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Evolutionarily Degenerate Biological Structures: Terminology Through Time, and the Question of Terminological Consensus

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Abstract

The existence of evolutionarily degenerate biological structures (EDBS) is a major concept in biology. Biologists have often used the terms "vestige," "rudiment," and their adjective forms "vestigial" and "rudimentary" for EDBS since the nineteenth century. Some authors have advocated stricter usage of the terms than others have. For example, some have advocated restriction of the term "rudimentary" to embryonic structures, whereas others have also applied it to postembryonic EDBS. Likewise, some have restricted the term "vestigial" to putatively functionless structures, whereas others have applied it to structures that retain some function. Here, I sought to determine whether a consensus has been reached in the usage of such terms for EDBS. A sample of 200 articles in primary scientific literature from the twentieth and twenty-first centuries shows that through both centuries it has been more common to call EDBS "rudimentary" than to restrict the term "rudimentary" to embryonic structures, and it has been more common to attribute function or possible function to structures called "vestigial" than to restrict the term "vestigial" to putatively functionless structures. The consensus in both centuries has been less-strict usage of such terms; such usage is, in several ways, more logical than strict usage.

Keywords: Vestigial structures, Rudimentary structures, Evolution, Scientific terminology.

Introduction

Biologists have long recognized the existence of biological structures that have become drastically reduced and/or have lost salient functions during the course of evolution (hereafter called evolutionarily degenerate biological structures or EDBS). Through the last three centuries, different authors have preferred different terms for such structures, but various forms of the terms "vestige" and "rudiment" have been the most popular. Some authors have suggested strict definitions for such terms (Brues, 1903; Lull, 1920; Hall, 2003), while others ignore strict definitions and use the terms more loosely (e.g. Miralles et al., 2012; Nweeia et al., 2012; Woon and Stringer, 2012). This study was undertaken to determine whether a consensus has developed in primary scientific literature of the twentieth and twenty-first centuries as to the proper level of strictness for terms for EDBS. Such terms are often spelled the same in English as they are in other languages. Below, therefore, for the sake of clarity, words in languages other than English are italicized.

Biologists used the noun "vestige," its adjective form "vestigial," and their cognates (hereafter collectively called V-terms), as well as the noun "rudiment," its adjective form "rudimentary," and their cognates (hereafter collectively called R-terms) for diminutive biological structures, even before such structures were widely recognized as evolutionary degenerate. In a French-language article, Saint-Hilaire (1798) called the tiny clavicles of the ostrich *rudiments* and called the flightless wings of the cassowary *vestiges*. Cuvier (1799) used the French terms *rudiment* and *vestige* for numerous diminutive animal organs in a treatise on animal anatomy. Both authors used the terms *rudiments*

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and *vestiges* synonymously and without implying evolutionary change. Several nineteenth-century biologists also used similar terms without evolutionary implications, implying only that the structures were relatively tiny in comparison to their homologs in related taxa. Examples include the use of the German words *Spur* (equivalent to "vestige") and *Rudiment* by Mayer (1825) for parts of the diminutive hindlimb skeletons of snakes and reduced-limbed lizards; the use of the Danish word *Rudiment* by Eschricht and Reinhardt (1861) for the pelves and hindlimbs of whales; and the use of R-terms by Strothers (1881) for whale hindlimbs.

The earliest published reference to apparently-degenerate structures as evidence of biological evolution is in Erasmus Darwin's 1791 book *Botanic Garden*. Darwin noted "apparently useless or incomplete appendages to plants and animals, which seem to shew they have gradually undergone changes from their original state" (p. 8). As examples he listed stamens without anthers, styles without stigmas, the halteres of flies, the side toes of pigs, and nipples on male mammals. He used no V-term or R-term for such structures.

In his French-language book *Philosophie Zoologique*, Lamarck (1809) was the earliest author to use such a term to express the opinion that such structures were the evolutionary remnants of more fully-expressed structures in the organisms' ancestors. Lamarck called the blind eyes of mole rats and olms vestiges. He used these and other examples to argue that biological evolution occurs and that an organ that is useless in an animal's environment degenerates through the generations.

Robert Chambers' (1844) *Vestiges of the Natural History of Creation* also cited such structures as evidence for biological evolution. Despite the book's title, Chambers used R-terms for such structures. Examples that he cited include ostrich wings, snake hindlimbs, and the human coccyx. In the category "rudimentary organs" he also included structures that appear and then vanish in the embryo (e.g. teeth in baleen whales), and—echoing Erasmus Darwin—structures that are present in a sex for which they are useless (e.g. male nipples). He considered rudimentary organs to be degenerate forms of more fully-developed ancestral organs in some cases and precursors to more fully-developed descendant organs in other cases.

Lamarck and Chambers explicitly cited fossil succession as evidence of biological evolution. Richard Owen subsequently did likewise, and to emphasize the point he cited specific examples of fossil species with morphology intermediate between older fossil species and modern species (Owen, 1846, 1849). He used the term "rudiments" for diminutive biological structures with larger homologs in related species (Owen, 1849, 1866), and implied that such diminutive structures are evolutionarily degenerate (Owen, 1849).

Charles Darwin (1860, 1871) largely followed Chambers' terminology. He used R-terms for putatively degenerate structures, for structures that are present in a sex for which they are useless, and for structures that appear and then vanish in the embryo. However, he coined the term "nascent organs" for precursors to more fully-developed descendant organs, rather than calling them "rudiments."

In the second half of the nineteenth century it became commonplace for biologists to explicitly opine that apparently-degenerate structures were indeed derived from ancestrally more fully-expressed structures. For EDBS Führbinger (1870) used the German terms *Rudiment* and *Spur*, Marsh (1879) used "rudiments" and "remnants," Cope (1864, 1892, 1894) and Rothschild (1900) used R-terms, and some authors interchangeably used R-terms and V-terms (Morgan, 1891; Bernard, 1893; Wiedersheim, 1895; Wortmann, 1898).

By the twentieth century the theory of biological evolution was accepted by most biologists, and the use of R-terms and V-terms for post-embryonic structures was understood to imply evolutionary degeneration. However, some authors insisted that R-terms be restricted to embryonic structures and not applied to EDBS, to which only V-terms should be applied (Brues, 1903; Lull, 1920; Hall, 2003).

Another call for terminological strictness came from biologists who included functionlessness in the definition of "vestigial," implying or stating outright that V-terms ought not be used for a structure with a known function (Bellairs, 1950; Kinsky, 1971; Scadding, 1981, 1982). Such terminological strictness began in the twentieth century. In contrast, some eighteenth-century and early twentieth-century authors explicitly opined that an EDBS could maintain a minor function even after having lost a major one (Darwin, 1860, 1871; Brues, 1903; Waddington, 1937; Stickel and Stickel, 1946).

In the primary scientific literature of the twenty-first century some authors advocate or employ terminological strictness of the two kinds mentioned above (Hall, 2003; Buckland-Nicks et al., 2011), whereas others do not. Because terminological consensus is important for communication, it would be useful to determine whether a consensus has developed regarding the degree of strictness in the use of terms for EDBS. If a consensus has developed, then it would be advisable for future authors to use terminology as per the consensus so as to communicate with maximum effectiveness.

