

# Trends in the evolution of life, brains and intelligence

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**Abstract:** The  $f_i$  term of Drake's equation – the fraction of life-bearing planets on which 'intelligent' life evolved – has been the subject of much debate in the last few decades. Several leading evolutionary biologists have endorsed the thesis that the probability of intelligent life elsewhere in the universe is vanishingly small. A discussion of this thesis is proposed here that focuses on a key issue in the debate: the existence of evolutionary trends, often presented as trends towards higher complexity, and their possible significance. The present state of knowledge on trends is reviewed. Measurements of quantitative variables that describe important features of the evolution of living organisms – their hierarchical organization, size and biodiversity – and of brains – their overall size, the number and size of their components – in relation to their cognitive abilities, provide reliable evidence of the reality and generality of evolutionary trends. Properties of trends are inferred and frequent misinterpretations (including an excessive stress on mere 'complexity') that prevent the objective assessment of trends are considered. Finally, several arguments against the repeatability of evolution to intelligence are discussed. It is concluded that no compelling argument exists for an exceedingly small probability  $f_i$ . More research is needed before this wide-ranging negative conclusion is accepted.

Received 17 November 2012, accepted 19 February 2013, first published online 26 March 2013

**Key words:** evolutionary trend, brain evolution, evolution of cognition, Drake's equation, complexity, convergence, allometry.

## Introduction

The subject of this review paper is the fifth term of Drake's equation,  $f_i$ , the fraction of life-bearing planets on which intelligence developed. It encompasses biological evolution, excluding earlier the apparition of life and later the cultural development making interstellar communication possible. Presently, a direct estimate of  $f_i$  is beyond reach because no life has yet been detected outside Earth. So, the scientific discussion of the possibility or probability of intelligent life elsewhere in the Universe must be rephrased as 'What was the *a priori* probability that intelligent life developed on Earth?' or more dramatically 'Was the development of intelligence (in)evitable?' The answer to this question has widely varied among biologists. For example, George Gaylord Simpson considered the apparition of human intelligence as a 'fluke' (Simpson 1964). Stephen Jay Gould, using his famous example of the 'tape of life', proposed a thought experiment – 'rerun the tape, he claimed, and each time the result will be different' and in most repeats conscious life will be absent (Gould 1996). Ward & Brownlee (2000) provided various arguments that intelligent life is rare. In contrast, cell biologist and Nobel prize winner Christian de Duve maintained that 'life is an obligatory manifestation of matter, written into the fabric of the universe', and thus 'there must be many sites of life, perhaps even intelligent life sometimes, in many parts of our galaxy and in others' (de Duve 1995, 2011).

What would happen if the tape of life were run again and is rarely discussed in the literature. This is not surprising given the speculative nature of this question. Most discussions bear on a different but related question, whether there are evolutionary trends to higher forms of organization, especially towards forms supporting the apparition of intelligent beings. The two questions are intimately related because the attainment of high enough levels of organization is presumably a necessary condition for the apparition of high intelligence. Indeed, if trends to some forms of higher organization were improbable, this would mean that forms of organization supporting intelligence would only rarely appear in independent runs of the tape.

The aim of this paper is to review some of the facts, interpretations and arguments that lie behind such dissenting views about the existence and nature of evolutionary trends in relation with the apparition of intelligence. We describe two significant aspects of biological evolution on Earth: the increase in organizational complexity, size and diversity of organisms (see section 'Trends in the evolution of structure, size and diversity of organisms') and the evolution of brains in particular (see section 'Trends in the evolution of brains'). The trends examined are directly related to the apparition of 'intelligence' in animals and humans (see section 'Trends in the evolution of intelligence'). In order to keep the length of the paper reasonable, we focus on factual quantitative data and leave aside the discussion of trend mechanisms and their

theoretical interpretation (see Carroll 2001; Chaline *et al.* 2009; Russell 2009; McShea & Brandon 2010; Bogonovich 2011), as well as cultural evolution (see e.g. Chaline *et al.* 2009; Rospars 2010). In the last section ‘Discussion: from biology to astrobiology’, the significance of the trends and their bearing on Drake’s equation are discussed in order to clarify several difficulties that tend to obscure the debate.

## Trends in the evolution of structure, size and diversity of organisms

### *Hierarchical structure from prokaryotes to multicellular organisms*

Until the 1960s the idea that complexity increases in evolution was widely accepted among evolutionary biologists. Numerous examples of increase in complexity were given by Lamarck, Darwin, Cope, Spencer, Gregory, Julian Huxley, Simpson and many others, and the consensus extended well beyond biologists. However, more recently, attempts to define complexity and to demonstrate its increase has led many authors to doubt that any increase actually took place. McShea (1991) contrasted the generality of the consensus with the paucity of the evidence and raised two main criticisms.

First, many examples were deliberately chosen in order to make a case for a *uniform trend* occurring in all lineages at all times, so neglecting many counter-examples. For instance, the skulls of Devonian fishes had more bones and were more complex than the human skull (Williams 1966). Therefore, the case for a strictly uniform trend in complexity must be replaced by the case for a mere *net trend*, i.e. occurring occasionally or only in some lineages (Ayala 1974). Moreover, no list of chosen examples can make a case for or against the existence of a net trend. Good evidence can only be provided in a large random sample where patterns of change should emerge as statistical regularities (Gould *et al.* 1987; McShea 1991, 1996).

Second, the criteria utilized to define complexity are often not consistent. For example, Stebbins (1969) identified eight grades of complexity: earliest self-reproducing systems, prokaryotes, single-cell eukaryotes, multi-cell eukaryotes, organisms with differentiated tissues and organs, organisms with well-developed limbs and nervous systems, homeotherms, human beings. He noted that these grades appeared in the fossil record in the expected order of increasing complexity and so supported the case for a trend. However, this scale is inconsistent. Complexity of the first five grades is apparently defined as the hierarchical depth, i.e. the number of levels of nested subunits, whereas the last three grades do not increase hierarchical depth (McShea 1991, 1996). Similar problems can be found in the similar scales proposed by other authors (e.g. Meyer 1954; Cailleux 1971; Pettersson 1996; Maynard Smith & Szathmáry 1995; Bonner 2004).

