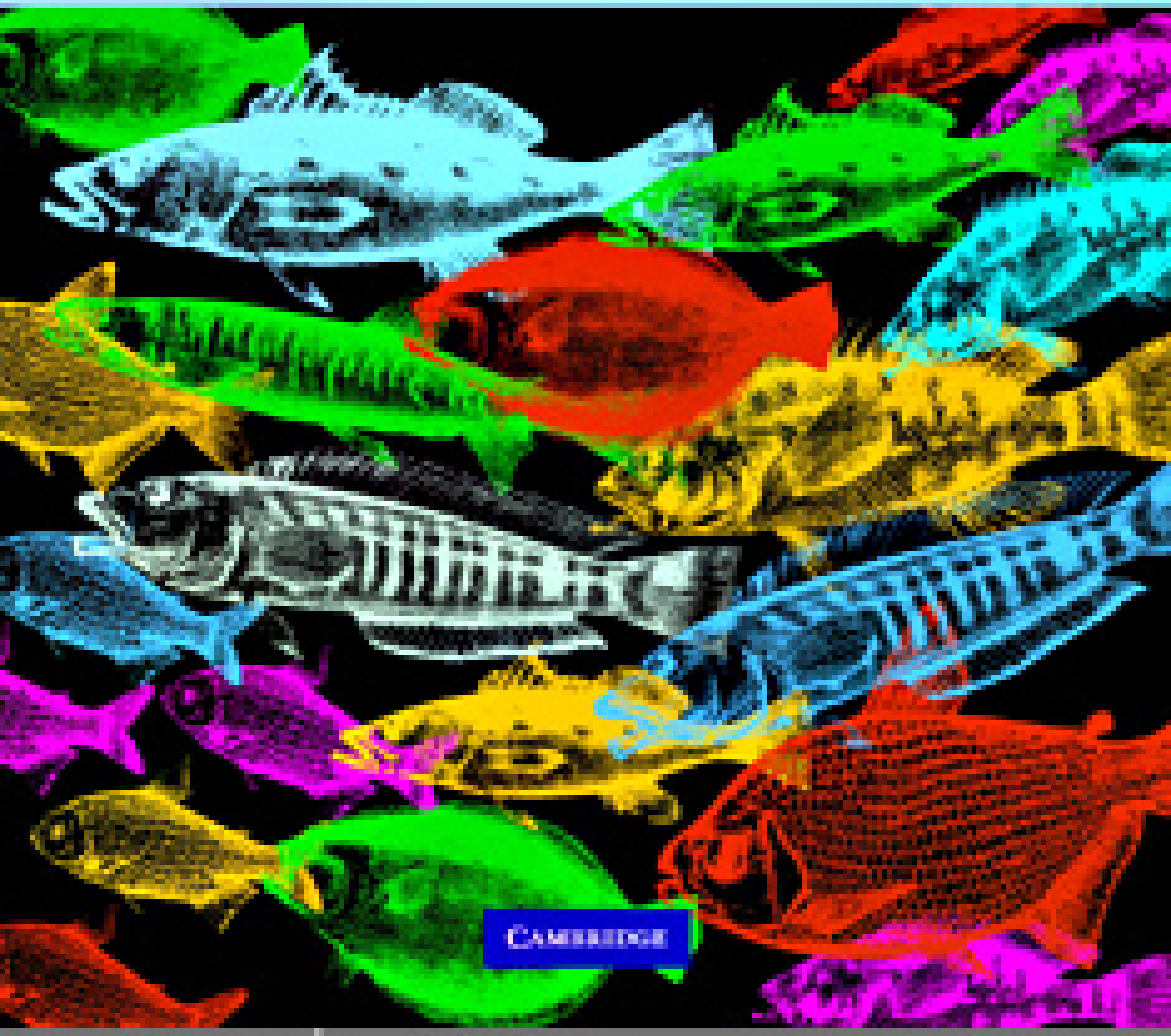
Darwin's Fishes

An Encyclopedia of Ichthyology, Ecology and Evolution

DANIEL PAULY



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An Encyclopedia of Ichthyology, Ecology, and Evolution

In *Darwin's Fishes*, Daniel Pauly presents a unique encyclopedia of ichthyology, ecology, and evolution, based upon everything that Charles Darwin ever wrote about fish. Entries are arranged alphabetically and can be about, for example, a particular fish taxon, an anatomical part, a chemical substance, a scientist, a place, or an evolutionary or ecological concept. Readers can start wherever they like and are then led by a series of cross-references on a fascinating voyage of interconnected entries, each indirectly or directly connected with original writings from Darwin himself. Along the way, the reader is offered interpretation of the historical material put in the context of both Darwin's time and that of contemporary biology and ecology.

This book is intended for anyone interested in fishes, the work of Charles Darwin, evolutionary biology and ecology, and natural history in general.

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CAMBRIDGE
UNIVERSITY PRESS

CAMBRIDGE UNIVERSITY PRESS
Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo

Cambridge University Press
The Edinburgh Building, Cambridge CB2 2RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org
Information on this title: www.cambridge.org/9780521827775

First published in print format 2004

ISBN-13 978-0-511-19235-7 eBook (Adobe Reader)
ISBN-10 0-511-19235-5 eBook (Adobe Reader)

ISBN-13 978-0-521-82777-5 hardback
ISBN-10 0-521-82777-9 hardback

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Foreword

This book by Professor Daniel Pauly is for people interested in fishes, in Charles Darwin, or just plain interested in natural history. Darwin is known for writing about many things, with superb works on orchids and barnacles and, of course, on natural selection. Many authors have written about him and we often hear reference to 'Darwin's finches'. I suspect few people connect Darwin with fishes: this now will change. Daniel Pauly has done a superb job in this book in showing us the many connections between Darwin and fishes. He does this in a delightful way, mixing subtle, cryptic humour with academic discussions. Pauly gives us a tour in discovering fascinating facts; it's a great way to learn about fishes.

Daniel Pauly is internationally known for his work on fish growth and mortality, tropical fisheries management, and ecosystem modelling. A recognized leader in studies of fish population dynamics, he is also well known for his insights into the historic and socio-economic factors that intervene when fish populations are exploited. These, combined with his wide interests in evolutionary subjects, allowed a masterful treatment of Darwin's contributions to ichthyology, the subject of this book.

The book is arranged like an encyclopedia, with items in alphabetical order. The generous cross-references allow the reader to start with a given term of interest and go on an exciting voyage of discovery, exploring all sorts of worlds. One can start from a given fish taxon (by common or scientific name) and be led through, for example, an anatomical part, to a biologist or other scientist, a scientific phenomenon, an ecological or evolutionary subject, a philosopher, a chemical element, a geographic location, some form of life other than a fish, a museum, and then back to some fish. All the topics, however, lead directly or indirectly to the work of Darwin, perhaps the most influential person in biology. The reader never knows where the journey will lead, perhaps to an old fossil, to Louis Agassiz, or to a species flock undergoing evolution. An exciting mixture of topics enters in as we take off in whatever direction we wish. Readers get into whole organismal biology (and respect for whole organismal biology is under serious threat in many so-called 'Biology' Departments), and it is fun to challenge ourselves in seeing just what we know or do not know on given subjects. Resources of interest to ichthyologists also

include an appendix list of Darwin's *Fish in Spirits of Wine* by Jacqueline McGlade and the list of *Beagle* specimens in the Natural History (London) and Zoology (Cambridge University) museums. Fishes came into Darwin's life, just as they do ours, in many fascinating ways, as readers will discover. The book does have limits, though, as Professor Pauly has been conservative in his definition of the term 'fishes'. After all, he could have included us: even we humans are fish derivatives!