Methods

I compiled a sample of 200 publications that mention EDBS, 100 apiece from the twentieth and twenty-first centuries. The twenty-first century was therefore sampled more densely, which is appropriate because of its higher publication rate. For the search I used online search engines such as JSTOR (www.jstor.org), Science Direct (www.sciencedirect.com), and Journal Finder (library.uncfsu.edu/journal-finder), as well as the help of nine graduate students who were instructed in the use of those three search engines. Students using Journal Finder were instructed to search within eight journals with frequent reference to EDBS (Am J Bot, Ann Bot, Evolution, Evolution and Development, Journal of Experimental Biology. Journal of Morphology, J Zool, and Proc Natl Acad Sci USA), which together provided 83 of the 200 articles. A publication was included in the sample only if it satisfied the following criteria: (1) it is an example of primary scientific literature (an article in a peer-reviewed journal), (2) it uses V-terms and/or R-terms in reference to EDBS, (3) it is not written from an explicitly anti-evolution perspective. The third criterion was used because of potential conflict between the second crite-

rion and publications written from an anti-evolution perspective. Once the sample of 200 articles was compiled, I examined the use of R-terms and V-terms to determine which articles were relevant to the question of prevailing level of strictness in the use of such terms for EDBS. An article was deemed relevant to R-term strictness level if it included explicit or implicit advocacy of restriction of R-terms to embryonic structures (by outright insistence on such restriction or by unambiguously employing such strict usage), or if it took the opposite stance by applying R-terms to EDBS. An article was deemed relevant to V-term strictness level if it included explicit or implied advocacy of restriction of V-terms to putatively functionless structures (by outright insistence on such restriction or by characterizing specific EDBS as functionless), or if it took the opposite stance by attributing a known or possible function to EDBS to which V-terms were applied.

Results

The results are detailed in Table 1 and summarized in Table 2. Of the 200 articles, 64 were deemed relevant to strictness level for R-terms: 39 from the twentieth century and 25 from the twenty-first century. Of these 64 articles, 59 (92%) applied R-terms to EDBS, while five (8%) advocated or applied restriction of R-terms to embryonic structures. Among the 39 relevant

Table 1. Usage of forms of the terms "vestige" and "rudiment" in reference to evolutionarily degenerate biological structures (EDBS) in 200 twentieth- and twenty-first century publications in primary scientific literature. EA = explicit advocacy of strict usage. F = function (known or possible) admitted for the EDBS in question, or for EDBS in general. L = EDBS in general, or the EDBS in question, characterized as functionless. R = form(s) of the term "rudiment" used for EDBS. SU = strict usage without explicit advocacy. V = form(s) of the term "vestige" used for EDBS.

Publication	Term used for EDBS	Level of strictness for R-terms	Level of strictness for V-terms
Brues, 1903	V	EA	F
Matthew, 1908	R, V		
Bechtel, 1921	V		
Osborn, 1921	R, V		
Camp, 1923	R		
Essex, 1927	V		
Sewertzoff, 1931	R		
Chubb, 1932	V		
Dawson, 1936	V		
Munro, 1937	V		
Waddigton, 1937	R, V		F
Fisher, 1940	V		
Colbert, 1941	V		
Pavan, 1945	R		
Stickel and Stickel, 1946	V		F
Stokely, 1947a	V		
Stokely, 1947b	R, V		
Bellair,s 1950	R		L
Bellairs and Underwood, 1951	R, V		F
Colbert and Mook, 1951	V		
Hosokawa, 1951	R		
Knobloch, 1951	V		L
Woods and Inger, 1957	R		
Boke, 1959	R, V		
Satchell, 1959	V		
Gans, 1960	V		
Emerson, 1961	V		L
Mlynarski and Madej, 1961	R		F
Stephenson, 1961	R, V		
Neville, 1963	V		
Radinsky, 1963	V		F
Gasc,1966	V		F
List, 1966	R, V		

Table 1. Continued.

Publication	Term used for EDBS	Level of strictness for R-terms	Level of strictness for V-terms
Gasc, 1968	R		
Frick and Taylor, 1968	R, V		
McDowell, 1969	V		
Kinsky, 1971	R, V		L
Patton and Taylor, 1971	R, V		
Heye,r 1972	V		
Patton and Taylor, 1973	R, V		
Taylor and Webb, 1976	R, V		L
Tidemann, 1976	R		
Greer, 1977	V		L
Carpenter et al., 1978	V		F
Lande, 1978	R, V		F
Webb and Taylor, 1980	R, V		
Brygoo, 1981	V		
Scadding, 1981	V		L
Slobodchikoff and Wismann, 1981	V		
Naylor, 1982	V		F
Scadding, 1982	V		L
Wilson, 1982	R, V		
Greer, 1985	R		F
Greer and Cogger, 1985	V		
Land, 1985	V		
Thomason, 1985	V		
van der Merwe, 1985	V		F
Boucher, 1986	V		
Stephens, 1986	V		
Brandoni and Brooks, 1987	V		
Greer and Mys, 1987	V		
Hancox, 1988	V		
Ludwig and Gibbs, 1989	V		
Morton and Thurston, 1988	V		
Carle and Whiton, 1990	R		
Grimaldi, 1990	R, V		
Heffner and Heffner, 1990	R, V		
Gillespie, 1991	V		
Mayer and Charlesworth, 1991	R, V		L
Renous et al., 1991	V		
Jouin et al., 1992	V		L
McFadden et al., 1994	V		F
Perle et al., 1994	V		
Triemer and Lewandowski, 1994	V		
Černý and Čižinauskas, 1995	V	SU	
Fong et al., 1995	R, V		L
Deckel, 1996	V		F
Elbrächter and Schnepf, 1996	V		
Gilson and McFadden, 1996	V		F
Call and Dilcher, 1997	V		F
Crespi and Vanderkist, 1997	V		
Tague, 1997	R, V		
Turc and Lecour, 1997	V		
Bhatnagar and Meisami, 1998	R		

Table 1. Continued.

Publication	Term used for EDBS	Level of strictness for R-terms	Level of strictness for V-terms
Doving and Trotier, 1981	V		
Doweld, 1998	R, V		
Murali et al., 1998	V		F
Argiriadi et al., 1999	V		F
Corley et al., 1999	V		
Cohn and Tickle, 1999	R		F
Douglas, 1999	V		F
Klasing, 1999	V		
Rodríguez-Riaño et al., 1999	V		
Weston et al., 1999	V		F
Scholtz, 2000	V		
Takeda, 2000	V	EA	
Gibert et al., 2000	V		
Sato et al., 2000	V		F
Tchernov et al., 2000	R		
Yan et al., 2000	V		
Walker-Larsen and Harder, 2001	V		L
Beardsley and Olmstead, 2002	V		
Bejder and Hall, 2002	V		F
Grimaldi et al., 2002	V		
Kearney, 2002	V		F
Narbona et al., 2002	V		
Peterkova et al., 2002	R, V		
Roxburgh and Penshow, 2002	V		
Rudall et al., 2002	V		
Sekiguchi et al., 2002	V		F
Strittmatter et al., 2002	R, V		
Tague, 2002	R, V		
Ashman, 2003	V		
Emig, 2003	V		
Grimaldi, 2003	V		
Hall, 2003	V	EA	F
Liman and Inman, 2003	V		
Zhang and Webb, 2003	V		
Eastman and Lannoo, 2004	V		
Engel and Grimaldi, 2004	V		
Kearney and Stuart, 2004	R		
Maslakova et al., 2004	V		
Pol and Norell, 2004	V		
Simões-Lopes and Gutstein, 2004	V		F
Streltsov et al., 2004	V		
Whiting et al., 2004	R		
Beutel and Weide, 2005	V		
Golonka et al., 2005	V		
Gotoh et al., 2005	V		
Kearney et al., 2005	V		L
Miura, 2005	V		F

Table 1. Continued.

