoptychius greenocki	М	360	45.0	(10)
	† Drvdenius insianis	М	360	10.0	(10)
	† Gonatodus punctatus	М	360	17.0	(10)
	+ Acrolepis ortholepis	М	360	30.0	(10)
	† Acrolepis sedawickii	М	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)
	† Pvaopterus humboldti	UP	260	60.0	(52)
	+ Flonichthys punctatus	I P	260	8.0	(10)
	† Reticulenis exsculnta	LIP	260	57.0	(10)
	† Bobasatriana canadensis	Tr	251	67.0	(26)
	† Apatolepis australis	MTr	228	14.0	(10)
	+ Mesembroniscus Iongisquamosus	MTr	228	80	(10)
	† Polypterus dageti	UK	98.6	54 1	(54)
	+ Mesopoma politum	M	360	7.0	(0,1)
	† Mesopoma planti	Pn	318	7.0	(55)
	† Dorvoterus hoffmanni	P	299	12.0	(52)
	+ Paleoniscum freislebeni	LIP	260	19.0	(26)
	+ Birgeria groenlandica	l Tr	251	84.0	(56)
	† Saurichthys seefeldensis	MTr	228	180.0	(9)
	+ Boreosomus aillioti	l Tr	251	13.0	(10)
	† Perleidus madagascarensis	L Tr	251	12.0	(26)
	+ Redfieldius gracilis	LITr	228	19.0	(26)
	+ Chondrosteus hindenburgi		200	300.0	(10)
	+ Dapedium pholidotum	1.1	200	26.0	(26)
	† Peipiaosteus pani	LU.I	161	60.0	(56)
	+ Protonsenburus liui	11.1	161	23.3	(52)
	+ Protoscaphirhynchus squamosus	I K	146	56.0	(10)
	+ Polyodon tuberculata	FC	55	260.5	(.3)
	+ Crossopholis magnicaudata	EC	55	.39.0	(10)
	Huso son	B	0	530.0	(3)
	Acinenser sinensis	B	0 0	130.0	(3)
	Scanbirbynchus spp	B	0	140.0	(3)
	Pseudoscanbirbynchus	B	0	56.0	(3)
	Psenburus aladius	B	0	300.0	(3)
	+ Paralepidotus ornatus	UTr	228	30.0	(57)
	+ Semionotus agassizii	LITr	228	29.0	(26)
	+ Pachchormus Acconus		200	94 N	(26)
	+ Caturus velifer		161	57.0	(26)
	+ Strobilodus aiganteus		161	177 0	(10)
	+ Amionesis dolloi		146	14.0	(10)
	t Calamonleurus ovlindrious		146	01 D	(26)
	+ Leoisosteus simplex		146	73.0	(26)
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Appendix	1. Continued
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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	IK	146	75.0	(26)
	+ Longileptolenis weidenothi	1.1	183	37.4	(49)
	† Humbertia operta	UK	100	10.0	(10)
	+ Lentolenides haertesi		150	54	(59)
	+ Lentolenides spratiformis	111	150	9.1	(59)
	+ Longilentolenis wiedenrothi		161	36.0	(49)
	+ Orthogonikleithrus boelli	111	161	4.5	(50)
	+ Orthogonikleithrus loichi	11	161	4.5	(53)
	+ Cavenderichthys talbragaronsis	11	183	10.1	(10)
	+ Cladoovolus gardnori		1/6	111.0	(26)
	+ Gillious arcuatus		140	157.0	(20)
	Gillicus alcualus + lebthyodootes standan		140	107.0	(10)
	+ Pachuthriagang prostorius		140	220.0	(10)
	† Pachythinssops propierus	UJ	150	38.0	(10)
	T Inrissops formosus	UJ	150	28.0	(10)
	T Antarctithrissops australis	UJ	150	30.0	(60)
	† Xipnactinus 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	(<i>3</i>)
	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	(<i>62</i>)
	† 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		100	28.0	(10)
	+ Diplomystus shanalionsis		1/6	20.0 5 5	(63)
	+ Paraclupea chotungoncic		140	0.0	(63)
	Talaciupea unelunyensis		24	3.0	(10)
	+ Engravia ourvetala	50	54	3.0	(10)
	T Erigraulis eurystole	EC	54 57	15.5	(39)
	T Kriighila eocaefia	EG	57	9.0	(∠0)
	† Santanaclupea silvasantosi	LK	125	12.0	(65)