These criticisms call attention to the importance of defining complexity consistently and operationally, which is a difficult task, especially when different taxa must be compared. One of the best illustrations of a trend in the history of life is provided by the symbiotic association of unicellular prokaryotes to form

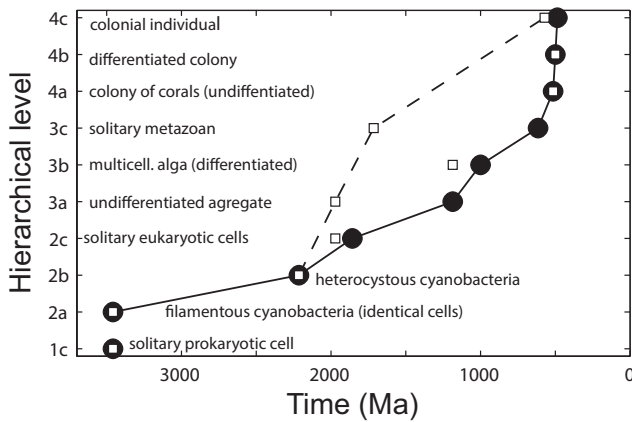
the first eukaryotic cell, the aggregation of single eukaryotic cells to form multicellular organisms, and finally, the association of multicellular organisms to form colonial individuals. The main difficulty is to devise a scale defining the levels of the hierarchic structure that is operational, consistent and of sufficient resolution. To be operational with fossil remains, the scale must be based on morphological criteria. To be consistent, a unique set of criteria representing change in a single direction must be applied to all levels, which excludes a specific definition of each level, for example a nucleus for eukaryotes and tissues for multicellular organisms. Finally, high resolution is desirable to analyse the pattern of increase. McShea (2001a, b) proposed a scale satisfying these criteria and provided the first rigorous proof for a trend in the hierarchical structuring of organisms. It illustrates many of the problems and patterns found in this type of studies.

McShea’s scale is based on two criteria, the number of levels of nestedness and the degree of individuation. *Nestedness* means that a higher level individual consists mainly of entities at the next lower level that are attached to one another. *Nestedness* defines the four main levels which are occupied by prokaryotic cells (level 1), aggregates of prokaryotic cells (level 2, e.g. eukaryotic cells), aggregates of level-2 organisms (level 3, e.g. eukaryotic multicellular organisms) and aggregates of level-3 organisms (level 4, e.g. colonial individuals). For each level of nestedness (in levels 2–4), three degrees of ‘*individuation*’ were recognized in the connected aggregates of lower-level entities: (a) undifferentiated, (b) differentiated and (c) differentiated with intermediate parts (e.g. microtubules and intracellular membranes of eukaryotic cells that are not homologous to former prokaryotic cells).

All organisms found were assigned to only 10 levels and all levels were occupied. It is remarkable, and so far unexplained, that no aggregate of, say, organisms of level 2a or 2b were found at level 3, as level 3 (and 4) individuals are composed of level 2c (respectively 3c) entities only. As no exceptions to this rule were recognized, the two-dimensional scale can be collapsed into a single-dimensional scale. The scale is crude, however, as a simple alga like *Volvox* occupies the same level 3c as a complex metazoan, like an insect or a vertebrate.

Next, fossils were assigned to a hierarchic level based on their morphology, sometimes relying on analogies with extant organisms. The time of first occurrence of each level was determined from published estimate for the stratigraphic unit in which each fossil was found. The resulting plot of hierarchical levels as a function of time is shown in Fig. 1(a). The data points show a regular increase in the hierarchical structure extending over the Precambrian and into the early Phanerozoic from ~3500 to ~500 Ma, all levels and sublevels arising in order. The lines are outer envelopes that document a trend in the maximum on the assumption that a hierarchical level, once achieved, was never lost. This is the best documented macroevolutionary trend observed over such a long period.

The lines are subject to several kinds of uncertainties: on fossil dating, on assigning a level to a fossil (as shown by the difference between the two lines), possible bias in fossil



**Fig. 1.** Trend in the hierarchical organization of organisms. Hierarchical levels based on nestedness (levels 1–4) and individuation (sublevels a–c). Only four levels were considered; although a few examples of aggregation at level 5 (supercolonies) are known in cyclostome bryozoans, siphonophores and ants, and level 6 might be reached by human society (McShea & Changizi 2003); because individuals in these aggregations are not attached to each other and difficult to detect in fossils, they were excluded (see, however, Pettersson 1976). Owing to imperfect preservation and/or absence of modern analogues, some specimens could not be assigned with confidence to a single level; each was assigned either to the lowest (restrictive view, solid circles, solid line) or to the highest level in its range (permissive view, empty square and dashed line), so that for five levels two times of first occurrence were determined. The lines are outer envelopes showing the trajectories on the assumption that a hierarchical level, once achieved, was never lost. Level 1c was not included in either line, because the first known solitary prokaryotic cells slightly post-dates the first prokaryotic filaments (level 2a). (The permissive view of the data indicates four skips: 2a before 1c, 3a before 2c, 3c before 3b and 4c before 4b. Although suspicious, this view raises the possibility that hierarchical saltations may be relatively easy and that lower levels might arise as reversals from higher level organisms.) Redrawn from McShea (2001b).

preservation and the sensitivity of the maximum to sample size. Assuming that these sources of errors can be neglected, several tentative conclusions can be drawn from (the restrictive view of) the data. First, skipping of levels occurs with much lower probability than single step increases from one sublevel to the next. Second, this incremental increase is not produced by a single lineage, as most first occurrences are from representatives of different and often distantly related groups. Third, the ‘waiting time’ for transition between successive maxima tends to decrease both with time and with increasing hierarchical level.