Publication	Term used for EDBS	Level of strictness for R-terms	Level of strictness for V-terms
Müller et al., 2005	V		
Napoleão et al., 2005	V		
Narbona et al., 2005	V		
Regoes et al., 2005	V		F
Ronse de Craene, 2005	R, V		
Witter et al., 2005	V		
Espinasa and Jeffery, 2006	V		F
Franz-Odendaal and Hall, 2006	V		F
Garnier et al., 2006	V		L
Gomez and Shaw, 2006	V		
Grant, 2006	V		F
Kohlsdorf and Wagner, 2006	V		
Ostrovsky et al., 2006	V		
Prince and Johnson, 2006	V		F
Rehorek and Smith, 2006	V	SU	
Rodríguez-Riaño et al., 2006	R, V		F
Sidell and O'Brien, 2006	V		
Bowsher et al., 2007	V		
Maxwell and Larsson, 2007	V		L
Mehta and Wainwright, 2007	V		
Tamatsu et al., 2007	V		
Watabe et al., 2007	V		
Brandley et al., 2008	V		
Gobin et al., 2008	V		L
Hunt et al., 2008	V		
Jonz and Nurse, 2008	V		F
McGowan et al., 2008	V		
Sherman et al., 2008	R, V		F
Witton and Naish, 2008	V		
Yoshizawa and Jeffery, 2008	V		
Bateman and Fleming, 2009	V		
Crottini et al., 2009	R		
Jerez and Tarazona, 2009	V		
Ostrovsky and Rodríguez, 2009	V		
Renvoisé et al., 2009	V		
Sauer and Hausdorf, 2009	V		F
Tekleva and Krassilov, 2009	R, V		
Wilkens and Purschke, 2009	R, V		
Burnham et al., 2010	V		
Campbell et al., 2010	V		
Senter, 2010a	R, V		F
Senter, 2010b	R, V		F
Zubidat et al., 2010	V		F
Barfod et al., 2011	V		
Buckland-Nicks et al., 2011	R, V		L
Chan-ard et al., 2011	R, V		
Gomes Rodrigues et al., 2011	V		
Moch and Senter, 2011	R, V		F
Ortega-Chávez and Stauffer, 2011	V		

Table 1. Continued.

Publication	Term used for EDBS	Level of strictness for R-terms	Level of strictness for V-terms
Siler and Brown, 2011	V		
Xu et al., 2011	R, V		L
Yu et al., 2011	V		L
Arkhipkin et al., 2012	R, V		F
Bensimon-Brito et al., 2012	V	EA	
Crole and Soley, 2012	R		F
Daver et al., 2012	V		
Hartstone-Rose et al., 2012	V		
Labonne et al., 2012	V		F
Miralles et al., 2012	R		F
Nweeia et al., 2012	R, V		L
Olympska, 2012	V		
Woon and Stringer, 2012	R, V		
Godefroit et al., 2013	V		
Gotoh et al., 2013	V		
Huang et al., 2013	V		
Hutson and Hutson, 2013	V		
Longo et al., 2013	V		F
Sato et al., 2014	V		F
Xu et al., 2014	V		

Table 2. . Number of articles using forms of the terms "vestige" and "rudiment" in specific ways in reference to evolutionarily degenerate biological structures in 200 twentieth- and twenty-first century publications in primary scientific literature. See Table 1 caption for abbreviations.

	1901-2000	2001-14	1901-2014
n	100	100	200
V	87	94	181
R	36	23	59
V&R	22	17	39
EA	2	2	4
SU	1	0	1
F	19	23	42
L	10	9	19

twentieth-century articles, 36 (92%) applied R-terms to EDBS, while three (8%) advocated or applied restriction of R-terms to embryonic structures. Among the 25 relevant twenty-first-century articles, 23 (92%) applied R-terms to EDBS, while two (8%) advocated or applied restriction of R-terms to embryonic structures. The ratio of less-strict to more-strict usage of R-terms is therefore equal between the two centuries, and the prevailing usage in both centuries has been to allow application of R-terms to EDBS.

Of the 200 articles, 61 were deemed relevant to strictness level for V-terms: 29 from the twentieth century and 32 from the twenty-first century. Of these 61 articles, 42 (69%) attributed a function or possible function to EDBS to which V-terms are applied, while 19 (31%) advocated restriction of V-terms to putatively functionless structures. Among the 29 relevant twentieth-century articles, 19 (65.5%) attributed a function or possible function to EDBS to which V-terms are applied, while 10 (34.5%) advocated restriction of V-terms to putatively functionless structures. Among the 32 relevant twenty-first-century articles, 23 (72%) attributed a function or possible function to EDBS to which V-terms are applied, while nine (28%) advocated restriction of V-terms to putatively functionless structures. In both centuries, therefore, the prevailing usage of V-terms applies them to structures with a known or suspected function.

Discussion

Although terminological strictness can be conducive to communication in some cases, the consensus found here indicates that this is not the case with V-terms and R-terms for EDBS. This is none too surprising, because less-strict usage of both sets of terms is more logical than stricter usage in several respects. For example, strict application of V-terms only to functionless structures is illogical because it is impossible to prove that a structure is functionless. A structure with no known function may have a function that is yet to be discovered (Scadding, 1981), and a structure that has lost a major function may retain a minor one (Darwin, 1860; Hall, 2003). Strict usage would therefore ultimately render V-terms inapplicable to any structure. It is more logical to apply the term "vestigial" to a structure that is demonstrably a vestige (a remnant of an ancestrally greater structure) than to define V-terms so strictly as to render them obsolete. A term is pointless if its definition is so strict as to prohibit its usage. In addition, rendering V-terms obsolete would provide ammunition to anti-evolution authors who employ the strict usage of V-terms to cast doubt upon biological evolution by claiming that vestigial structures do not exist because functionlessness cannot be demonstrated (Bergman and Howe, 1990; Sarfati, 2002). It would be incongruous for evolutionary biologists to deliberately provide support for the anti-evolution movement.

Less-strict usage of R-terms for EDBS is logical from an evo-devo perspective. The evolutionary process that produces EDBS often includes the arresting of the structure's development at an early stage (Brues, 1903; Bejder and Hall, 2002; Espinasa and Jeffery, 2006; Rehorek and Smith, 2006), and biologists have long used R-terms for structures in early developmental stages. Because EDBS can therefore be considered to be persistently rudimentary, R-terms are appropriate for EDBS. A recent call for terminological strictness recommended that a given EDBS be called a "rudiment" in the embryo and a "vestige" in the adult (Hall, 2003), but such terminological differentiation is unnecessary, because a structure with immature morphology is morphologically still a rudiment, even if it is in a mature body. To insist that a persistent rudiment not be called a rudiment merely because it persisted as one, is no more logical than to insist that a town not be called a town because it has never grown into a city. Also, biologists frequently use the term "rudimentation" for the evolutionary process that produces EDBS (Berger Dell'Mour, 1985; Tague, 2002; Maxwell and Larrson, 2007). It is linguistically logical to call the product of rudimentation a rudiment.

Stricter usage is not only illogical but is also in opposition to the consensus. As shown here, prevailing usage in primary scientific literature applies R-terms to EDBS and V-terms to structures that retain a function. The few calls for greater terminological strictness have therefore been met with an implicit veto by the rest of the scientific community. It is therefore recommended here that R-terms not be restricted to embryonic structures and that V-terms not be restricted to putatively functionless structures.

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References

Argiriadi MA, C Morisseau, BD Hammock, and DW Christianson (1999) Detoxification of environmental mutagens and carcinogens: structure, mechanism, and evolution of liver epoxide hydrolase. Proc Natl Acad Sci USA 96: 10637-10642.

Arkhipkin AI, VA Bizikov, and D Fuchs (2012) Vestigial phragmocone in the gladius points to a deepwater origin of squid (Mollusca: Cephalopoda). Deep-Sea Res I 61: 109-122.

Ashman T-L (2003) Constraints on the evolution of males and sexual dimorphism: field estimates of genetic architecture of reproductive traits in three populations of gynodioecious *Fragaria virginiana*. Evolution 57: 2012-2025.

Bandoni SM and DR Brooks (1987) Revision and phylogenetic analysis of the Gyrocotylidea Poche, 1926 (Platyhelminthes: Cercomeria: Cercomeromorpha). Can J Zool 65: 2369-2389.