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	FC	54	22.0	(10)	
	† Esox lepidotus	PC	61	70.0	(10)	
	† Umbra krameri	FC	54	17.0	(.3)	
	+ I Imbra perpusilla	EC	54	3.0	(10)	
	Dallia pectoralis	B	0	33.0	(3)	
	+ Estesesov tiemani	PC	61	30.0	(67)	
	+ Beurlenichthys ouricuriensis	IK	125	6.0	(65, 68)	
	+ Boltyshia brevicauda	PC	61	8.0	(10)	
	+ Prostomias maroccanus	IK	125	17.0	(10)	
	+ Dactylopogon grandis	LIK EK	95	44.0	(10)	
	† Hakelia laticauda	LIK OK	95	9.0	(10)	
	+ Lentosoma elongatus	UK OK	95	8.0	(10)	
	+ Nomatonatus longisninnus		95	14.0	(10)	
	+ Tachynoctos longipos		95	27.0	(10)	
	+ Sardinaidas manastarii		95	19.0	(10)	
		UK	95	7.0	(10)	
	† Diponta antoigua † Dipontorux spinosus	UK	95	14.0	(10)	
	+ Ainichthya vilifar	UK	95	14.0	(10)	
	+ Puopostoroidos	UK	95	0.0 7.0	(10)	
	+ Stichocontrus livatus	UK	95	7.0	(10)	
	+ Enchoduc macroptorus	UK	95	0.0	(10)	
	+ Loptocodon roctus	UK	95	23.0	(10)	
	+ Palacalyeus draganaia	UK	95	23.0	(10)	
	+ Halae migralania	UK	95	40.0	(10)	
	† Halec microlepis	UK	95	18.0	(10)	
	† Phylactocephalus microlepis	UK	95	15.0	(10)	
	Apaleopholis lamatus	UK	95	31.0	(10)	
	† icnthyotringa furcata	UK	95	15.0	(10)	
	† Sarainius cordieri	UK	95	14.0	(10)	
	T Ctenocephalichtys loreti	UK	95	5.0	(10)	
	T Myripristis nomopterygius	ME	49	11.0	(10)	
	† Paraspinus cupulus	UK	95	16.0	(10)	
	† Stichoberyx polyaesmus	LK	125	8.0	(10)	
	† Acrogaster neckell	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)	
	† Iubantia 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	Ν	Avg. (cm)	Avg. (In 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

Family	Ν	Avg. (cm)	Avg. (In 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	0.0	-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	31	0.6	-0.8	0.3
Bedotiidae	11	81	20	0.4	-0.2	-0.6
Belonidae	43	68.7	4.0	0.8	-1.0	17
Bembridae	6	22.7	31	0.4	-1.7	31
Berveidae	9	50.8	3.8	0.5	_0.3	_0.9
Blenniidae	325	87	2.0	0.5	0.0	0.0
Bothidae	117	16.2	27	0.5	-0.2	0.0
Bovichtidae	4	33.6	32	0.9	0.2	0.0
Brachaeluridae	2	99.0	4.6	0.3	_	-
Brachionichthvidae	2	11.5	24	0.4	_	_
Bramidae	19	51.4	3.8	0.6	-1.5	3.6
Bregmacerotidae	12	6.4	17	0.7	-1.2	0.7
Bythitidae	61	16.5	25	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
Callichthvidae	173	52	16	0.4	0.9	3.4
Callionymidae	123	10.7	21	0.7	-0.5	_0.7
Callorhinchidae	3	112.1	47	0.2	-1.7	-
Caproidae	8	15.7	26	0.6	0.0	-0.9
Caracanthidae	4	4.5	15	0.3	-2.0	4.0
Carangidae	141	68.9	4 1	0.5	0.2	-0.3
Caranidae	33	19.8	29	0.4	_0.1	-0.7
Carcharbinidae	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	R	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	32	-	- -	-
Centrolonhidae	25	63.7	4.0	07	_0.6	_0 5
Centrophoridae	14	1173	47	0.3	0.0	_0.5 _1 २
Centrophonidae	1	22.0	, 3.1	-	- -	-1.5
Centronomidae	, 22	85.9	4.3	0.6	0.2	_1 2
Cepolidae	15	41.3	3.6	0.5	_1 0	20
	10	11.0	0.0	0.0	1.0	2.0