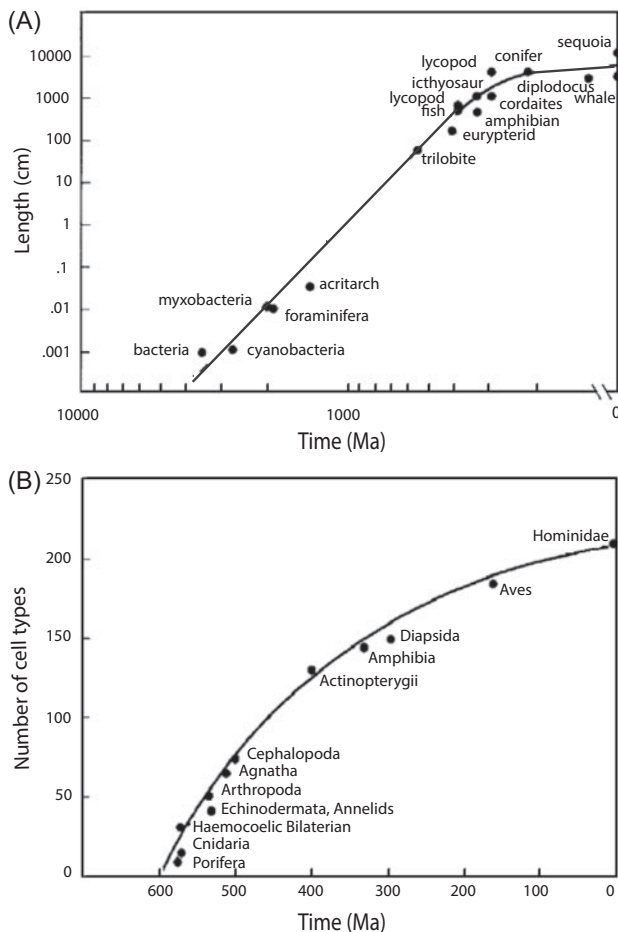
Fourth, two opposite processes can take place in the course of evolution – aggregation or disaggregation (McShea 2001b). For example, a solitary multicellular organism can form a colony or the members of a colony can return to a solitary existence. Thus, the observed increase in maximum hierarchical structuring can result from a higher probability of aggregation over disaggregation (‘biased changes’) or from an equal probability of both (‘unbiased changes’). In the unbiased case, a trend occurs because at the lowest level further

decrease is not possible. The prokaryotic cell being the lowest level compatible with autonomous life, the global trend can be interpreted as a passive diffusion away from this lower boundary (or ‘left wall’, Gould 1996). In the biased case, forces would be at work favouring aggregation. The biased mechanism is favoured by the fact that the transition from protists to multicellular organisms occurred several times (Bonner 1998), whereas no case of a reverse transition from a multicellular organism to a solitary protist or from a eukaryotic cell to a solitary bacterium is known. However, few major increases are known at the lowest levels so that a few reversals would be enough to balance numbers of increases and decreases; in the present state of knowledge, the discovery of two or three species of free-living protists having arisen from a metazoan cannot be excluded (McShea 2001b).

Although a direct test on the major transitions is not possible, discrimination of trend mechanisms can be based on the minor transitions, i.e. changes in the degree of individuation. Marcot & McShea (2007) selected 22 clades spanning at least one instance of a minor transition for which phylogenies and relevant hierarchical data were available. The 22 clades include one group of cyanobacteria, eight groups of protists and 13 groups of metazoans (bryozoans, cnidarians, arthropods and mammals). All statistical analyses based on these data failed to reject the null hypothesis of symmetrical rates of increase and decrease (measured as changes per sampled phylogenetic branch). The only exception concerns differentiation (sublevels c) for which a significant bias was found in favour of decreases, i.e. reversal from differentiated to undifferentiated. According to these results, the clear trend of increasing the hierarchical structure throughout life history could arise from diffusion away from a lower boundary.

#### *Evolution of size and its consequences*

Hierarchical complexity is related to a characteristic simpler to define and measure – size. The maximum size of both animals and plants has increased progressively over geological time (Cailleux 1971, 1976; Bonner 1998). This is illustrated in Fig. 2(A). For example, the transition from prokaryotic to eukaryotic cells entailed a ten-fold increase in size. For Bonner (2006) size is not just a by-product of evolution but a prime mover of all other changes, ‘a supreme regulator of all matters biological’ (p. 2). First, in any environment, whether an ocean, a pond or a forest, there is always an array of organisms of different sizes that are adapted to their own-sized niche. As a result of Darwinian natural selection, all size levels are filled up and if one is vacated it is soon filled. However, the largest size level is always open and available to be filled by bigger organisms to escape the competition with the smaller ones. ‘This simple fact explains why the world has evolved from one in which there was nothing larger than bacteria to today’s, in which we have blue whales and giant sequoias’ (p. 65) and it is worth noting that the argument holds for any character, including ‘intelligence’. Second, any increase in size entails a number of consequences that are all rooted in physics. The strength and the weight of a limb or a branch do not vary identically when size increases: strength varies as the square of the linear dimensions and



**Fig. 2.** Size and number of cell types through time. (A) Log–log graph of the maximum sizes of organisms. (B) Estimated maximum numbers of cell types of early members of various groups. Redrawn from Bonner (2006); data from Valentine *et al.* (1994).