Barfod AS, M Hagen, and F Borchsenius (2011) Twenty-five years of progress in understanding pollination mechanisms in palms (Arecaceae). Ann Bot 108: 1503-1516.

Bateman PW and PA Fleming (2009) to cut a long tail short: a review of lizard caudal autotomy studies carried out over the last 20 years. J Zool 277: 1-14.

Beardsley PM and RG Olmstead (2002) Redefining Phrymaceae: the placement of *Mimulus*, tribe Mimuleae, and Phryma. Am J Bot 89: 1093-1102.

Bechtel AR (1921) The floral anatomy of the Urticales. Am J Bot 8: 386-410

Bejder L and BK Hall (2002) Limbs in whales and limblessness in other vertebrates: mechanisms of evolutionary and developmental transformation and loss. Evol Dev 4: 445-458.

Bellairs A d'A (1950) The limbs of snakes with special reference to the hind limb rudiments of *Trachyboa boulengeri*. Br J Herpetol 1: 73-83.

Bellairs A d'A and G Underwood (1951) The origin of snakes. Biol Rev 26: 193-237.

Bensimon-Brito A, ML Cancela, A Huysseune, and PE Witten, Vestiges, rudiments, and fusion events: the zebrafish caudal fin endoskeleton in an evo-devo perspective. Evol Dev 14: 116-127.

Bergman J and G Howe (1990) "Vestigial Organs" are fully functional. Creation Research Society Books, Kansas City, MO.

Berger-Dell'Mour HAE (1985) The lizard genus *Tetradactylus*: a model case of an evolutionary process. In: K-L Schuchmann (ed.) Proceedings of the International Symposium on African Vertebrates. Zoologisches Forschungsinstitut Und Museum Alexander Koenig, Bonn, pp. 495-510.

Bernard HM (1893) Notes on the Chernetidae, with special reference to the vestigial stigmata and a new form of trachea. J Linn Soc Lond Zool 24: 410-430.

Beutel RG and D Weide (2005) Cephalic anatomy of *Zorotypus hubbardi* (Hexapoda: Zoraptera): new evidence for a relationship with Acercaria. Zoomorphology 124 (2005): 121-136.

Bhatnagar KP and E Meisami (1998) Vomeronasal organ in bats and primates: extremes of structural variability and its phylogenetic implications. Micr Res Tech 43: 465-475.

Boke NH (1959) Endomorphic and ectomorphic characters in *Pelecyphora* and *Encephalocarpus*. Am J Bot 46 (1959): 197-209.

Boucher LM (1986) vestigial larval shells in the planktonic veligers of two gymnodorid nudibranchs. J Moll Stud 52: 30-34.

Bowsher JH, GA Wray, and E Abouheif (2007) Growth and patterning are evolutionarily dissociated in the vestigial wing discs of the red imported fire ant, Solenopsis invicta. J Exp Zool Mol Dev Evol 308B: 769-776.

Brandley MC, JP Huelsenbeck, and JJ Wiens (2008) rates and patterns in the evolution of snake-like body form in squamate reptiles: evidence for repeated re-evolution of lost digits and long-term persistence of intermediate body forms. Evolution 62: 2042-2064.

Brues CT (1903) The structure and significance of vestigial wings among insects. Biol Bull 4: 179-190.

Brygoo ER (1981) Systématiques des lézards scincidés de la région malagache. Bull Mus Natl Hist Nat 3: 675-688.

Buckland-Nicks JA, M Gillis, and TE Reimchen (2011) Neural network detected in a presumed vestigial trait: ultrastructure of the salmonid adipose fin. Proc Roy Soc B 279: 553-563.

Burnham DA, A Feduccia, LD Martin, and AR Falk (2010) Tree climbing—a fundamental avian adaptation. J Syst Palaeont 9: 103-107.

Call VS and DL Dilcher (1997) The fossil record of *Eucommia* (Eucommiaceae) in North America. Am J Bot 84: 798-814.

Camp CL (1923) Classification of the lizards. Bull Am Mus Nat Hist 48: 289-480.

Campbell DR, SG Weller, AK Sakai, TM Culley, PN Dang, et al. (2010) Genetic variation and covariation in floral allocation of two species of *Schiedea* with contrasting levels of sexual dimorphism. Evolution 65: 757-770.

Carle FL and DC Wighton (1990) Odonata. In: DA Grimaldi (ed.) Insects from the Santana Formation, Lower Cretaceous, of Brazil. American Museum of Natural History, New York, pp. 51-68.

Carpenter CC, JB Murphy, and LA Mitchell (1978) Combat bouts with spur use in the Madagascan boa (*Sanzinia madagascariensis*). Herpetologica 34: 207-212.

Černý H and S Čižinauskas (1995) The clavicle of newborn dogs. Acta Vet Brno 64: 139-145.

Chambers R (1844) Vestiges of the natural history of creation. John Churchill, London.

Chan-ard T, S Makchai, and M Cota (2011) *Jarujinia*: a new genus of lygosomine lizard from central Thailand, with a description of one new species. Thail Nat Hist Mus J 5: 17-24.

Chubb SH (1932) Vestigial clavicles and rudimentary sesamoids. Am Nat 66: 376-381.

Cohn MJ and C Tickle (1999) Developmental basis of limblessness and axial patterning in snakes. Nature 399: 474-479.

Colbert EH (1941) The osteology and relationships of *Archaeomeryx*, an ancestral ruminant. Am Mus Novit 1135: 1-24.

Colbert EH and CC Mook (1951) The ancestral crocodilian *Protosuchus*. Bull Am Mus Nat Hist 97: 143-182.

Cope ED (1864) On a blind silurid, from Pennsylvania. Proc Acad Nat Sci Phila 16: 231-233

Cope ED (1892) On degenerate types of scapular and pelvic arches in the Lacertilia. J Morphol 7: 223-244.

Cope ED (1894) On the lungs of the Ophidia. Proc Am Philos Soc 33: 217-224.

Corley LS, JR Blankenship, AJ Moore, and PJ Moore (1999) Developmental constraints on the mode of reproduction in the facultatively parthenogenetic cockroach *Nauphoeta cinerea*. Evol Dev 1: 90-99.

Crespi BJ and BA Vanderkist (1997) Fluctuating asymmetry in vestigial and functional traits of a haplodiploid insect. Heredity 79: 614-630.

Crole M and J Soley (2012) Gross anatomical features of the tongue, lingual skeleton and laryngeal mound of *Rhea americana* (Palaeognathae, Aves): morpho-functional considerations. Zoomorphology 131: 265-273.

Crottini A, J Dordel, J Köhler, F Glaw, A Schmitz, et al. (2009) A multilocus phylogeny of Malagasy scincid lizards elucidates the relationships of the fossorial genera *Androngo* and *Cryptoscincus*. Mol Phyl Evol 53: 3445-350.

Cuvier G (1799). Leçons d'anatomie comparée. Baudouin, Paris.

Darwin C (1860) On the origin of species by means of natural selection. John Murray, London.

Darwin C (1871) The descent of man, and selection in relation to sex. John Murray, London.

Darwin E (1791) Botanic garden, volume 1. J. Johnson, London.

Daver G, G Berillon, and D Grimaud-Hervé (2012) Carpal kinematics in quadrupedal monkeys: towards a better understanding of wrist morphology and function. Journal of Anatomy 220: 42-56.

Dawson MI (1936) The floral morphology of the Polemoniaceae, Am J Bot 23: 501-511.

Deckel AW (1996) Behavioral changes in Anolis carolinensis following injection with fluoxetine. Beh Br Res 78: 175-182.

Douglas SE (1999) Evolutionary history of plastids. Biol Bull 196: 397-399.