Family	Ν	Avg. (cm)	Avg. (In 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
Cheimarrhichthvidae	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	34	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	0.0	0.3
Cirrhitidae	28	15.5	2.6	0.5	1.0	12
Citharidae		25.6	3.2	0.3	_0.9	0.1
Citharinidae	102	19.9	23	1 1	0.4	_1 1
Clariidae	102	40.8	3.4	0.8	0.4	-0.2
Clinidae	79	14.5	25	0.6	0.5	0.3
Clupeidae	202	20.0	27	0.7	_0.2	_0.3
Cobitidae	137	11.5	22	0.6	0.5	0.0
Cojidae	5	37.4	3.6	0.0	_0.3	_2 1
Colocongridae	5	56.9	4.0	0.3	1.0	22
Comenhoridae	2	18.5	29	0.0	-	
Congiopodidae	6	39.9	3.6	0.5	_0.2	0.9
Congridae	121	57.9	3.9	0.6	_0.1	27
Corvohaenidae	2	168.5	5.1	0.0	-	
Cottidae	190	16.3	2.6	0.7	03	0.2
Cottocomenhoridae	6	10.0	3.0	0.2	_1 1	1.8
Cranodanididae	2	36.0	3.6	0.2		-
Creediidae	16	5 1	1.6	0.0	_0 3	-0.6
Crenuchidae	75	47	1.5	0.4	-0.3	-0.2
Cryptacanthodidae	3	79.3	4.2	0.7	-1.5	- 0.2
Ctenoluciidae	7	70	3.6	3.6	0.4	15
Curimatidae	98	12.6	2.4	0.5	-0.6	-0.1
Cyclonteridae	19	12.0	2.4	0.8	-0.0	-0.1
Cvematidae	2	15.5	2.2	0.0	-	-
Cynodontidae	1/	36.2	2.7	0.0	0.4	_0.6
Cynodoniidae	112	21.0	2.0	0.7	0.4	-0.0
Cynrinidae	1805	21.0	2.3	0.0	0.1	-0.1 _0.1
Cyprinidae	100	70	2.0	0.3	1.0	-U.I
Cyprinodonilidae	120	7.U 45.0	1.0	0.4	1.2	1.5
Dactulanteridae	3 7	40.U 25 0	3.0 2.4	0.2	1./	-
Dactylopienude	1	JJ.∠	0.4 1 7	0.7	0.1	1.8
Dactyloscopidae	30	5.9	1./	0.4	0.1	0.4
Dalatildae	64	/8.2	4.0	0.7	1.2	2.3
Dasyalluae	60	130.4	4.0	0.0	-0.3	-0.4
Dentatherinidae	1	5.0	1.6	-	-	-