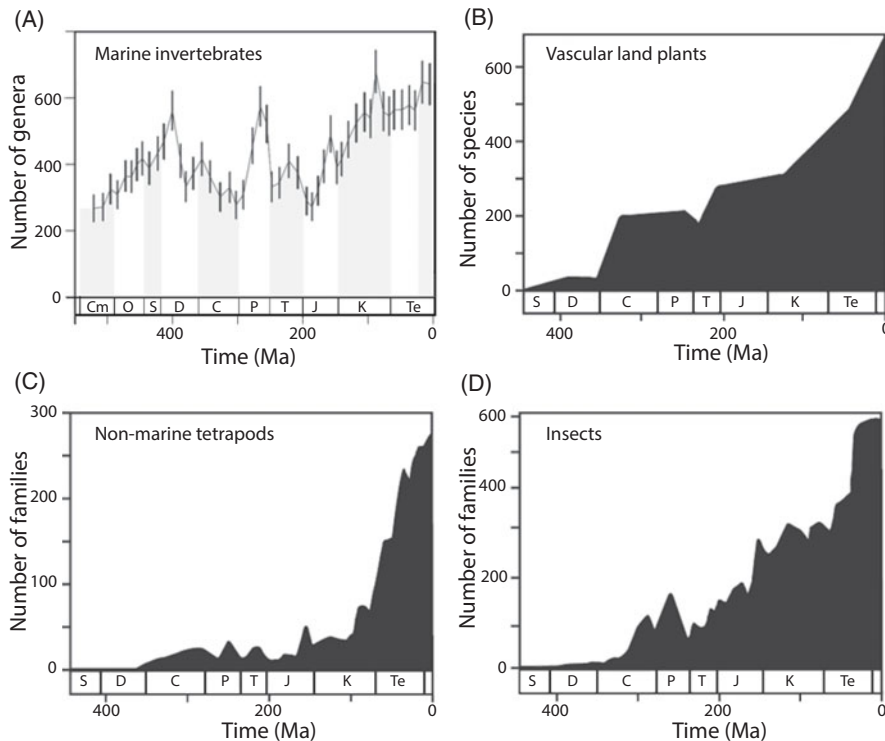
weight as the cube, so that strength varies as (weight)<sup>2/3</sup>. The same relationship holds for diffusion that occurs through a surface, such as oxygen in lungs and nutrients in intestines. These simple relations explain why the legs of an elephant are much bigger in proportion than those of a dog, and why the internal surface of lungs, intestines and other organs folds. However, simple changes in shape are not sufficient to support a large increase in size. To get oxygen to its internal tissues, a large aerobic animal needs a circulatory system with gills or lungs, heart, capillaries etc. As size increases the demands of the surface-size rule moulds much of the shape of large organisms and dictates an enormous increase in complexity.

These consequences of size increase provide complementary ways to measure complexity. With some exceptions (in bacteria, protists, eggs) the size of cells and the nucleocytoplasmic ratio (ratio of the size of the nucleus to that of the cytoplasm) are remarkably constant in most organisms, likely as a consequence of an adequate surface–volume ratio. Thus, the easiest way to become bigger is to add more cells and then to specialize the cells. For example, the microscopic alga *Volvox* is a sphere of ~50 000 cells forming a single layer. These cells belong to only two types, the numerous vegetative

cells (they are photosynthetic and have two flagella that move the colony) and the reproductive cells (without flagella). Some filamentous cyanobacteria have two types of vegetative cells, the photosynthetic cells and those that fix nitrogen; they are separated because the nitrogen-fixating enzymes are inhibited by oxygen. Many more types of cells are present in large animals and plants. Therefore, the number of cell types of an organism can be considered as an indicator of the division of labour among its cells and a measure of its complexity. Rough estimates of the number of cell types and of the total number of cells in different organisms from small colonial forms to large animals and plants have been gathered by Bell & Mooers (1997) and shown to be correlated in a log–log plot. Although these estimates are not accurate, because they have not been obtained with standardized protocols and consistent definition of cell types, they are nonetheless informative. Knowing that the number of cells and cell types increases with the size of organisms and that the maximum size of organisms has increased through time, it can be inferred that the maximum number of cell types must have also increased with time. This inference has been verified by Valentine *et al.* (1994). They plotted the number of cell types for extant species considered as representatives of their body plans against time of origin for their body plans (Fig. 2(B)). Only the specimens having the maximum number of cell types at different times were kept. McShea (1996) objected that the estimates for the four most recent taxa (amphibians, diapsid reptiles, birds and hominids) are probably too high because their cells have been studied much more intensively. In this interpretation, a steep increase in the maximum number of cell types would have occurred in the early Phanerozoic with little change after that. More counts will be needed to reduce the uncertainties.

Increase in size has many other effects that have been revealed by allometric studies: larger organisms move faster, they have longer generation time (Bonner 1965) and they live longer (Lindstedt & Calder 1981). These consequences are all significant as they favour animals that develop slowly, invest heavily in a small number of offspring (K-strategy), and rely on complex behaviours.

The increase in maximum size and maximum number of cell types must not be interpreted as an overall trend applicable to all organisms. Examples of decrease in size and in number of cell types are known (Bonner 2004, 2006). Finarelli & Flynn (2006) used ancestral character state reconstruction to demonstrate that large body size was acquired independently in at least four terrestrial clades of caniform carnivorans, and that the body size decreased in at least one clade. It is not known whether the evolution of size is biased or unbiased. However, increase and decrease are not symmetrical events because size decrease is far less demanding than size increase. Size increase demands correlated changes in the organism, otherwise it is not viable. Size is ‘a dictator that holds complete sway over what an organism will look like and how it will function’ (Bonner 2006, p. 148). In contrast, size decrease may permit a decrease of strength or surfaces but it does not require it, except in extreme cases of reduction where lack of space may force to shed some of the ancestral structures.



**Fig. 3.** Trend in biodiversity of different groups expressed as number of families, genera or species plotted as a function of time. (A) Genera of marine invertebrates from the Cambrian explosion to the present (modified from Alroy *et al.* 2008). (B) Species of vascular land plants (Niklas *et al.* 1985). (C) Families of non-marine tetrapods (Benton 1985). (D) Families of insects (Labandeira & Sepkoski 1993). Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous; Te, Tertiary. (B–D) Modified from Benton & Emerson (2007).

### Evolution of biodiversity

It is currently believed that all life originated from a single species. All extant organisms inherit from this species the same genetic code and molecular mechanisms for protein synthesis. The last universal common ancestor (luca) lived  $\sim 3.5$  Ma ago according to fossil and molecular evidence (Knoll 2003). Luca's descendents diversified through time and biodiversity increased from the initial single species to an estimated  $\sim 10$ – $20$  million species today (May 1990; Wilson 1992). However, the pattern of increase is still debated, as illustrated by the successive analyses of the fossil record of marine invertebrates. Analyses have focused on marine invertebrates because invertebrates are more numerous than vertebrates and preservation is more reliable in marine environments. Sepkoski (1984, 1996) compiled an encyclopaedic database of marine invertebrates in the fossil record based on the paleontological literature that provides the first and last known occurrences of more than 30 000 genera in  $\sim 4000$  families. The number of genera in the database plotted as a function of time, from the Cambrian explosion to the present (Fig. 3(A)), shows a steady increase during the early Cambrian. The rise apparently stopped after  $\sim 100$  Ma and was followed by a plateau for  $\sim 200$  Ma terminated by the massive late Permian extinction. After this catastrophic event, diversity recovered, then increased again up to its present level which is two times higher than the peak observed during the Paleozoic.