Døving KB and Trotier D (1998) Structure and function of the vomeronasal organ. J Exp Biol 201: 2913-2925.

Doweld AB (1998) Carpology, seed anatomy and taxonomic relationships of *Tetracentron* (Tetracentraceae) and *Trochodendron* (Trochodendraceae). Ann Bot 82 (1998) 413-443.

Eastman JT and MJ Lannoo (2004) Brain and sense organ anatomy and histology in hemoglobinless antarctic icefishes (Perciformes: Notothenioidei: Channichthyidae). J Morphol 260: 117-140.

Elbrächter M and E Schnepf (1996) *Gymnodinium chlorophorum*, a new, green, bloom-forming dinoflagellate (Gymnodiniales, Dinophyceae) with a vestigial prasinophyte endosymbiont. Phycologia 35: 381-393.

Emerson AE (1961) Vestigial characters of termites and processes of regressive evolution. Evolution 15: 115-131.

Emig CC (2003) Proof that *Lingula* (Brachiopoda) is not a living-fossil, and emended diagnoses of the family Lingulidae. Camets Géol 2003/01: 1-8.

Engel MS and DA Grimaldi (2004) New light shed on the oldest insect. Nature 427: 627-630.

Eschricht DR and J Reinhard (1861) Om Nordhvalen (*Balæna Mysticetus* L.) navnlig med Hensyn til dens Udbredning i Fortiden og Nutiden og til dens ydre og indre Særkjender. Bianco Lunos Bogtrykkeri, Copenhagen.

Espinasa L and WR Jeffery (2006) Conservation of retinal circadian rhythms during cavefish eye degeneration. Evol Dev 8: 16-22.

Essex B (1927) Studies in reptilian degeneration. Proc Zool Soc Lond 4: 879-945.

Fisher HI (1940) The occurrence of vestigial claws on the wings of birds. Am Midl Nat 23: 234-243.

Fong DW, TC Kane, and DC Culver (1995) Vestigialization and loss of nonfunctional characters. Ann Rev Ecol Syst 26: 249-268.

Franz-Odendaal TA and BK Hall (2006) Modularity and sense organs in the blind cavefish, *Astyanax mexicanus*. Evol Dev 8: 94-100.

Frick C and BE Taylor (1968) A generic review of the stenomyline camels. Am Mus Novit 2353: 1-51.

Fürbinger M (1870) Die Knochen und Muskeln der Extremitäten bei den

Schlangenähnlichen Sauriern. Wilhelm Engelmann, Leipzig.

Gans C (1960) Studies on amphisbaenids (Amphisbaenia, Reptilia) 1. A taxonomic revision of the Trogonophiinae, and a functional interpretation of the amphisbaenid adaptive pattern. Bull Am Mus Nat Hist 119: 129-204.

Garnier S, N Gidaszewski, M Charlot, J-Y Rasplus, and P Alibert (2006) Hybridization, developmental stability, and functionality of morphological traits in the ground beetle *Carabus solieri* (Coleoptera, Carabidae). Biol J Linn Soc 89: 151-158.

Gasc J-P (1966) Les rapports anatomiques du membre pelvien vestigial chez les squamates serpentiformes B.—*Python sebae* (Seba). Bull Mus Natl Hist Nat 38: 99-110.

Gasc J-P (1968) Contribution a l'ostéologie et a la myologie de *Dibamus novaeguineae* Gray (Sauria, Reptilia). Discussion systématique, Ann Sci Nat Zool Paris 10: 127-150.

Gibert J-M, E Mouchel-Viehl, E Quéinnec, and JS Deutsch (2000) Barnacle duplicate engrailed genes: divergent expression patterns and evidence for a vestigial abdomen. Evol Dev 2: 194-202.

Gillespie RG (1991) Predation through impalement of prey: the foraging behavior of *Doryonychus raptor* (Araneae, Tetragnathidae). Psyche 98: 337-350.

Gilson PR and GI McFadden (1996) The miniaturized nuclear genome of a eukaryotic endosymbiont contains genes that overlap, genes that are cotranscribed, and the smallest known spliceosomal introns. Proc Natl Acad Sci USA 93: 7737-7742.

Gobin B, F Ito, and J Billen (2008) Degeneration of sperm reservoir and the loss of mating ability in worker ants. Naturwissenschaften 95: 1041-1048.

Godefroit P, H Demuynck, G Dyke, D Hu, F Escuillé, et al. (2013) Reduced plumage and flight ability of a new jurassic paravian theropod from china. Nature Comm 4 (1394): 1-6.

Golonka AM, AK Sakai, and SG Weller (2005) Wind pollination, sexual dimorphism, and changes in floral traits of *Schiedea* (Caryophyllaceae). Am J Bot 92: 1492-1502.

Gomes Rodrigues H, C Charles, L Marivaux, M Vianey-Liaud, and L Viriot (2011) Evolutionary and developmental dynamics of the dentition in Muroidea and Dipodoidea. (Rodentia, Mammalia), Evol Dev 13: 361-369.

Gomez NN and RG Shaw (2006) Inbreeding effect on male and female fertility and inheritance of male sterility in *Nemophila menziesii* (Hydrophyllaceae). Am J Bot 93: 739-746.

Gotoh A, S Sameshima, K Tsuji, T Matsumoto, and T Miura (2005) Apoptotic wing degeneration and formation of an altruism-regulating glandular appendage (gemma) in the ponerine ant *Diacamma* sp. from Japan (Hymenoptera, Formicidae, Ponerinae). Dev Genes Evol 215: 69-77.

Gotoh A, F Ito, and J Billen (2013) Vestigial spermatheca Morphology in Honeybee Workers, *Apis cerana* and *Apis mellifera*, from Japan. Apidologie 44: 133-143.

Grant JB (2006) Diversification of gut morphology in caterpillars is associated with defensive behavior. J Exp Biol 209: 3018-3024.

Greer AE (1977) On the adaptive significance of the loss of an oviduct in reptiles. Proc Linn Soc NSW 101: 242-249.

Greer AE (1985) The relationships of the lizard genera *Anelytropsis* and *Dibamus*. J Herpetol 19: 116-156.

Greer AE and HG Cogger (1985) Systematics of the reduce-limbed and limbless skinks currently assigned to the genus *Anomalopus* (Lacertilia: Scincidae). Rec Austr Mus 37: 11-54.

Greer AE and B Mys (1987) Resurrection of *Lipinia rouxi* (Hediger, 1934) (Reptilia: Lacertilia: Scincidae), another skink to have lost the left oviduct. Amph-Rept 8: 417-426.

Grimaldi DA (1990) A phylogenetic, revised classification of genera in the Drosophilidae (Diptera). Bull Am Mus Nat Hist 197: 1-139.

Grimaldi DA (2003) A revision of cretaceous mantises and their relationships, including new taxa. Am Mus Novit 3412: 1-47.

Grimaldi DA, MS Engel, and PC Nasciembene (2002) Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. Am Mus Novit 3361: 1-71.

Hall BK (2003) Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution. Biol Rev 78: 409-433.

Hancox M (1988) Dental anomalies in the Eurasian dadger. J Zool 216: 606-608.

Hartstone-Rose A, RC Long, AB Farrell, and CA Shaw (2012) The clavicles of *Smilodon fatalis* and *Panthera atrox* (Mammalia: Felidae) from Rancho La Brea, Los Angeles, California. J Morphol 273: 981-991.

Heffner RS and HE Heffner (1990) Vestigial hearing in a fossorial mammal, the pocket gopher (*Geomys bursarius*). Hearing Res 46: 239-252.

Heyer RR (1972) A new limbless skink (Reptilia: Scincidae) from Thailand with comments on the generic status of the limbless skinks of Southeast Asia. Fieldiana Zool 58: 109-129.