Family	Ν	Avg. (cm)	Avg. (In 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	32	0.2	-0.3	12
Diretmidae	4	31.6	3.4	0.3	-0.1	-4.6
Doradidae	73	22.8	28	0.7	0.7	0.1
Draconettidae	10	9.8	23	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	53	0.6	_	_
Elassomatidae	5	3.6	13	0.2	21	4.5
Eleginopidae	1	60.0	4 1	_	_	_
Eleotridae	131	15.4	25	07	0.1	-0.3
Elopidae	6	99.8	4.6	0.1	1 1	1.8
Embiotocidae	22	28.1	33	0.4	_0 1	_1.0
Empelichthyidae	16	35.0	3.4	0.4	-0.4	0.1
Engraulidae	139	13.8	2.5	0.0	-0.4 -0.3	0.1
Engradidae	105	50.0	2.5	0.0	-0.5	-0.2
Enbipoidao	15	46.3	3.9	-	-	- 01
Epinopidae	20	40.3	3.7	0.5	-0.3	1.5
Erothictidae	10	7.0	1.6	0.7	-0.2	1.5
Ereuniidaa	01	7.2	1.0	0.0	1.3	2.3
Enthripidaa		23.0 46 E	3.2	0.2	-1.4	- 1.2
Erytinnidae	11	40.5	3.0	0.7	0.5	-1.5
Escrimeyendae	I C	4.1	1.4	- 0.7	-	-
Esocidae	6	101.5	4.5	0.7	-0.4	-1.8
Euclichthyluae	1	35.0	3.0	-	—	-
	I F	15.0	4.0	-	-	-
Evennannenidae	5	15.0	2.7	0.2	0.1	-4.0
Exocoelidae	57	20.7	3.2	0.3	-0.1	-0.3
Fistulariluae	4	157.5	5.0	0.5	-1.8	3.0
	40	9.4	2.2	0.4	0.1	0.1
Gauluae	24	00.0	4.0	0.7	0.0	-0.2
Galaxildae	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
Geotrildae	4	35.8	3.4	0.7	0.1	-5.6
Generate	50	21.9	3.0	0.4	-0.4	0.3
Gibberichtnyldae	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	-

Family	Ν	Avg. (cm)	Avg. (In 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
Heterenchelvidae	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
Hexatrvgonidae	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

Family	Ν	Avg. (cm)	Avg. (In 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	53	0.4	-	_
Melamphaidae	25	7.9	1.9	0.6	-0.7	-0.4
Melanocetidae	4	13.2	26	0.2	18	3.5
Melanonidae	2	23.4	31	0.3	-	_
Melanotaeniidae	67	87	21	0.3	-0.1	0.4
Menidae	1	30.0	3.4	_	_	_
Merlucciidae	20	87.3	4.4	0.5	-1.0	01
Microdesmidae	40	91	21	0.5	-0.3	0.0
Microstomatidae	19	16.8	2.8	0.4	_0.2	_1.4
Miraninnidae	4	47	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	-0.3
Monacanthidao	100	24.0	2.0	0.5	-1.0	2.1
Monocontridao	2	24.0	2.5	0.7	-0.1	-0.1
Monodostulidas	5	10.5	2.7	0.4	-1.0	_
Managasthidaa	15	22.1	3.0	0.5	-2.0	4.4
Moridaa	15	7.1	1.9	0.3	0.7	-0.5
Morinauidae	00	29.9	3.2	0.6	-0.5	2.1
Marranuidae	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	/2	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
Olvridae	4	10.9	2.4	0.3	-0.8	1.9
Omosudidae	1	23.0	3.1	_	_	_
Oneirodidae	46	10.6	22	0.6	-0.7	_በ
	10	10.0		0.0	0.7	0.0

Family	Ν	Avg. (cm)	Avg. (In 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
Percichthvidae	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
Petromvzontidae	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
Pholidichthvidae	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
Polvodontidae	2	260.5	5.6	0.2	_	-
Polyprionidae	- 5	202.0	5.3	0.2	-0.8	21
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
	0.10		· ·	•••	•••	0.0

Family	Ν	Avg. (cm)	Avg. (In 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	25	0.9	0.2	-0.7
Pseudotriakidae		295.0	57	_	_	_
Pseudotrichonotidae	2	7.5	20	0.3	_	_
Psilorhynchidae	6	7.2	19	0.2	0.4	-16
Psychrolutidae	30	24.3	3.0	0.6	_0.7	0.1
Ptilichthvidae	1	34.0	3.5	-	-	-
Bachycentridae	1	200.0	5.3	_	_	_
Padijoophalidao	1	76.0	1.2	_	_	_
Paiidao	154	70.0	4.3	-	- 0.1	- 0.2
Raglasidas	04	70.0 469 E	4.2	0.0	1.2	-0.2
Regalecidae	3	408.5	4.0	2.8	-1.3	-
Retropinnidae	6	14.7	2.5	0.6	1.0	-0.9
Rhamphichthyldae	/	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	/	104.6	4.6	0.3	-0.4	-2.5
Rhyacichthyidae	2	21.5	3.1	0.2	-	-
Rivulidae	225	6.1	1./	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

Family	Ν	Avg. (cm)	Avg. (In 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