However, the number of genera in Sepkoski's database does not necessarily reflect actual biodiversity because paleontologists collected more and smaller fossils from young loose sediments, present in large volume, than from old hard rocks. Also, they collected, with a higher probability, the best preserved fossils and more often near their home in Europe and North America than in distant locations. Although counting genera (or families) instead of species partly corrects for these defects, because genera are less difficult to count than species and their number depends less on local effort by individual paleontologists, the Meso-Cenozoic increase in diversity could be interpreted as a result of biased sampling (Raup 1976). To address these shortcomings, Sepkoski's database was improved to take into account some of the biases in sampling and fossil preservation. In the first study, Alroy *et al.* (2001) compared two periods of  $\sim 150$  Ma, one during the Paleozoic plateau and the other during the Meso-Cenozoic rise, and concluded that the Meso-Cenozoic rise might be an artefact. In the second study, Alroy *et al.* (2008) extended their analysis to all periods of the last 600 Ma with refined statistical methods correcting a wrong weighing assumption of the previous work. They found that the Meso-Cenozoic rise reappears, although not as much as in Sepkoski's curve. The recent number of genera is only 30% higher than the Paleozoic peak, not two-fold higher. The authors conclude that saturation has been reached. This may indicate that the

carrying capacity of the oceans, which depends on the way that energy is captured in marine ecosystems, has been reached (Sepkoski 1996). However, critics believe that the methods used are too conservative, minimize recent biodiversity and call for a third iteration (Kerr 2008).

The diversity on land deserves special attention because  $90 \pm 5\%$  of all living macroscopic species are found on land. Only 5% (Benton 2009) or 15% (May 1994) of species live in oceans, although the oceans cover  $\sim 70\%$  of Earth's surface. The pre-eminence of terrestrial over marine diversity dates from the mid-Cretaceous period ( $\sim 110$  Ma). It is ultimately related to the low cost of mobility on land resulting from physical differences between air and water in density, viscosity, specific heat and diffusion coefficient of oxygen (Vermeij & Grosberg 2010). Life on land started primarily with cyanobacteria in the Precambrian. Multicellular organisms would have followed in the Ordovician ( $\sim 470$  Ma). The earliest fossils on land are from the Silurian (425 Ma) for vascular plants and arthropods, the Devonian for tetrapods (400 Ma), trees and flying insects (375 Ma). The diversification on land has been studied in various groups from the Silurian (430 Ma) (reviewed in Benton & Emerson 2007), including vascular land plants (Niklas *et al.* 1985), non-marine tetrapods (Benton 1985; Sahney *et al.* 2010) and insects (Labandeira & Sepkoski 1993; Mayhew 2007). The curves for the three groups are globally increasing (Fig. 3(B)–(D)). Apparently, the curve for vascular land plants presents several phases like the curve for marine invertebrates. In contrast, the curve for insects is closer to linear and that for non-marine tetrapods is exponential. These curves were not corrected for biases in sampling and preservation. Although the fossil terrestrial record is patchy and incomplete because sedimentation is more sporadic on land than in oceans, Benton (2010) maintains that the counts correctly reflect diversity. The evidence for geological artefacts is limited, the order of fossils in the rock is internally consistent (e.g. no mammals in Cambrian deposits was ever found) and in broad agreement with the molecular phylogenies. Moreover, fossil diversity and rock volume parallel each other, indicating that both may be controlled by a third cause, such as changing sea level. So, even if over-estimated, the observed increases in diversity seem difficult to explain by biased sampling. Overall, life on land seems to have increased exponentially and if an equilibrium level has been reached this is only recently. This is well illustrated by tetrapods (Fig. 3(C)) that increased from 1 to 27 000 species in the course of the last 400 Ma (Benton 2010). With this exponential diversity of life, the world is increasingly divided into finer ecological niches, which means that a greater number of species offers more opportunities for the apparition of new species.

Fast diversifications, called adaptive radiations, are frequently observed, for example the diversifications of terrestrial plants in the Devonian ( $\sim 400$  Ma) and of the mammalian orders during the Mesozoic. Such evolutionary success is frequently attributed to two conditions, a key innovation and an ecological opportunity. Examples of innovations are the apparition of the flower in the Cretaceous ( $\sim 110$  Ma), or of echolocation for bats, the mammalian group with the largest

number of species. In fact, molecular phylogenetics suggests that the notion of a single key innovation is often too restrictive and must be replaced by a whole sequence of innovations (for plants, see Donoghue 2005). The second condition for success is a corresponding evolutionary opportunity, for example the 'empty' Devonian land environment for plants and the habitats vacated by dinosaurs for mammals.

Five major mass extinctions took place at the end of Ordovician (440 Ma), Devonian (360 Ma), Permian (250 Ma), Trias (199 Ma) and Cretaceous (65 Ma). According to Raup (1991) the percentage of species that disappeared in these successive crises was 45, 25, 55, 35 and 35%, respectively. For Erwin (2006),  $\sim 95\%$  of species died out during the Permian crisis. However, all extinctions were followed by rapid rebounds (Sepkoski 1984; Benton & Emerson 2007; Alroy *et al.* 2008). After most of them, the global diversity rose to levels even higher than those prior to the extinction.