Hosokawa H (1951) On the pelvic cartilages of the *Balaenoptera*-foetuses, with remarks on the specificial and sexual difference. Sci Rep Whales Res Inst 5: 5-15.

Huang D, A Nel, C Cai, Q Lin, and MS Engel (2013) Amphibious flies and paedomorphism in the Jurassic Period. Nature 495: 94-97.

Hunt G, MA Bell, and MP Travis (2008) Evolution toward a new adaptive optimum: phenotypic evolution in a fossil stickleback lineage. Evolution 62: 7100-710.

Hutson JD and KN Hutson (2013) Using the American alligator and a repeated-measures design to place constraints on in vivo shoulder joint range of motion in dinosaurs and other fossil archosaurs. J Exp Biol 216: 275-284.

Jerez A and OA Tarazona (2009) Appendicular skeleton in *Bachia bicolor* (Squamata: Gymnophthalmidae): osteology, limb reduction and postnatal skeletal ontogeny. Acta Zool 90: 42-50.

Jonz MG and CA Nurse (2008) New developments on gill innervation: insights from a model vertebrate. J Exp Biol 211: 2371-2378.

Jouin C (1992) The ultrastructure of a gutless annelid, *Parenterodrilus* gen. nov. *taenioides* (= *Astomus taenioides*) (Polychaeta, Protodrilidae). Can J Zool 70: 1833-1848.

Kearney M (2002) Appendicular skeleton in amphisbaenians (Reptilia: Squamata). Copeia 2002: 719-738.

Kearney M and BL Stuart (2004) Repeated evolution of limblessness and digging heads in worm lizards revealed by DNA from old bones. Proc Biol Sci 271: 1677-1683.

Kearney M, JA Maisano, and T Rowe (2005) Cranial anatomy of the extinct amphisbaenian *Rhineura hatcherii* (Squamata, Amphisbaenia) based on high-resolution x-ray computed tomography. J Morphol 264: 1-33.

Kinsky FC (1971) The consistent presence of paired ovaries in the kiwi (*Apteryx*) with some discussion of this condition in other birds. J Ornithol 112: 334-357.

Klasing KC (1999) Avian gastrointestinal anatomy and physiology. Sem Av Exot Pet Med 8 (2): 42-50.

Knobloch IW (1951) Are there vestigial structures in plants? Science 113: 465.

Kohlsdorf T and GP Wagner (2006) Evidence for the reversibility of digit loss: a phylogenetic study of limb evolution in *Bachia* (Gymnophthalmidae: Squamata). Evolution 60: 1896-1912.

Labonne G, R Laffont, E Renvoise, A Jebrane, C Labruere, et al. (2012) When less means more: evolutionary and developmental hypoth-

eses in rodent molars. J Evol Biol 25: 2102-2111.
Lamarck J-BPA de (1809) Philosophie zoologique. Luminil-Lesueur, Paris.
Land MF (1985) Fields of view of the eyes of primitive jumping spiders. J Exp Biol 119: 381-384.
Lande R (1978) Evolutionary mechanisms of limb loss in tetrapods. Evolution 32: 73-92.
Liman ER, DP Corey, and C Dulac (2003) Relaxed selective pressure on an essential component of pheromone transduction in primate evolution. Proc Natl Acad Sci USA 100: 3328-3332.
List JC (1966) Comparative osteology of the snake families Typhlopidae and Leptotyphlopidae. Ill Biol Monogr 36: 1-112.
Longo S, M Riccio, and AR McCune (2013) Homology of lungs and gas bladders: insights from arterial vasculature. J Morphol 274: 687-703.
Ludwig M and SP Gibbs (1989) Evidence that the nucleomorphs of *Chlorarachnion reptans* (Chlorarachniophyceae) are vestigial nuclei: morphology, division, and DNA-DAPI fluorescence. J Phycol 25: 385-394.
Lull RS (1920) Organic evolution. MacMillan, New York.
Marsh OC (1879) Polydactyle horses, recent and extinct. Am J Sci 17: 499-505.
Maslakova SA, MQ Martindale, and JL Norenburg (2004) Vestigial prototroch in a basal nemertean, *Carinoma tremaphoros*. Evol Dev 6: 219-226.
Matthew WD (1908) Osteology of *Blastomeryx* and phylogeny of the American Cervidae. Bull Am Mus Nat Hist 24: 535-562.
Mayer C (1825) Die Hintere Extremität der Ophidier. N Acta Phys-Med Acad Leop-Carol 2: 819-842.
Mayer C (1829) Fernere Unterschungen über die hintere Extremität der Ophidier und über die Schuppen der Cäcilia. Z Physiol 3: 249-256.
Mayer SS and D Charlesworth (1991) Cryptic dioecy in flowering plants. Tr Ecol Evol 6: 320-325.
Maxwell EE and HCE Larrson (2007) Osteology and myology of the wing of the Emu (*Dromaius novaehollandiae*), and its bearing on the evolution of vestigial structures. J Morphol 268: 423-441.
McDowell SB (1969) *Toxicocalamus*, a New Guinea genus of snakes of the family Elapidae. J Zool 159: 443-511.
McFadden GI, PR Gilson, CJB Hofmann, GJ Adcock, and U-G Maier (1994) Evidence that an amoeba acquired a chloroplast by retaining part of an engulfed eukaryotic alga. Proc Natl Acad Sci USA 91: 3690-3694.
McGowen MR, C Clark, and J Gatesy (2008) The vestigial olfactory receptor subgenome of odontocete whales: phylogenetic congruence between gene-tree reconciliation and supermatrix methods. Syst Biol 57: 574-590.
Mehta RS and PC Wainwright (2007) Biting releases constraints on moray eel feeding kinematics. J Exp Biol 210: 495-504.
Miralles A, M Anjeriniaina, CA Hipsley, J Müller, F Glaw, et al. (2012) Variations on a bauplan: description of a new Malagasy "mermaid skink" with flipper-like forelimbs only, (Scincidae, *Sirenoscincus* Sakata & Hikida, 2003). Zoosystema 34: 701-719.
Miura T (2005) Developmental regulation of caste-specific characters in social-insect polyphenism. Evol Dev 7: 122-129.
Mlynarski M and Z Madej (1961) The rudimentary limbs in Aniliidae (Serpentes). Br J Herpetol 3: 1-6.
Moch JG and P Senter (2011) Vestigial structures in the appendicular skeletons of eight african skink species (Squamata, Scincidae). J Zool 285: 274-280.
Morgan CL (1891) Animal life and intelligence. Edwin Arnold, London.
Morton B and MH Thurston (1989) The functional morphology of *Propeamussium lucidum* (Bivalvia: Pectinacea), a deep-sea predatory scallop. J Zool 218: 471-496.
Müller H, OV Oommen, and P Bartsch (2005) Skeletal development of the direct-developing caecilian *Gegenophis ramaswamii* (Amphibia: Gymnophiona: Caeciliidae). Zoomorphology 124: 171-188.
Munro SS (1937) The effect of testis hormone on the preservation of sperm life in the vas deferens of the fowl. J Exp Biol 15: 186-196.
Murali R, DJ Sharkey, JL Daiss, and HM Krishna Murthy (1998) Crystal structure of Taq DNA polymerase in complex with an inhibitory Fab: the Fab is directed against an intermediate in the helix-coil dynamics of the enzyme. Proc Natl Acad Sci USA 95: 12562-12567.
Napoleão P, PS Reis, LC Alves, and T Pinheiro (2005) Morphologic characterisation and elemental distribution of *Octopus vulgaris* Cuvier, 1797 vestigial shell. Nucl Instr Meth Phys Res B 231: 345-349.
Narbona E, PL Ortiz, and M Arista (2002) Functional andromonoecy in *Euphorbia* (Euphorbiaceae). Ann Bot 89: 571-577.
Narbona E (2005) Dichogamy and sexual dimorphism in floral traits in the andromonoecious Euphorbia boetica. Ann Bot 95: 779-787.
Naylor BG (1982) Vestigial organs are evidence of evolution. Evol Theory 6: 91-96.
Neville AC (1963) Motor unit distribution of the dorsal longitudinal flight muscles in locusts. J Exp Biol 40: 123-136.
Nweeia MT, FC Eichmiller, PV Hauschka, E Tyler, JG Mead, et al. (2012) Vestigial tooth anatomy and tusk nomenclature for *Monodon Monoceros*. Anat Rec 295: 1006-1016.
Olympska E (2012) Morphology and affinities of Eridostracina: Palaeozoic ostracods with moult retention. Hydrobiologia 688: 139-165.
Ortega-Chávez N and WF Stauffer (2011) Ontogeny and structure of the acervulate partial inflorescence in *Hyophorbe lagenicaulis* (Arecaceae; Arecoideae). Ann Bot 108: 1517-1527.
Osborn HF (1921) The evolution, phylogeny and classification of the Proboscidea. Am Mus Novit 1: 1-15.
Ostrovsky AN, AV Grischenko, PD Taylor, P Bock, and SF Mawatari (2006) Comparative anatomical study of internal brooding in three anascan bryozoans (Cheilostomata) and its taxonomic and evolutionary implications. J Morphol 267: 739-749.
Ostrovsky AN, A O'Dea, and F Rodríguez (2009) Comparative anatomy of internal incubational sacs in cupuladriid bryozoans and the evolution of brooding in free-living cheilostomes. J Morphol 270: 1413-1430.
Owen R (1846) A history of British fossil mammals, and birds. John van Voorst, London.
Owen R (1849) On the nature of limbs. John van Voorst, London.
Owen R (1866) Anatomy of vertebrates. Longmans, Green, and Co., London.
Patton TH and BE Taylor (1971) The Synthetoceratinae (Mammalia, Tylopoda, Protoceratidae). Bull Am Mus Nat Hist 145: 119-218.
Patton TH and BE Taylor (1973) The Protoceratinae (Mammalia, Tylopoda, Protoceratidae) and the systematics of the Protoceratidae. Bull Am Mus Nat Hist 150: 347-414.
Pavan C (1945) Observations and experiments on the cave fish *Pimelodella kronei* and its relatives. Am Nat 80: 343-361.
Perle A, LM Chiappe, R Barsbold, JM Clark, and MA Norell (1994) Skeletal morphology of *Mononykus olecranus* (Theropoda: Avialae) from the Late Cretaceous of Mongolia. Am Mus Novit 3105: 1-29.
Peterková F, M Peterka, L Viriot, and H Lesot (2002) Development of vestigial tooth primordia as part of mouse odontogenesis. Conn Tiss Res 43: 120-128.
Pol D and MA Norell (2004) A New gobiosuchid crocodyliform taxon from the Cretaceous of Mongolia. Am Mus Novit 3458: 1-31.
Prince JS and PM Johnson (2006) Ultrastructural comparison of *Aplysia* and *Dolabrifera* ink glands suggest cellular sites of anti-predator protein production and algal pigment processing. J Moll Stud 72: 349-357.