Darwin receives special respect from biologists. So should fishes. If it were not for fishes we would not have evolved – which cannot be said for finches and other birds. True, Darwin has his detractors, but then so do fishes. Darwin was not the first to suggest that life evolves: such people as his grandfather, Erasmus Darwin, and Jean-Baptiste Lamarck believed life evolved, but we tend to overlook that. What has captivated us is Darwin's explanation of the driving force of evolution, natural selection. Alfred Russel Wallace had the same explanation for evolution as Darwin, but we tend to overlook that also. One can excuse ichthyologists trying to explain the vast diversity of colour in tropical reef fishes from wondering if something else other than natural selection is at play. But let's remind the creationists that our knowledge that evolution has occurred, and is still occurring, is not based on the theory of what its driving force(s) may or may not be.

Darwin has certainly been a major figure in giving us the impetus to make our classifications reflect evolutionary history. It is through his theory of evolution that we explain similarities between taxa and give a modern rationale to our classifications. Our knowledge of evolution and the historical connections of life with explanations of why life is as it is gives biology a unique place among the sciences. In Darwin's day, about 9000 species of fish were recognized as valid, compared with over 28 000 now. We have a concept of species today, as evolutionary lineages separated by irreversible discontinuities (see Nelson 1999), different from that of Darwin, and yet that is not what explains the different number of species recognized. Active ichthyologists of Darwin's day dealing with higher fish classification included Albert Günther of the British Museum and in America Theodore Gill and Edward Drinker Cope. Ironically I think the latter two employed more evolutionary thinking in their work than did the fellow in the British Museum, who as this book points out, studiously avoided references to evolution.

Not surprisingly, many fish species, starting with *Pimelometopon darwini*, have 'Darwin' as part of their scientific or common name, and this book presents all of these (first-order) eponyms, along with second-order eponyms, various retronyms, and one whimsical 'reverse eponym', the unfortunate Mr Fish. There is also Darwin's bass, but that is a book by Paul Quinnett, entitled *Darwin's Bass, The Evolutionary Psychology of Fishing Man*. One can get easily hooked on both Pauly's and Quinnett's books and come out a winner.

Pauly's book is an adventure in learning. This scholarly work is also a wonderful source of quotes, for research papers, public talks, university classes, student essays, or cocktail parties, and the exact source is given for all quotes, so you can pretend you found them yourself. The book will be of interest to both the old-timer and

the beginning student of ichthyology (alas, are we not all ultimately beginners) as well as for those with a fondness for Darwin but knowing little or nothing of fishes. It's a good full meal, from the 'dry-run' introduction, through the main course of entries, to Jacqueline McGlade's wine list, and the dessert of finely annotated references.

We can enjoy fishes in so many wonderful ways and I thank Daniel Pauly for presenting yet another way.

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University of Alberta

Preface and acknowledgments

The idea for this book emerged in the late 1980s when I attempted to find an interesting Darwin quote to add to a volume I was then editing on the impact of El Niño on Peruvian fishes and fisheries. I remembered from earlier readings that Darwin had been in Peru, where he collected specimens of the species which Leonard Jenyns later described as *Engraulis ringens*, the Peruvian anchoveta.

But I did not find any suitable quote: the indexes of books by, or about, Darwin that I consulted all covered 'finches' but not 'fishes'. Still, the pun was obvious, and I decided to write a short essay on Darwin's work on fishes, to be titled *Darwin's Fishes*, if only to get it out of my system.

However, caught in the iron grip of the Law of Unintended Consequences, I ended up writing a book-size chrestomathy. Fortunately, I had the help of Darwin (who contributed about 45 000 of his words, i.e. almost one third of the entire book) and, as we shall see, the help of friends who provided relevant information and helped verify facts.

The book now completed, I will attempt to cover my tracks, and pretend that this was written to fill the 'major gap in scholarship' that is usually recruited in such cases. Thus, I refer to Gruber (1981, p. xix), who, in an influential review of Darwin's work, pointed out that "[w]e need to fill many gaps in our knowledge of detail, and we need new approaches to synthesis. The details wanting are by no means fussy bits. They are, rather, organized chunks or even macro-chunks – for example, a longitudinal and critical reconstruction of Darwin's half-century of work on earthworms." I shall leave the subterranean task of working through *Darwin's Grubs* to my vermiphile colleagues: it is *Darwin's Fishes* that I herewith offer as a latitudinal 'macro-chunk' and 'critical reconstruction'.

This reconstruction of Darwin's work on fishes (and other aquatic organisms interacting with fishes) is 'critical' in that I checked Darwin's work at three levels: (a) within the body of Darwin's formal publications and other writings, by following the development of his ideas and use of the supporting facts, and probing these for internal consistency; (b) with regard to Darwin's use of source material, by accessing the references he cited and appraising his interpretation of the information therein; and (c) by evaluating Darwin's hypotheses in light of present knowledge.

No continuous narrative would have allowed presentation of this multi-layered material in coherent fashion (I did try, and the section below, on 'Darwin and ichthyology' builds on such an earlier attempt), and hence the decision to present it in the form of two lists: (i) 478 alphabetized entries, forming the bulk of this book, and (ii) 958 (mostly) annotated references, used to present Darwin's marginalia and his other comments on publications he had read, and to put his ecologically oriented work in the taxonomy-dominated context of the ichthyology of his time. This enabled the writing up of this material in the form of small, hopefully digestible items (Gruber may have called them 'micro-chunks'), liberally cross-referenced. Moreover, this allowed the book to become largely self-referential, i.e. it enabled me to create entries for explanatory items normally tucked away, in the form of endnotes or glossaries, into the back matters of a book. The price paid for this convenience of access is that Darwin's own narrative had to be 'chunked' into pieces, especially when he illustrated a topic – e.g. **sexual selection** – through a series of examples, referring to different fish species, as in *Descent of Man*. Here, all I can suggest to the reader interested in these topics is to access the original texts, which is a good thing to do anyway.

Another part of the price paid for attempting to include and reference, in agonizing detail, all I could find which Darwin ever wrote about fishes, is that many sections of this book read like laundry lists. I have attempted to cover this up, mainly through levity, the result being that this book will probably irritate serious scholars, but still bore students to tears. This is aggravated by the fact that I have been unable to resist the frequent use of inordinately long, or otherwise difficult words (e.g. 'chrestomathy'), and smuggling some of my pet ideas into this book, e.g., on oxygen's role in fish growth, even if their link to the specifics of Darwin's writings may be seen as tenuous. The cavillers will have a field day, especially among the historians, to whom the natural scientists' easy judgments ('X was wrong about that!') is anathema, given their difficulty in conceiving of a craft that would legitimately reach that way into times past.

On the other hand, Charles Darwin (CD) passed the tests put to him with flying colours, and even passed the anachronical hurdle in (c) above. (I have emphasized the few errors I found, both because CD is such a worthy target, and because without such emphasis, this book may be perceived as a hagiography.) Thus, my overall conclusion is that CD's writings on fishes reflect a generally judicious selection, correct citation and interpretation of his sources, and based thereon, the formulation of hypotheses that have largely withstood the test of time. Moreover, in the process of digging through the literature of Darwin's time and reading his voluminous *Correspondence*, I discovered a person different from most of his contemporaries – even within his social class – and, as well, from the unimaginative compiler of facts that many, often misled by his own *Autobiography*, still see in Darwin. My impression now is that, like Michelangelo, Darwin so well perceived the best thoughts of his time that they enabled him to see glimpses of the future.