### Convergent evolution

A remarkable feature of evolutionary processes is the ubiquity of convergence. Convergent evolution occurs when descendants resemble each other more than their ancestors did. Classical examples of convergences are provided by marsupials. The evolution of marsupials in Australia paralleled the evolution of placental mammals in other parts of the world. There are Australian marsupials resembling mice, moles, anteaters, squirrels, cats, wolves, etc. (Simpson & Beck 1965; Chaline & Marchand 2002). Many innovations appeared several times in widely separated lineages. For example, the transition from protists to multicellular organisms occurred at least 13 times independently (Bonner 1998); the camera eye appeared at least 40 times in groups as different as medusa, annelids, cephalopods, vertebrates with enough differences in detail to attest their independent apparition (Salvini-Plawen & Mayr 1977). Ants of genera *Atta* and *Acromyrmex* domesticated different fungi at least five times  $\sim 50$  Ma ago. Molecular phylogenetic studies indicate that convergent evolution may have been more frequent than thought previously. For examples, analyses revealed morphological and ecological convergences between species of lizards, from different families in Australia and North America (Melville *et al.* 2005) and from the same genus in Caribbean islands (Losos *et al.* 1998). In the latter case, 'ecomorphs' of different islands, undistinguishable from morphology and ecology, were shown to be the result of independent evolutionary transitions. Many more examples are documented in Conway Morris (2003, 2010, 2011).

### Trends in the evolution of brains

One of the most significant cell differentiations found in metazoans is the apparition of the nerve cell or neuron. Neurons are present in all extant animals, except sponges, and make up a large proportion of the cells in any individual. For example, of the 959 cells that constitute the small nematode worm, *Caenorhabditis elegans*, 302 are neurons. A likely reconstruction of the evolution of nervous systems involves the following steps: first, a primitive neuron connected a sensory

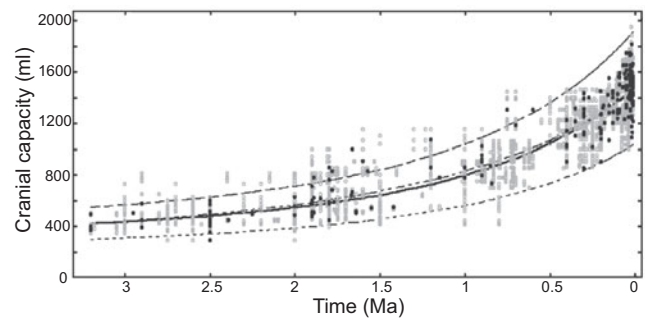
site to a contractile or secretory cell; several neurons connected to one another via synapses; interneurons intercalated between sensory neurons and motor neurons, then differentiated in two classes, excitatory and inhibitory; neural networks developed and grew into ganglions; cephalic ganglions fused to create primitive brains; finally, as the body grew in size, the brain also grew in size. The evolution of brain size and complexity is well documented in the vertebrates and mammals.

#### Evolution of brain size (encephalization)

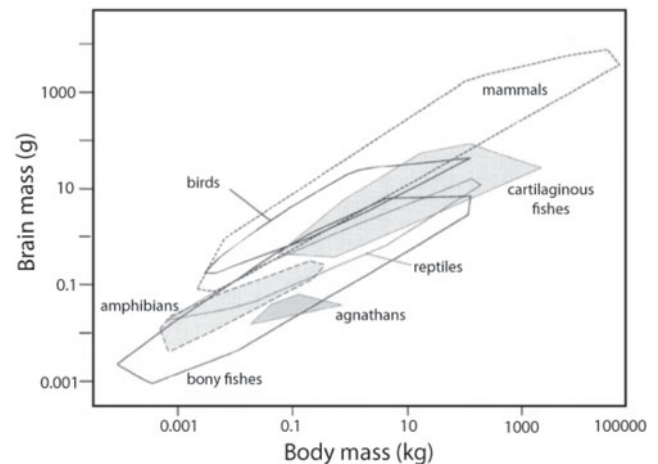
Brains and other soft tissues are not preserved in the fossil record. Therefore, information is limited to endocranial casts (endocasts) of fossil skulls that show only the size and shape of the brain (Krubitzer & Kaas 2005). Natural endocasts form when sediment fills the endocranial cavity. Subsequent weathering removes the fossilized bone, exposing the cast. In most mammals, endocasts closely approximate brain volume (Gittleman 1986). Preservation can be excellent, but the number of complete endocasts is small. Other methods hold promise to determine more endocranial volumes, computerized tomography of fossil crania (e.g. Marino *et al.* 2004) and indirect methods based on correlations of endocranial volume with better preserved parts of the skulls (Finarelli & Flynn 2007). Brain size can be measured by volume or mass as the density of brain tissue is  $\sim 1.0 \text{ g ml}^{-1}$  (Marino *et al.* 2003).

The few endocasts from mammal-like reptiles and the earliest mammals indicate that these taxa possessed relatively small brains. Apparently, brain size varied little until  $\sim 60 \text{ Ma}$  ago, when the major radiations of marsupial and placental mammals began (Northcutt & Kaas 1995). During 3.5 Ma of human evolution, an enormous increase in brain size has occurred, from  $450 \text{ cm}^3$  in Australopithecines to  $\sim 1350 \text{ cm}^3$  in modern *Homo sapiens* and  $1500$  (range  $1200\text{--}1750 \text{ cm}^3$ ) in extinct *Homo neanderthalensis* (Roth & Dicke 2005). Several studies provide detailed data on this trend during the last  $\sim 3.2 \text{ Ma}$ , for 3–8 species of extinct and extant primates from genera *Cercopithecus*, *Paranthropus*, *Australopithecus*, *Pan* and *Homo* (McHenry 1994; Kappelman 1996; Rapoport 1999; Falk *et al.* 2000, 2009; Elton *et al.* 2001; Leonard *et al.* 2003; Neill 2007). Lent *et al.* (2012) included five other genera (*Parapithecus*, *Aegyptopithecus*, *Proconsul*, *Sahelanthropus* and *Ardipithecus*), extending the time range to  $\sim 35 \text{ Ma}$  ago. The most extensive report (de Miguel & Henneberg 2001), based on more than 2161 fossil specimens of a dozen species dated from 3.2 Ma to 10 ka, shows that the trend is gradual with no apparent discontinuities (Fig. 4). The best-fit curve to the data is a double exponential function of time which explains 90% of the total variance.