Radinsky L (1963) The perissodactyl hallux. Am Mus Novit 2145: 1-8.

Regoes A, D Zourmpanous, G Léon-Avila, M Van Der Giezen, J Tovar, et al. (2005) Protein import, replication, and inheritance of a vestigial mitochondrion. J Biol Chem 280: 30557-30563.

Rehorek SJ and TD Smith (2006) The primate Harderian gland: does it really exist? Ann Anat 188: 319-327.

Renous S, J-P Gasc, and A Raynaud (1991) Comments on the pelvic appendicular vestiges in an amphisbaenian: Blanus cinereus (Reptilia, Squamata). J Morphol 209: 23-38.

Renvoisé E, AR Evans, A Jebrane, C Labruère, R Laffont, et al. (2009) Evolution of mammal tooth patterns: new insights from a developmental prediction model. Evolution 63: 1327-1340.

Rodríguez-Riaño T, A Ortega-Olivencia, and JA Devesa (1999) Types of androecium in the Fabaceae of SW Europe. Ann Bot 83: 109-116.

Rodríguez-Riaño T, FJ Valtueña, and A Ortega-Olivencia (2006) Megasporogenesis, megagametogenesis and ontogeny of the aril in *Cystius striatus* and C. *multiflorus* (Leguminosae: Papilionoideae). Ann Bot 98: 777-791.

Ronse De Craene LP (2005) Floral developmental evidence for the systematic position of *Batis* (Bataceae). Am J Bot 92: 752-760.

Rothschild LW (1900) A monograph on the genus *Casuarius*. Trans Zool Soc Lond 15: 109-148.

Roxburgh L and B Penshow (2002) Ammonotely in a passerine nectarivore: the influence of renal and post-renal modification on nitrogenous waste product excretion. J Exp Biol 205: 1735-1745.

Rudall PJ, RM Bateman, MF Fay, and A Eastman (2002) Floral anatomy and systematics of Alliaceae with particular reference to *Gilliesia*, a presumed insect mimic with strongly zygomorphic flowers. Am J Bot 89: 1867-1883.

Saint-Hilaire EG (1798 [Bonaparte year 8]) Observations sur l'aile de l'autruche. In: Insitut d'Égypte (ed.) Mémoires sur l'Égypte, publiés pendent les campanges du Général Bonaparte, dans les anées VI et VII, tome primier. Didot l'Aine, 1798 Paris, pp. 79-87.

Sarfati J (2002) Refuting evolution 2. Master Books, Green Forest, AR.

Satchell GH (1959) Respiratory reflexes in the dogfish. J Exp Biol 36: 62-71.

Sato S, I Tews, and RJM Wilson (2000) Impact of a plastid-bearing endocytobiont on apicomplexan genomes. Intl J Parasitol 30: 427-439.

Sato T, C Nagasato, Y Hara, and T Motomura (2014) Cell cycle and nucleomorph division in *Pyrenomonas helgolandii* (Cryptophyta). Protist 165: 113-122.

Sauer J and B Hausdorf (2009) Sexual selection is involved in speciation in a land snail radiation on Crete. Evolution 63: 2535-2546.

Scadding SR (1981) Do "vestigial organs" provide evidence of evolution? Evol Theory 5: 173-176.

Scadding SR (1982) Vestigial organs do not provide scientific evidence for evolution. Evol Theory 6: 171-173.

Scholtz CH (2000) Evolution of flightlessness in Scarabaeoidea (Insecta, Coleoptera). D Entomol Z 1: 5-28.

Sekiguchi H, M Moriya, T Nakayama, and I Inouye (2002) Vestigial chloroplasts in heterotrophic stramenopiles *Pteridomonas danica* and *Ciliophrys infusionum* (Dictyochophyceae). Protist 153: 157-167.

Senter P (2010a) Vestigial skeletal structures in dinosaurs. J Zool 280: 60-71.

Senter P (2010b) Vestigial structures exist even within the creationist paradigm. Rep Nat Ctr Sci Educ 30 (4): 18-26.

Sewertzoff AN (1931) Studien über die Reduktion der Organe der Wirbeltiere. Zool Jb Abt Anat Ont Tiere 53: 611-700.

Sherman TD, AJ Bowling, TW Barger, and KC Vaughn (2008) The vestigial root of dodder (*Cuscuta pentagona*) seedlings. Intl J Pl Sci 169: 998-1012.

Siler CD and RM Brown (2011) Evidence for repeated acquisition and loss of complex body-form characters in an insular clade of Southeast Asian semi-fossorial skinks. Evolution 65: 2641-2663.

Sidell BB and KM O'Brien (2006) When bad things happen to good fish: the loss of hemoglobin and myoglobin expression in Antarctic icefishes. J Exp Biol 209: 1791-1802.