Another impression I now have is that the 'taxon-centred' approach used here would lead to many new insights if applied to other large groups, such as insects or

mammals, and to biologists other than CD (e.g. Linnaeus or Huxley), whose work, like his, covered a wide range of taxa.

Now, all that is left to do is to thank the friends and colleagues who helped me with *Darwin's Fishes*. Foremost among these is the team, led by Rainer Froese, that created *FishBase*, the computerized encyclopedia of fishes. Rainer was forced – as I was – by the nature of his project to move into areas he had never dreamt of getting into. In this case, the Law of Unintended Consequences turned him into an expert on fish nomenclature. Whatever nomenclatural consistency this book has is due in part (50%) to Rainer Froese. The other 50% are for William Eschmeyer of the California Academy of Sciences, and an honorary member of the FishBase Team. I could not have done without his extraordinary *Catalog of Fishes*, now incorporated in FishBase, and his answers to my queries.

Thanks also to Jacqueline McGlade, for contributing her transcription of *Fish in Spirits of Wine* to this effort, and to Adrian Friday for a list of the fishes collected by CD still in the University Museum of Zoology, Cambridge. As well, thanks are due to Ms Aque Atanacio, the FishBase artist, who processed all the graphs, while Amy Poon, with the assistance of Ms Elsie Wollaston and her staff at the UBC Library, dug up a huge chunk of the ancient references cited here. Thanks also to the students of my *Darwin's Fishes* course, given since 1995 at the University of British Columbia (lately as 'Bio 445'), and in which many of the epistemological and ethical issues touched upon here are further developed.

Maria-Lourdes 'Deng' Palomares wrote the neat 'macro' that kept my word processing program in check, forcing it to maintain the page layout I wanted. I immensely appreciated this, her draft index to the fishes, and the many other ways she contributed to the material incorporated in this book.

The following persons provided information beyond the call of duty (specific topics, if any, are in parentheses), or read the whole or part of the draft, and must now therefore (if somewhat paradoxically), be absolved of responsibility for any remaining errors (which are obviously all my fault): Patrick Armstrong, Nicolas Bailly, Anthony Chow (typhoid fever); Villy Christensen, Philippe Cury, Jonathan Entwisle, Patti Gilbertson, Rune Hagen (king cod), Kristin Kaschner (fish sounds), Mark Kraulis (sexual selection), Sven Kullander, Jessica Meeuwig, Judith Myers (water beetles) Jørgen Nielsen, Tom Okey, Sandra Wade Pauly (yes, my wife, neither last nor least), Torstein Pedersen (king cod), Tony Pitcher, David Preikshot (more references), Neil Rainer (typhoid fever); Donna Shanley (kid stories); Kostas Stergiou, Ray Symonds, Ann Tautz, Peter Tyedmers, Anne van Dam (things Dutch), Michael Vakily, Maria Helena Vieira (Cape Verde Islands), Joseph Wible (Darwiniana), Cindy Young (image processing), and Dirk Zeller.

Conventions used in the text

Most of the material in *Darwin's Fishes* is presented as an alphabetical list of entries, each relating to a particular term or 'headword' (printed in **bold**). [Note that German characters with umlauts, e.g. ä, ü, are alphabetized as if the 'e' were spelled out, i.e. ae, ue.] The entries are liberally cross-referenced by means of asterisks in front of words that are headwords, and by the use of '*see*' and '*see also*'. Charles Darwin is referred to as 'CD' throughout.

CD's own words are differentiated from mine by being presented in this font. Underlinings within CD quotes are his own, except in the entry on *electric organs (II). My few underlinings correct small errors such as incorrect dates of references.

The editors of CD's **Correspondence, *Marginalia, *Notebooks* and other material not originally intended for publication did a marvellous job deciphering his handwriting and producing texts suitable for scholarly study. Notably, they provide lists of symbols and fonts allowing the distinction of different 'layers' in CD's writing (e.g. to distinguish original text from later emendations). In this book only a few symbols have been retained from the *Correspondence* and *Notebooks* and also used for the transcription of **Fish in Spirits of Wine*. These are:

<....> indicating a deletion by CD;
<<..>> indicating an insertion by CD; and
[.....] indicating editors' (or my) notes within the text.

The superscript numbers indicating foot- or endnotes are largely CD's, with a few provided by the editors of work from which quotes were extracted. The original numbers were changed in only a few cases, to ensure their uniqueness within each alphabetic entry. In the annotations to CD quotes, I use 'n.' to refer to items originally in such notes.

Darwin and ichthyology

This book, consisting mainly of alphabetized entries and of quotes ripped from their context, makes it hard for the reader to gain an overall view of its major topic: Darwin's relationships to ichthyology, both as a user of, and a contributor to, the insights in that discipline.

The brief introduction which follows, adapted from Pauly (2002a), attempts to compensate for this by linking Charles Darwin (CD; 1809–82) to various themes, arranged in four periods, and themselves linked to some of the major entries of this book, where detailed information and the relevant quotes are presented.

The years before the *Beagle*

Contrary to a widespread view, CD's youth and student years prepared him well for the *naturalist role he assumed during the voyage of the **Beagle*.

CD's schooling appears to have been typical of that of boys of his social class and time, even if he recalled, in his **Autobiography* (p. 46) that he was doing no good at school. Far more interesting, at least here, is his extraordinary devotion to *angling, which started at an early age, and apparently lasted until well into the *Beagle* years. An extensive *correspondence attests to this devotion, and related activities and readings, notably of Izaak *Walton's *Compleat Angler*. Indeed, Walton's classic, which identifies (and names!) distinct populations of *Trout and other fish species in the British Isles, may have contributed, a decade or so later, to CD's dawning perception of within-species *variation as a motor of *evolution.

CD's angling years were also a period of avid *beetle collection, and this introduced him to Leonard *Jenyns, who later described the fish CD collected during the voyage of the *Beagle*.

Only two elements are highlighted here of CD's student years in Edinburgh: his dissection of a *Lumpfish under the guidance of his then mentor Robert *Grant, and his relationship with John *Edmonton.

The importance of the written account of the Lumpfish dissection derives from the fact that it is the first bit of scientific writing by CD ever found, and from the profound understanding of the relationship between scientific 'fact' and 'theory' that this account documents. Indeed, the mature way of *'seeing' illustrated by this

account, while establishing that CD then was already a keen observer, quick to formulate and test fruitful hypotheses, also establishes that Grant, an early evolutionist, cannot have had on CD as little intellectual influence as claimed in his *Autobiography*.

The relationship with John *Edmonton, a former South American slave of African ancestry established in Edinburgh, from whom CD took private lessons in taxidermy, is also important, as it appears to have opened his mind to respecting people outside his narrow class and ethnic background, thus enabling him to learn from the people he met in his later travels and readings, and, ultimately, to formulate a theory that encompassed all of humanity, and embedded us within the same nature. This contrasts with the divisive schemes propagated by less open-minded contemporaries, e.g. Louis *Agassiz and Richard *Owen, whose religious prejudices, combined with social opportunism, ultimately undermined their science.