However, these studies do not take into account the relationship between brain mass and body mass—a classical example of allometric relationship. It has been shown on extant species that the magnitude  $y$  of a wide variety of anatomical and physiological phenomena, including brain size is a power function of the body size  $x$ ,  $y = ax^b$  (Huxley 1932; Teissier 1936; Schmidt-Nielsen 1984). The classical plot of brain mass as a function of body mass for species of various vertebrates, established by Jerison (1973), shows, as expected from the



**Fig. 4.** Trend in hominid brain size (cranial capacity  $V$  in  $\text{cm}^3$ ) over 3.2 Ma based on 217 fossil adult specimens (grey points) of a dozen species, *Australopithecus afarensis* ( $\geq 3200 \text{ ka}$ ), *Australopithecus africanus* ( $\geq 2900$ ), *Australopithecus garhi* ( $\geq 2500$ ), *Australopithecus aethiopicus* ( $\geq 2390$ ), *Australopithecus boisei* ( $\geq 2250$ ), *Australopithecus robustus* ( $\geq 2000$ ), *Paranthropus robustus* ( $\geq 2000$ ), *Homo habilis* ( $\geq 1900$ ), *Homo erectus* ( $\geq 1800$ ), archaic *H. sapiens* ( $\geq 750$ ), *Homo heidelbergensis* ( $\geq 600$ ), *H. sapiens neanderthalensis* ( $\geq 350$ ), *H. sapiens* ( $\geq 300$ ). The line of best fit, determined on the average capacities for each hominid fossil by date (black dots), is a double exponential function,  $V = 306.63 \times 4.83^x$ , with  $x = 0.9995^t$  and  $t$  time before present expressed in ka; it explains 90% of the total variance. Most data points are included within the 99% confidence interval around this curve (dashed curves). Non-parametric testing based on the chronological rank of specimens indicates that the trend is highly significant ( $p = 10^{-4}$ ). Modified from de Miguel & Henneberg (2001).



**Fig. 5.** Brain mass as a function of body mass for the major groups of vertebrates in a double-logarithmic graph. Each polygon encloses the data for various species of a given group. In each group, for a given body size, there is a ten-fold range in brain size. Modified from van Dongen (1998).

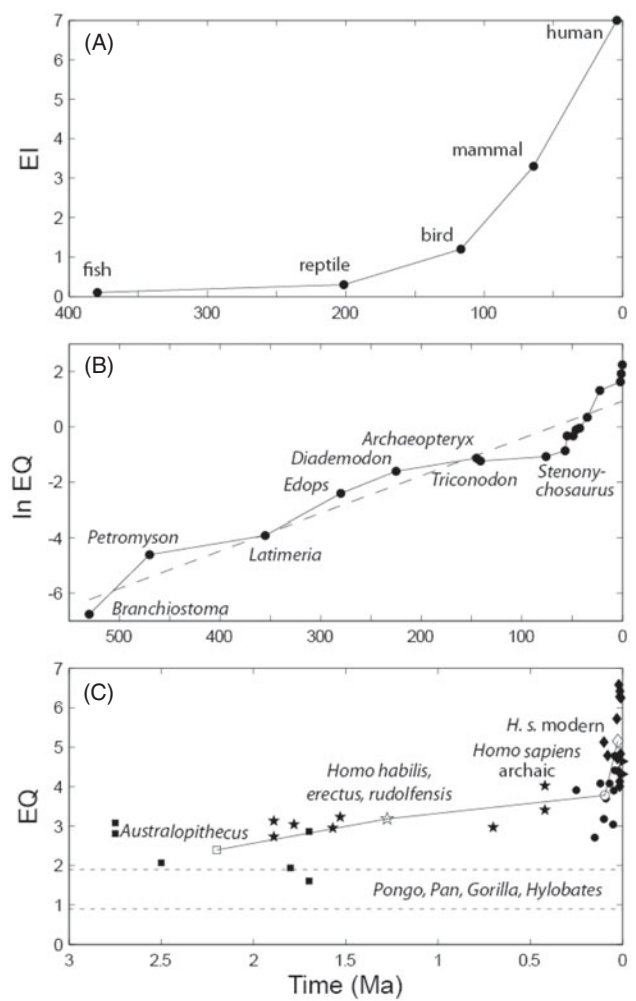
power law, that the logarithm of the brain mass ( $\log y$ ) is a linear function of the logarithm of the body mass  $x$  (Fig. 5). It shows also that the slopes  $b$  but not the intercepts  $\log a$  are the same for the 'lower' vertebrates (fishes, amphibians and reptiles) and the 'higher' vertebrates (birds and mammals). Thus, the points for 'lower' and 'higher' vertebrates fall approximately on two parallel lines. Slope  $b < 1$  indicates that

when the body enlarges, the brain also enlarges, but not in proportion (negative allometry). Therefore, brain is the largest in the largest animals but, when measured as a percentage of body mass, is largest in the smallest animals. For example, the human brain represents 2% of its body mass but up to 10% of the body mass of shrews, the smallest mammals (Van Dongen 1998; Roth & Dicke 2005). In most radiations, brain size varies approximately 10-fold, but across all vertebrate radiations slopes range from 0.21 (agnathans like lampreys) to 0.74 (mammals) and brain size varies enormously (~30-fold) for a given body size (Northcutt 2002).

Knowing this allometric rule, it becomes possible to remove the confounding effect of body size and to investigate the evolution of brain size as if all animals had the same size. One measure of relative brain size is the deviation of a species point from the overall line characterizing the group studied – the encephalization quotient (EQ; Bauchot & Platel 1972; Jerison 1973, 1991; Mace *et al.* 1980). EQ can be interpreted as the amount of additional brain matter an animal has over its basic somatic needs. Traditionally, following Jerison, EQ has been considered as a measure of ‘intelligence’. It is not necessary to adopt this interpretation to find an interest in EQ measurements. Estimates of *maximum* EQ reached at different evolutionary times were published by Meyer (1954) for 16 species of mammals over ~70 Ma, by Russell (1983) on 18 fossil species over 530 Ma, and by Kappelman (1996) on 48 fossil specimens of eight species of hominids over the last 3 Ma (Fig. 6). All curves show an increasing trend with a doubling time that apparently shortens with time. As the body mass of fossils must be reconstructed for determining the EQ, the uncertainties on brain mass and body mass cumulate. Russell (1983) estimated the error on EQ values to be ±15% and on times to be ±2%.