Simões-Lopes PC and CS Gutstein (2004) Notes on the anatomy, positioning and homology of the pelvic bones in small cetaceans (Cetacea, Delphinidae, Pontoporiidae). Lat Am J Aq Mamm 3 (2004): 1-6.

Slobodchikoff CM and K Wismann (1981) A function of the subelytral chamber of tenebrionid beetles. J Exp Biol 90: 109-114.

Stephens PJ (1986) The fused thoracic-abdominal ganglion of the hermit crab (Pagurus pollicaris): neuromuscular relationships in the thoracic and abdominal flexor muscles. J Exp Biol 123: 201-216.

Stephenson NG (1961) The comparative morphology of the head skeleton, girdles and hind limbs in the Pygopodidae. J Linn Soc Zool 44: 627-644.

Stickel WH and LF Stickel (1946) sexual dimorphism in the Pelvic Spurs of *Enygrus*. Copeia 1946: 10-12.

Stokely PS (1947a) The post-cranial skeleton of *Aprasia repens*, Copeia 1947: 22-28.

Stokely PS (1947b) Limblessness and correlated changes in the girdles of a comparative morphological series of lizards. Am Midl Nat 38: 725-754.

Streltsov VA, JN Varghese, JA Carmichael, RA Irving, PJ Hudson, et al. (2004) Structural evidence for evolution of shark Ig new antigen receptor variable domain antibodies from a cell-surface receptor. Proc Natl Acad Sci USA 101: 12444-12449.

Strothers J (1881) Of the bones, articulations, and muscles of the rudimentary hind-limb of the Greenland right whale (*Balaena mysticetus*). J Anat Physiol 15: 141-176.

Strittmatter LI, V Negrón-Ortiz, and RJ Hickey. Subdioecy in *Consolea spinosissima* (Cactaceae): breeding system and embryological studies. Am J Bot 89: 1373-1387.

Tague RG (1997) Variability of a vestigial structure: first metacarpal in *Colobus guereza* and *Ateles geoffroyi*. Evolution 51: 595-605.

Tague RG (2002) Variability of metapodials in primates with rudimentary digits: *Ateles geoffroyi*, *Colobus guereza*, and *Perodicticus potto*. Am J Phys Anthropol 117: 195-208.

Takeda N (2000) Development of a penis from the vestigial penis in the female apple snail, *Pomacea canaliculata*. Biol Bull 199: 316-320.

Tamatsu Y, K Tsukahara, M Hotta, K Shimada (2007) Vestiges of vibrissal capsular muscles exist in the human upper lip. Clin Anat 20: 628-631.

Taylor BE and SD Webb (1976) Miocene Leptomerycidae (Artiodactyla, Ruminantia) and their relationships. Am Mus Novit 2596: 1-22.

Tchernov E, O Rieppel, H Zaher, MJ Polcyn, and LL Jacobs (2000) A fossil snake with limbs. Science 287: 2010-2012.

Tekleva MV and VA Krassilov (2009) Comparative pollen morphology and ultrastructure of modern and fossil gametophytes. Rev Palaeobot Palyn 156: 130-1368..

Thomason JJ (1985) The relationship of structure to mechanical function in the third metacarpal bone of the horse, *Equus caballus*. Can J Zool 63: 1420-1428.

Tiedemann VF (1976) Vergleichend anatomische Unterschungen an Muskeln und Knochen des Beckengürtels von *Ophisaurus harti* Blgr., *Ophisaurus apodus* Pall. und *Ophisaurus koellikeri* Gthr. Ann Naturhist Mus Wien 80: 325-335.

Triemer RE and CL Lewandowski (1994) Ultrastructure of the basal apparatus and putative vestigial feeding apparatuses in a quadri-

flagellate euglenoid (Euglenophyta). J Phycol 30: 28-38.

Turc O and J LeCoeur (1997) Leaf primordium initiation and expanded leaf production are co-ordinated through similar response to air temperature in pea (*Pisum sativum* L.). Ann Bot 80: 265-273.

Van Der Merwe M (1985) The vestigial teeth of *Miniopterus schreibersii natalensis* (Mammalia: Chiroptera). J Zool 207: 483-489.

Waddington CH (1937) The morphogenetic function of a vestigial organ in the chick. J Exp Biol 15: 371-376.

Walker-Larsen J and LD Harder (2001) vestigial organs as opportunities for functional innovation: the example of the *Penstemon* staminode. Evolution 55: 477-487.

Watabe M, T Tsubamoto, and K Tsogbaatar (2007) A New tritylodontid synapsid from Mongolia. Acta Palaeontol Pol 52: 263-274.

Webb SD and BE Taylor (1980) The phylogeny of hornless ruminants and a description of the cranium of *Archaeomeryx*. Bull Am Mus Nat Hist 167: 117-158.

Weston RF, I Qureshi, and JH Werren (1999) Genetics of a wing size difference between two *Nasonia* species. J Evol Biol 12: 586-595.

Whiting AS, JW Sites Jr., and AM Bauer (2004) Molecular phylogenetics of Malagasy skinks (Squamata: Scincidae). Af J Herpetol 53: 135-146.

Wiedersheim R (1895) The structure of man. An index to his past history. MacMillan, New York.

Wilkens V and G Purschke (2009) Pigmented eyes, photoreceptor-like sense organs, and central nervous system in the polychaete *Scoloplos armiger* (Orbiniidae, Annelida) and their phylogenetic importance. J Morphol 270: 1296-1310.

Wilson CL (1982) Vestigial structures and the flower. Am J Bot 69: 1356-1365.

Witter K, H Pavlikova, P Matulova, and I Misek (2005) Relationship between vestibular lamina, dental lamina, and the developing oral vestibule in the upper jaw of the field vole (*Microtis agrestis*, Rodentia). J Morphol 265: 264-270.

Witton MP and D Naish (2008) A reappraisal of azhdarchid pterosaur functional morphology and paleoecology. PLoS ONE 3 (5:e2271): 1-16.

Woods LP and RF Inger (1957) The cave, spring, and swamp fishes of the family Amblyopsidae of central and western United States. Am Midl Nat 58: 232-256.

Woon JTK and MD Stringer (2012) Clinical anatomy of the coccyx: a systematic review. Clin Anat 25: 158-167.

Wortman JL (1898) The extinct Camelidae of North America and some associated forms. Bull Am Mus Nat Hist 10: 93-142.

Xu X, C Sullivan, JN Choiniere, D Hone, P Upchurch, et al. (2011) A monodactyl nonavian dinosaur and the complex evolution of the alvarezsauroid hand. Proc Natl Acad Sci USA 108: 2338-2342.

Xu X, Z Zhu, R Dudley, S Mackem, C-M Chuong, et al. (2014) An integrative approach to understanding bird origins. Science 346: 1253293.1-1253293.10.

Yan HY, ML Fine, NS Horn, and WE Colón (2000) Variability in the role of the gasbladder in fish audition. J Comp Physiol A 186: 435-445.

Yoshizawa M and WR Jeffery (2008) Shadow response in the blind cavefish *Astyanax* reveals conservation of a functional pineal eye. J Exp Biol 211: 292-299.

Yu Q, D-X Liu, W Luo, and Y-H Guo (2011) Function and evolution of sterile sex organs in cryptically dioecious *Petasites tricholobus* (Asteraceae). Ann Bot 108: 65-71.

Zhang J and DM Webb (2003) Evolutionary deterioration of the vomeronasal pheromone transduction pathway in catarrhine primates. Proc Natl Acad Sci USA 100: 8337-8341.

Zubidat AE, RJ Nelson, and A Haim (2010) Photoentrainment in blind and sighted rodent species: responses to photophase light with different wavelengths. J Exp Biol 213: 4213-4222.