CD's years in Cambridge, where he performed rather well as a student, again contrary to a widespread belief fuelled by a misleading account in the *Autobiography*, are documented in various biographies, most of which emphasize the role of his mentor there, the botanist John *Henslow. Nothing peculiar to ichthyology is reported from this period, which ends when Captain Robert *FitzRoy accepted CD as his companion and effective *naturalist on the *Beagle*, after *Jenyns had refused the offer.

The *Beagle* years (1831–6)

CD's plan, when he embarked on the *Beagle*, was to collect enough material and observations to write, on his return, an account similar to von Humboldt's *Voyage aux régions équinoxiales du Nouveau Continent* (1805–39), which he greatly admired. Moreover, as ichthyology, in the early nineteenth century, was completely dominated by French taxonomists, as illustrated by the **Histoire Naturelle des Poissons*, CD also planned to collect fish specimens that would prove to be new species; the more the better. Thus, he concentrated his fish sampling effort in areas not previously, or little, explored by French vessels. Hence the thoroughness of his collecting work in Southern South America, and his more limited samples from the Indo-Pacific.

CD's conservative sampling strategy, dictated in part by the difficulties in preserving and shipping specimens back to England (with Henslow at the receiving end), did pay off, as illustrated by a letter of October 1839 to Jenyns, in which he congratulates himself: I am astonished & glad to hear how many new things you seem to have found – four new genera is something. There would have been more, had not a part of the *collection rotted away.

One important reason why the strategy worked is that Jenyns did a very competent job of describing CD's fishes, successfully navigating the waters between the Scylla of lumping distinct species, and the Charybdis of splitting mere variations into named species. (*FishBase was the main source of updated *names, i.e. the main tool I used to establish the correspondence between his species names and those now considered valid; see also the **Index to the Fishes**).

CD clearly believed, long before he conceived *sexual selection (through which he explained sex-related differences in the *colours of fish and other animals), that the colours of animals matter, and the descriptions of the live colours of most of his specimens, e.g. in *_Fish in Spirits of Wine_, attest to this. Moreover, he did not let his imagination colour his descriptions, basing them, rather, on the colour-coded charts in a book he took with him for that very purpose (Syme 1821). Thus, we can attribute to CD the first rigorous treatment of colours in biology in general, and in ichthyology in particular.

This attention to details which other naturalists may have overlooked is also evident from other aspects of his field work, for example, by his collection in the *Cape Verde, *Falkland or *Galápagos Islands. Notably, this involved performing simple – we might call them Baconian – *experiments, on the behaviour, *ecology, or physiology of various animals, including fishes. This involved, for example, cutting open a marine *iguana in the Galápagos (try that now!) to settle a longstanding dispute on whether they feed on underwater vegetation or on fish, dropping marine fishes into freshwater to see if they would adapt, and more.

The return of the *Beagle* to the *Foundations of Origin* (1837–44)

Particularly revealing to anyone who ever edited a book is the series of letters CD sent to Jenyns, upon his return from the voyage of the *Beagle*, to convince him to start, then to complete the job of describing the specimens CD called my fishes. These letters are fully documented in Burkhardt *et al.* (1986), with additional context provided in this book.

CD even used nationalism: For the credit of English zoologists, do not despair and give up; for if you do, then will it be said that there was not a person in Great Britain with knowledge sufficient to describe any specimen which may be brought here. (Dec. 4, 1837).

As well, CD pleaded with Jenyns for the incorporation, into the fishes' descriptions, of his field notes on colours and behaviour. Jenyns went along, and this made *Fish* (Jenyns 1840–2) rather lively, at least by the standards of the the taxonomic literature of the time. One example, from p. 87: "In Mr Darwin's notes, it is stated that [*_Salarias atlanticus_] bites very severely, having driven its teeth through the finger of one of the officers in the ships company. Its two very long sharp canine teeth at the back of the lower jaw are well calculated to inflict such a wound."

The point about CD, though, is not any of this, but that he discovered *natural selection. His post-*Beagle* *notebooks, now available in their entirety (Barrett *et al.* 1987), make clear that this discovery happened in the autumn of 1838, with various scholars even venturing specific dates.

This led to an immediate change in the way CD read: before, he absorbed ideas from a wide range of books, almost haphazardly, with what we might wish to call an 'open mind'. He describes his reading during this period thus: I worked on true Baconian principles and without any theory collected facts on a wholesale scale . . .

This statement has misled many – because it describes a period which ended when CD hit on natural selection. Thereafter, his readings became more targeted, with all that he read being evaluated (often through critical *marginalia pencilled right onto the offending pages) in terms of its support – or lack thereof – for the nascent theory.

The role played by fish in this phase of CD's personal evolution is hard to pin down. The distributions of fishes clearly played an important role. Notably, CD expected isolated islands to have a relatively large fraction of endemics among their coastal fishes, and one even gets the impression, with regard to the Galápagos at least, that he expected to be able to document, using fish species distributions, the peculiar role that isolated islands play in generating biodiversity, now commonly illustrated with *Darwin's Finches. This couldn't be done at the time, owing to the state of fish *taxonomy, and CD gradually abandoned this theme. However, he continued to discuss fish *distributions when contrasting freshwater with marine habitats, and insisting that the former served as refuge to ancient *ganoid fishes, which have apparently been saved from fatal competition by having inhabited a protected station. (*Origin, VI*, p. 105).

In **Foundations of Origin*, two manuscripts CD wrote in 1842 and 1844 to ensure that his discovery would not be lost (he had his wife promise to publish them, should he die prematurely), 'fish' also served as CD's shorthand for ancestral *vertebrates, especially in terms of their anatomy, habitat, and perceived tendency toward *hermaphroditism, a feature much emphasized in subsequent writings, and fully documented in this volume.

Also of note is CD's membership of the Strickland Commission, which originated the predecessor to the *International *Code of Zoological Nomenclature* (Strickland *et al*. 1843). None of this, however, added to our knowledge of fishes *per se*.

The mature Darwin (1845–82)

CD's contributions to *ichthyology, for the period from 1845 to his death, were both indirect and direct. The indirect contribution, obviously, is that he developed the evolutionary context within which biology must now be done, if it is to mean anything, notwithstanding *creationism.

That story, culminating in the 1859 publication of the first edition of **Origin of Species*, has been told in uncounted biographies and texts, and does not need rehashing here.

However, *Origin*, which ran in six editions during CD's lifetime, contains a multitude of direct references to fishes, notably on sexual selection, on relict forms (variants of the ganoid story, see above), on the position of fishes along the *complexity *scale, and on various *difficulties of the theory, i.e. the seeming lack of transitory forms to explain through natural selection the evolution of *eyes in fishes and other animals; *flying fishes; *swimbladders, erroneously presented as lung precursors; *electric fishes; the metamorphoses of *flatfishes; the pregnancy of male

*seahorses; the sudden appearance of *teleosts in the *fossil record; and more. Also discussed are the impact of sea-surface temperatures and geographic barriers on ichthyofauna formation, including an interesting *volte-face* from the first edition, concerning the impact of the Isthmus of *Panama; and the results of his field experiments on how seeds in fish stomachs are distributed by piscivorous *birds. Overall, *Origin* is a firework of ichthyological ideas.

Many of these ideas are amplified in the books CD later wrote to boost the argument in *Origin*, notably **Variations* (1871, 1877), and **Descent* (1871, 1877), his only works with sections explicitly dedicated to fishes. In *Variations*, a two-page section deals with the origin and forms of *Goldfish. In *Descent*, a section discusses the *sex ratios of *Pike, *salmonids and *cyprinids, and another discusses the secondary sexual characters of a large number of fish *species, from *sharks and *rays to highly derived teleosts.

Thus, CD would have had a strong impact on ichthyology, had he decided to gather his thoughts on this group into a small book, similar, say, to the one he devoted to **Worms*. He never assembled that book, however, and his impact on the discipline remained indirect – or absent, as illustrated by *Günther's *Introduction to the Study of Fishes*.

The present volume may be seen as a belated entry on CD's behalf.

Darwin's Fishes: a dry run

Presenting aspects of the work of Charles Darwin (CD) in alphabetic form appears never to have been done so far. Thus, it may be useful to provide examples of how this book can be used to extract structured information from its entries and annotated references. This 'dry run' may then serve as:

1 Another introduction to those who skip prefaces and/or introductory essays (which one should not, as this is where the authors usually best explain themselves); and
2 An instructor's guide for the daring colleague considering using *Darwin's Fishes* as main text or supplementary reading for a course in ichthyology, evolutionary biology, or in the history of science.

First to the structure of *Darwin's Fishes*. This book presents all that CD ever wrote on fishes. The bulk of this material is presented in the form of alphabetized **entries**. Another, if small, part of CD's writing on fishes is presented here as annotation to references. This, plus the fact that most references also include my own annotations (and translations, where appropriate), and that all references are cross-linked to all entries where they are cited, make the bibliography an integral part of *Darwin's Fishes*, and not what it might seem at first sight: a grave for the dead bones of scholarship. This integration with the main entries also applies to CD's field notes on fishes, presented here both as a whole (*see* **Appendix I** and/or '***Fish in Spirits of Wine***') and as short quotes within the relevant entries.

Thus, following up on a topic will usually require starting from its main entry, then linking to both the related entries and the references. This is illustrated here with sequences of quotes and comments dealing with three topics, each documenting one typical entry in *Darwin's Fishes*, and pertaining to:

1 A (group of) fish species CD was interested in;
2 A concept which CD documented with fish examples; and
3 A person with whom CD debated fish-related issues.

Parrotfishes CD sampled parrotfishes in both *Tahiti and the *Cocos Islands. While the species in question were not new to science, CD's thoughts about the ecological role of parrotfishes turned out to anticipate his later work on the slow work of earthworms: he believed that parrotfishes, by consuming corals and defecating calcium carbonate, had created the chalk layers that characterize the *Cretaceous, only to be rebuffed by a naturalist, William Buckland, who was often wrong, but not on this. CD also tested whether parrotfishes contain poison, which they do. He also misspelled parrotfish (genus *Scarus*) to **Sparus*, which earlier editors of his work failed to notice.

Thus, if you turn to the entry on parrotfishes (p. 154) you will see that it is linked through the asterisked entries to:

Ciguatera A form of ichthyotoxicity of reef fishes, increasingly affecting the international fish trade and to which CD exposed himself when he consumed a *barrow-cooter (his *spelling again) and, possibly, a parrotfish.

Cocos Islands The atolls, now officially known as 'Cocos (Keeling) Islands,' visited by the **Beagle* in April 1836, where CD tested his just-developed theory of coral reef formation (outlined in **Coral Reefs* and predictably rejected by *Agassiz), sampled eleven species of fish (all asterisked), none new to science and a small fraction of the 533 fish species occurring there.

Porgies Fishes of the genus *Sparus*, a misspelling of *Scarus*. CD sampled a porgy in the *Galápagos.

Shoals Referring to a group of fishes, but differing from 'school.' Shoal also pertains to an area of shallow waters, such as the *Abrolhos.

Tahiti where CD sampled ten species of fish (all asterisked), whose range was later briefly discussed, and where he performed a memorable trip inland, described in further entries (*see* **Food-fish; Otters**).

There are other ways than shown above to follow up on the parrotfishes entry. For example, it would have been possible to first visit some of the references cited in that entry (e.g. Valenciennes (1840) or **Fish*, i.e. Jenyns (1840–2)). This would have led to details on the monumental **Histoire Naturelle des Poissons*, the major source of data on fishes at the time, or to CD's annotation on the book in which the specimens he collected were described.

Sexual dimorphism We take this entry to illustrate how *Darwin's Fishes* deals with concepts, in this case one proposed by CD himself. Here we find a definitional quote by CD, and a cross link to *sexual selection, usually the cause of sexual dimorphism. Also, we find a link to *FishBase, an Internet-accessible global database on fish that can be used to test the hypothesis implicit in the CD quote, i.e. that in fish, the females are always larger than the males.

Contrary to the information CD was given on this by *Günther and others, not all fish species have females that are larger than the males (the *Cichlidae represent one of many exceptions). However, this rule does apply to the majority of fish species, and it is sufficiently true to cast doubt on a related belief CD held, which I call the *reproductive drain hypothesis. The belief here is that growth

and reproduction act as 'antagonists', i.e. that fish either grow fast or have a high fecundity, but not both. CD favourably cites *Spencer to that effect, and refers to his 'explanation' of the antagonism. Spencer, however, only asserts its existence, and the few examples he gives (Cod, Stickleback) contradict him: Cod grow faster to larger sizes than Sticklebacks, though they have a much higher fecundity. I refer to the entry on *oxygen to explain this apparent paradox, one of the cases where I smuggled a pet theory into *Darwin's Fishes*.

Here again, tracking the references allows identifying further links. Thus, the annotations to Spencer (1864–7) connects not only back to the *reproductive drain hypothesis, but also to *social Darwinism, to which he contributed the key ingredients, and to *survival of the fittest, the term he invented and passed on to a reluctant CD.

Agassiz Our last example is an entry on a person, Jean-Louis Rodolphe Agassiz. The text of the entry betrays that I do not like the man, despite having grown up in a city (La Chaux-de-Fonds, Switzerland, although I am French) whose main street and one of its schools bear his name. He was just too bigoted to now serve as a role model to anyone. And it did not help that he ended up rejecting just about any scientific advance he encountered, be it evolution by *natural selection, or the elegant theory of reef formation outlined in **Coral Reefs*.

In his own entry, Agassiz is cross-referenced to *cavefishes, *classification, *creationism, *evolution, and *taxonomy. As in the above two examples, these entries lead to other entries, etc., and thus to more material on Agassiz' often weird scientific stands (though he did get his glaciers right). We can also sample the virulence of his racism (even within the context of his time) more directly through the references cited in the main entry, i.e. through the annotations to Morton (1854), in which CD suggests he (Agassiz) should be ashamed of what he wrote.

Finally: while navigating through this book, refer to the section on 'Conventions used in the text', and try the entry on *spelling if you think something looks wrong. And please read the Preface if you have not already done so.

Entries (A to ZZZ)

A The first letter of the Roman alphabet, and hence the place where the systematic reader and the author of an encyclopedia first meet. It is therefore the place where the reader is urged not to judge this book by its first letter(s) – just as it shouldn't be judged by its cover. Rather, continue to read further down, 'alphabetically' as it were, or browse. You can do this randomly, or by following the links connecting the entries in this book.

Thus, you can go from here to *Darwin the person (a.k.a. *CD), or to *a* *darwin, the unit of evolutionary change. (Note the subtle introduction of 'a,' the indefinite article, also much used by CD). Or, if you don't already know, you can find out what a *chrestomathy is, or look at the references, either to see if you are cited (you might be if you are an ichthyologist, or a Darwin scholar), or to read some of the nasty remarks CD penned about authors such as Chambers, or *Lamarck. Or you can check on the epistemological problem posed by CD's often strange *spelling.

In this book, CD's writings are always in this font; *italics* are used for emphasis, for Latin or French expressions, and for scientific names (*see also* **ZZZ**).

Aberrant Forms or groups of animals or plants which deviate in important characters from their nearest allies, so as not to be easily included in the same group with them, are said to be aberrant (*Origin VI*, p. 430; see **Cavefishes, Lungfishes, Seahorses**).

Abnormal contrary to the general rule (*Origin VI*, p. 430; *see, for example*, **Analogous organs; Flatfish controversy (II); Monstrosities**).

Abrolhos Reefs named from the Portuguese 'abre olhos,' i.e. 'open your eyes'. Given the soft nature of ships' hulls relative to reefs, there are several places where opening one's eyes was recommended by Portuguese sailors, and two of these are mentioned by CD.

One of these places is the Abrolhos Archipelago, off Brazil (about 18°S, 38°35′W), visited by the *Beagle* in late March 1831. CD noted, while in the vicinity of the Abrolhos, that since leaving Bahia, the only living things that we have seen were a few *sharks & *Mother Carey's chickens (*Diary*, March 24–6, 1832).

The ecosystems of the Brazilian Abrolhos have been relatively well studied (Telles 1998; Ferreira and Gonçalves 1999), and it is hoped that the establishment of a marine park in the area (Dutra 1999) will help overcome the effects of various stresses, notably overfishing.

Another of these places is Houtman's Abrolhos, located on the northwest coast of Australia (28°S), and briefly described in **Coral Reefs* (pp. 234–5). CD noted that: Dampier also repeatedly talks about the immense quantities of Cuttle fish bones floating on the surface of the ocean, before arriving at the Abrolhos *shoals. (*Notebook R*, p. 23; Dampier 1703). However, cuttlefish are molluscs, and do not belong to *Darwin's fishes as defined in this book. Thus, I don't know how these cuttles smuggled themselves in here. Perhaps because of CD's *spelling.

Acanthoclinus fuscus *See* **Roundheads.**

Acanthopterygians A superorder of fishes, characterized by spiny fins and *ctenoid scales, and which includes the perch-like fishes and closely allied groups, i.e. the majority of the over 28,000 extant species of fish.

It is therefore not surprising that *Jenyns, who described CD's fish *collection, should have had problems with the Acanthopterygians. Thus CD's encouragements to Jenyns: I admire the ingenuity, with which you perceive a fishy smell about my book, my silence, & daresay the very name of me: – Moreover this fishy smell, as far as I remember of it in *Henslow's Museum was not very savoury, so that I fear the very idea of me must disturb your nostril. – Far from thinking you have done little, I am delighted to hear that the Acant. are so nearly ready: with respect to the time could you let

me have the fish by the end of November, as the latest, so as to produce a number by the final day of the year, or on the 1st of the ensuing March. [. . .]. Have you any idea of the bulk of your M.S. for the Acant. portion of the Fish? [. . .].

I am really very sorry that you find my fish such a troublesome job – ill luck to them they have caused me trouble & plague also, – but I trust you will eventually be repaid in their having led you to study some of the groups of foreign fish – & I feel sure, that whatever you do in them, as far as it goes, will be good work, & a step in the good science of Natural History (*Correspondence*, July 15, 1839).

***Acanthurus* spp.** *See* **Surgeonfishes.**

Achirus lineatus *See* **Sole, Lined.**

Agassiz, Jean-Louis Rodolphe Swiss–American biologist and geologist (1807–73) whose early work on fossil (Agassiz 1833–44) and recent fishes (Spix and Agassiz 1829–31; Agassiz 1846) and on the slow work of glaciers won him enough fame for a ticket to America in 1846, where, after ingratiating himself with the most illiberal part of the local elite (see annotation to Morton 1854), he founded Harvard's Museum of Comparative Zoology (Winsor 1991; Tort 1996, pp. 33–7). From this new base, he undertook various expeditions, notably to collect Amazon fishes (Agassiz and Agassiz 1868), and to describe coral reefs in Florida (Agassiz 1883).

Agassiz corresponded extensively with CD, and the fishy part of this correspondence, e.g. on *cavefishes, is documented in this book. However, Agassiz remained to his dying day a prisoner of religious prejudices. Grove and Lavenberg (1997, p. 8) write with reference to an expedition that Agassiz led to the *Galápagos, in 1878, that "curiously the finding of new, different species did not change Louis Agassiz' vigorous opposition to the Darwinian theory of *evolution". Indeed, Agassiz' research programme was geared toward detecting the working of God's mind in the *taxonomy and *classification of living and extinct organisms (Winsor 1991). Agassiz was the last prominent biologist to hold on to such a dream, now the nightmare of biology teachers in less enlightened parts of the world. (*See also* **Creationism.**)

Agriopus hispidus *See* **Pigfishes.**

Albicore CD's *spelling for 'Albacore,' i.e. *Thunnus alalunga* (Bonnaterre, 1788).

As noted by CD, Albacore feed on *flying fishes, which feed on small *crustaceans (*Journal*, Dec. 6, 1833). What supported the latter, i.e. the basis of pelagic *food webs, eluded him, however, as *phytoplankton had not yet been discovered. (*See also* **Plankton.**)

***Aleuteres* spp.** *See* **Filefishes.**

Algae A class of plants including the ordinary seaweeds and the filamentous freshwater weeds (*Origin VI*, p. 430; *see* **Blennies**; **Damselfishes**; **Kelp**; **Lizards**; **Parrotfishes**; **Plankton**).

Alosa *See* **Herrings.**

Altruism An action by, or feature, of a given individual, appearing to benefit a different and unrelated individual.

Altruism represented a serious problem for CD's theory of *natural selection. Thus, after reading in McClelland (1839, p. 230) that Fishes are bright to be caught, he noted: I must utterly deny this. – If this could be passed – farewell my thesis (**Marginalia* 550). CD then developed this point: It has been asserted that animals are endowed with instincts, not for their own individual good or for that of their own social bodies, but for the good of other species, though leading to their own destruction: it has been said that fishes migrate that birds & other animals may prey on them;[2] this is impossible on our theory of the natural selection of self-profitable modifications of instinct. But I have met with no facts, in support of this belief worthy of consideration. (**Big Species Book* p. 520; n. 2 cites Linnaeus (1762), p. 389, and Alison (1847), pp. 7, 15).

CD rightly saw in altruism a clear test of his theory (*see also* **Difficulties**), which thus meets *Popper's criterion of falsifiability: As in nature selection can act only through the good of the individual, including both sexes, the young, & in social animals the community, no modification can be effected in it for the advantage of other species; & if in any organism structure formed exclusively to profit other species could be shown to exist, it would be fatal to our theory. Yet how often one meets with such statements, as that the fish in the Himalayan rivers are bright-coloured, according [to] an excellent naturalist, that birds may catch them! How the fish came to be bright-coloured I can no more pretend to explain than how the *Gold-fish, which Mr *Blyth <informs me he> believes to be a domestic *variety of a dull-coloured Chinese fish, has gained its golden tints, or than how the *Kingfisher, which preys on these fish, comes to be so brilliantly *coloured, without, as far as we can see, any direct relation to its habits. (*Big Species Book*, p. 382; the excellent naturalist is McClelland, cited above. *See also* **Handicap principle**.)

Strangely enough, a Russian school of self-described 'Darwinian' evolutionists emerged which saw altruism of the kind CD rejected as the motor of *evolution (Todes 1989; Sapp 1994). This school included a noted ichthyologist, Karl Fedorovich Kessler, who interpreted fish reproduction, schooling and migrations as forms of 'mutual aid' (Todes 1989, pp. 109–12).

'Mutual aid' is tempting, though it is not what seems to be happening in nature. Rather, the detailed study by Hamilton (1964) and others, first of social insects, then of other social animals, demonstrated conclusively that 'helping,' for an animal, can lead to increased survival and reproduction of kin, i.e. siblings, cousins, etc. Their increased fitness increases the 'inclusive fitness' of the helper, thus compensating for the cost of helping, which can go, for example in the worker caste among eusocial insects, as far as forgoing reproduction. Or put differently: an animal can opt to spread its genes by helping its relatives reproduce successfully, and thereby spread the shared genes, which can be seen as the ones that 'selfishly' benefit from the whole arrangement (Dawkins 1989).

Thus, CD need not have worried about altruism ultimately undermining his theory. In fact, altruism became one of the exceptions that probed the rule.

Amblyopsis *See* **Cavefishes**.

Amblyrhynchus *See* **Lizards**.

Ammocœtus(-es) Larval form of *lampreys, resembling *lancelets in shape and behaviour, and used once by CD to illustrate forms that lack *complexity.

Amphibians A class of vertebrates which includes the frogs, toads and newts (i.e. the 'batrachians'), sporting a mix of features which renders them in some ways 'intermediate' between primitive fishes and early reptiles (though one must be wary of such linear *scale).

CD suggested once that the *lungfish *Lepidosiren* mediates between fish and amphibians: Unknown form probably intermediate between mammals, Reptiles & Birds as intermediate as Lepidosiren now is between Fish and Batrachians (*Corresp.* to C. *Lyell, Sept. 23, 1860). He did this only once, presumably because the lungfishes, at the time, were perceived to *be* amphibians.

The larval form of amphibians, the tadpole, provides a model for the early chordates. The similarities between larval *seasquirts and tadpoles are particularly striking, and are commented upon by CD. (*See also* **Vertebrate origins; Lancelet; Ontogeny**.)

Amphidromy(-ous) A questionable form of *diadromy, referring to fishes that migrate between freshwater and the sea, but not for the purpose of breeding, as *anadromous and *catadromous species do.

Amphioxus *See* **Lancelet**.

Anadromy(-ous) Refers to fish whose adults leave the sea and ascend rivers to spawn; most *salmon and *shads are anadromous. (*See also* **Diadromy**.)

Analogous organs Organs whose similarity depends upon similarity of function, as in the wings of insects and *birds. Such structures are said to be analogous and to be analogues of each other. (*Origin VI*, p. 430). Analogous organs constrast with 'homologous' organs, derived from the same body parts, such as the wings of *bats and birds, both ultimately derived from the forelegs of ancestral lower vertebrates. *Owen contributed greatly to the differentiation of these two concepts, a necessary step in the understanding of organic *evolution. CD discussed the implications of analogous organs under the heading Similar & peculiar organs in beings far remote in the scale of nature, viz.: – I have already alluded to the remarkable case of *Electric organs occurring in genera of fish, as in the *Torpedo & *Gymnotus almost as remote as possible from each other: but the organs differ not only in position, & in the plates being horizontal in one & vertical in the other, but in the far more important circumstance of their nerves proceeding from widely different sources[1] (**Big Species Book*, pp. 374–5; n. 1 cites Owen (1846) who, on pp. 217–18, describes two types of electric organ. However, Owen does not explicitly mention their nerves having different sources, though it may be implied.)

Also: According to our theory when we see similar organs in allied beings we attribute the similarity to common descent. But it is impossible to extend this doctrine to such cases, as those just given of the [. . .] Torpedo & Gymnotus, the Echnida & Hedgehog &c, – excepting in so far that community of descent, however remote the common ancestor may have been, would give something in common to the general organisation. Just in the same way [. . .] we have seen that the occurrence of similar monsters in the most diverse members of the same great class may be attributed to a like organisation from common descent, being acted on by like *abnormal causes of change [. . .].

It is not, I think, at all surprising that natural selection should have gradually given a fish & a *whale something of the same forms, from fitting them to move through the same element; just as man in a small degree has given by his selection something in common to the form of the grey-hound & race-horse. A similar doctrine, I infer, must be extended to the above given remarkable cases of similar, though very peculiar & complex structures, in beings remote in the *scale of nature. Such cases are not common; & in some of them the parallelism, as we have seen in the electric organs of fishes & in the eye of Cephalopod & mammal is not absolutely strict. (*Big Species Book*, pp. 375–6.)

Androgynous *See* **Hermaphrodite**.

Anelasma squalicola *See* **Barnacles**.

Angling Young CD was an avid angler, and this led his older brother Erasmus Darwin to write to him: "As to the tackle you are quite welcome to have it all except the line whose beauties you don't appear to appreciate properly." (*Correspondence*, June 1825).

Three years later, CD described his passion in letters to his cousin W. D. Fox: The reason I delayed answering is that I have been on an expedition for a few days. For you must know that I am become a 'Brother of the Angle' under the superintendence of M[r] Slaney (MP. for our town of Shrewsbury), who pronounces me a very flourishing Pupil. (*Corresp*. Aug. 19, 1828). The term Brother of the Angle, emphasized by CD, is from Izaak *Walton's *Compleat Angler*, first published in 1753. One cannot help but wonder how much this work, and its many references to local variants (or *races) of widely distributed fish *species, such as Brown *trout, may have influenced CD's later thinking on *variation. Also, angling led him to keep a field list of fishes, based on Neill (1808; Browne 1995, p. 78; DAR 5: 28–35).

CD remained devoted to angling until shortly before the voyage of the *_Beagle_: I have been intending to write every hour for the last fortnight, but *really* have had no time: I left Shrewsbury this day fortnight ago, & have since that time been working from morning to night in catching fish or *beetles. This is literally the first idle day I have had to myself: for on the rainy days I go fishing, on the good ones Entomologizing. [. . .] And now I give you some account of our Welch trip. [. . .] Old E & myself staid a few days longer & had some pretty good trout fishing. (*Correspondence*, Aug. 25, 1830).

Later, CD was to remember his passion: I had a strong taste for angling, and would sit for any number of hours on the bank of a river or pond watching the float; when at Maer[1] I was told that I could kill the worms with salt and water, and from that day I never spitted a living worm, though at the expense, probably, of some loss of success (**Autobiography*, p. 27; n. 1 identifies the house as that of CD's uncle, Josiah Wedgwood). CD's experience with angling can be assumed to have contributed to the skill he displayed during the voyage of the *Beagle*, while acquiring his *collections of fish specimens, and while *fishing to supply the *Beagle* crew with fresh food.

Anguilla *See* **Eel; Eels.**

Annelids (-idae) A class of worms in which the surface of the body exhibits a more or less distinct division into rings or segments, generally provided with appendages for locomotion and with gills. It includes the ordinary marine worms, the earthworms, and the leeches (*Origin VI*, p. 431; by ordinary marine worms, CD means bristle worms, or polychaetes, of which he often uses the genus *Nereis* as a representative. Hence his vision of chalk-making nereidous animals in the *Cretaceous. *See also* **Dohrn.**)

***Aphritis* spp.** *See* **Thornfishes.**

Apistus A genus of scorpionfishes to which *Jenyns (*Fish*, p. 163) assigned a specimen collected by CD at *King George's Sound, Australia. He also felt that this specimen, though sharing a number of features with *Apistus niger*, now *Tetraroge niger* (Cuvier, 1829), Family Tetrarogidae, was 'distinct' from it.

This is confirmed by Gomon *et al.* (1994), who point out that the range of *T. niger* does not extend to southern Australia. This leaves open the true identity of the specimen collected by CD.

***Aplochiton* spp.** *See* **Galaxiidae.**

Aplodactylus punctatus *See* **Marblefishes.**

Arripis georgianus *See* **Ruff.**

Artificial selection The process wherein a human breeder chooses which of the progeny of a plant or animal should survive and reproduce. The long-term results of such selection are preferred *breeds or *races. It was CD who first noted the similarity between such selection and the process he called *natural selection.

In fact, the two processes differ only when seen from our perspective as 'selectors'. From the selectee's (e.g. a *Goldfish's) point of view, we are as much part of its environment as, say, its *parasites. Thus, we can also conceive artificial selection as being, from the selectee's point of view, a way of establishing itself in a new niche: the material culture that humans create (including aquaria in pet shops).

Ascension Island A small island in the Southeastern Atlantic, 1290 km to the northwest of *Saint Helena Island, visited by the *Beagle* on July 19–23, 1836. CD took the opportunity for studying the geology of Ascension Island, but does not appear to have sampled its marine life.

Later, however, CD did comment on the fishes of Ascension Island: Fish of Teneriffe. St. Helena & Ascension most species like & *identical* with S. America. & many very *close*:[5] see full paper.[6] L'Institut 1838. p. 338 (*Notebook E*, p. 406; n. 5 refers to Valenciennes (1838a), p. 338; 6 to Valenciennes (1838b), i.e. a summary of Valenciennes (1837–44)).

According to Edwards (1990, p. 45), Ascension Island has a total of 72 species of bottom-dwelling neritic fish, with the following affinities: widespread warm Atlantic species 24; Western and Central Atlantic 21; Central Atlantic 16; Eastern and Central Atlantic 4; *endemic species: 7 (i.e. 10%, similar to the percentage of endemic fishes in the *Galápagos).

Assuming that 'most' means over 50%, it may perhaps be argued that, indeed, most species [of Ascencion are] like & identical with S. America – but this may stretch CD's description too far.

Ascidians *See* **Seasquirts**.

Aspidophorus chiloensis *See* **Poachers**.

Asterisk The symbol*, used in this book to identify terms with an entry of their own. Often written 'Asterix' by French schoolchildren. Find out why.

Asymmetry The results of differences between the 'sides' of structures with one or more longitudinal axes, such as the body of an animal. Echinoderms and coelenterates – CD's *Zoophites – whose bodies are radially symmetrical, have many opportunies for asymmetries (see, for example, Edwards 1966). Some echinoderms, such as the sand dollars and the sea cucumbers, sport variable mixtures of bilateral and radial symmetry, resulting in various asymmetries, depending on one's standpoint. Hence CD's definition of assymetrical as having two sides unlike (*Origin VI*, p. 431) is incomplete.

The bilaterally symmetrical vertebrates only rarely have genes coding for external asymmetries (although asymmetry of internal organs is the rule). Notable exceptions are the *Cichlidae, the *flatfishes, and the *Jenynsiinae, wherein species and/or populations may be defined by the orientation of their asymmetry. Another exception is the *lancelet, whose slight asymmetry may be vestigial (*see* **Dohrn**).

Except in these groups, externally visible asymmetries can therefore be used, in the context of *sexual selection, to evaluate whether a potential partner has suffered from developmental errors, *parasites, predator attacks, or diseases (see Morris *et al*. 2003; Reimchen 1988, 1992, 1997; Sasal and Pampoulie 2000), all of which invariably generate asymmetric injuries. Indeed, many animals, including fishes, generate colour patterns of intricate symmetry, i.e. in which asymmetries are easily detected. Such a *handicap may help females evaluate the true fitness of males.

Laterality is a form of asymmetry reflected in the preferred use, by animals, of (appendages on) their left or right side. It is known as 'handedness' in humans.

***Atherina* spp.** *See* **Silversides**.

Autobiography Short name of the manuscript initially titled *Recollections of the development of my mind and character* written by CD between 1876 and 1881, initially for the benefit of his family, and of which a bowdlerized version was published after his death by his son Francis, along with a selection of his letters, also expurgated (Darwin 1887). A version, with "original omissions restored" was published by CD's granddaughter (Barlow 1958), but serious damage had already been done in terms of casting CD as a conventional, vaguely religious country squire dabbling in nature studies. This may have been accentuated by CD's description of his seemingly unfocused readings during a brief, specific period, from mid-1837 to the autumn of 1838, on p. 119 of his *Autobiography*, which has misled generations of CD's biographers: I worked on true Baconian principles and without any theory collected facts on a wholesale scale . . . The point here is that CD not only misrepresents Bacon (1620), but most of his own practice, in which 'facts', at least from the end of 1838 to the very end of his working life, were collected *only* to test clearly formulated hypotheses, notably *natural selection.

Here is one of CD's most famous quotes on this: About thirty year ago there was much talk that geologists ought only to observe and not theorise; and I well remember some one saying

that at this rate a man might as well go into a gravel-pit and count the pebbles and describe the colours. How odd it is that anyone should not see that all observations must be for or against some view if it is to be of any service (*Correspondence* to Henry Fawcett, Sept. 18, 1861). Similarly, he told Anton *Dohrn, on September 26, 1870, in response to a question on how he started his various studies: I begin always with a priori solutions, if anything happens to interest me. I have generally hundreds of hypotheses before I know the facts; I apply one after the other, till I find one which covers the whole ground. But I am exceedingly careful and slow in printing (Groeben 1982, p. 94). Indeed, CD was an originator of the 'hypothetico-deductive method' usually attributed to *Popper (Ghiselin 1969). Here we can give only glimpses of this, e.g. in CD's *experiments with fishes, which, indeed, were never printed.

Azores An archipelago consisting of nine small volcanic islands west of the Portuguese mainland, and the last stopover of the **Beagle* before she arrived in Falmouth on October 2, 1836, and completed her voyage. Armstrong (1992c) thus called Terceira, where the *Beagle* anchored, "Charles Darwin's Last Island".

While performing his usual land-based explorations, CD did not collect marine organisms from the Azores. Indeed, during the last phase of the voyage of the *Beagle*, CD sampled very few marine animals in general, and fishes in particular.

Thus, CD did not sample *Scorpaena azorica* Eschmeyer 1969, originally described as an *endemic but since reported from the Mediterranean (Golani 1996), nor any of the many other fishes from that archipelago (Santos *et al*. 1997). Moreover, in his haste to get back home, CD reported, in both the *Diary* and the *Journal*, his arrival in Terceira as having occurred on September 20, and the departure from the Azores on September 25. The more patient *Beagle* log reports these dates as September 19, and 23, respectively (Armstrong 1992c, p. 60).