However, this trend in maximum does not imply a uniform trend for two reasons. First, six separate linear evolutionary sequences (morphoclines) have been recognized in vertebrates: (1) lampreys to hagfishes in agnathans; (2) squalomorph to galeomorph sharks in cartilaginous fishes; (3) polypteriforms to teleosts in bony fishes; (4) amphibians to reptiles; (5) reptiles to birds; and (6) reptiles to mammals (Northcutt 2002). Brain size has increased *independently* in some members of each of these radiations (Fig. 7). As a result, many cartilaginous fishes have brains as large for their body size as those of birds and mammals. Second, in many members of each vertebrate radiation relative brain size has not increased, and it has even decreased in some members (Northcutt 2002). For example, relative size decreased in lungfishes and amphibians (Roth *et al.* 1993) whose brain and body are composed of a smaller number of bigger cells (Bonner 2006). In bats, relative to the ancestral state, brain size has been reduced in fast flyers, while it has increased in manoeuvrable flyers adapted to complex habitats (Safi *et al.* 2005). The fossil hominid, *Homo floresiensis*, on the island of Flores in Indonesia, has a smaller brain than its putative ancestor, *Homo erectus* (Falk *et al.* 2005).

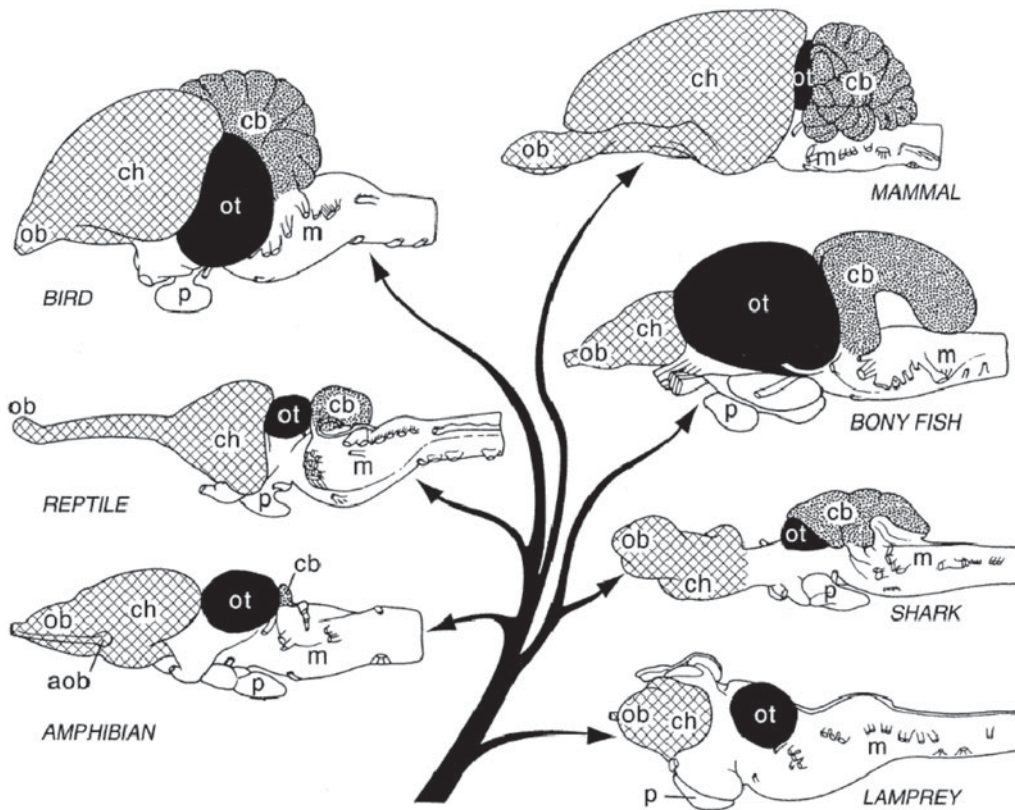
That brain size can be subject to bi-directional selection has been confirmed by a detailed study of caniform carnivorans



**Fig. 6.** Trend in maximum encephalization. (A) Mean encephalization index (EI) for five groups of vertebrates over ~400 Ma; EI is the ratio of cerebral hemispheres over inferior brain centres (redrawn from Meyer 1954). (B) Encephalization quotient (EQ) for 18 fossil organisms over 530 Ma. The first three organisms (*Branchiostoma*, *Petromyson* and *Latimeria*) are extant and taken as representative of the maximum level of encephalization in existence for the time indicated (Paleozoic era). The 10 Cenozoic organisms are *Plesiadapis*, *Tetonius*, *Heptodon*, *Homacodon*, *Necrolemur*, *Leontinia*, *Argyrocetus*, *Homo habilis*, *H. erectus* and *H. sapiens*. The regression line (dashed) is  $\ln EQ = 0.0135 \times (531 - t) - 6.23$  (redrawn from Russell 1983). (C) EQ for 48 fossil specimens of eight hominid species (*Australopithecus*, squares; early *Homo* species, stars; archaic *Homo sapiens*, circles; modern *H. sapiens*, diamonds) over the last 3 Ma; the empty symbols are means (on time and on EQ) for each group; the two dashed lines are mean ± standard deviation for extant apes (redrawn from Kappelman 1996).

(dogs, bears, skunks, otters, sea lions etc.; Finarelli & Flynn 2007). The distribution of caniform EQs remained relatively stable from 36 to 8 Ma. At ~6 Ma, median and maximum EQs both began to increase, whereas over the whole 36 Ma period, the minimum EQ tended to decrease. If a lower bound for caniform encephalization exists and this boundary is near the ancestral caniform value, the trend of increased





**Fig. 7.** Lateral views of the brains of extant species representative of the main groups of vertebrates and their phylogenetic relationship. The brains of most vertebrates possess the same number of divisions. aob, accessory olfactory bulb (cross-hatched); cb, cerebellum (stippled); ch, cerebral hemispheres (cross-hatched); m, medulla oblongata; ob, olfactory bulb (cross-hatched); ot, optic tectum (black); and p, pituitary gland. The brains are not drawn to the same scale; the variation in both overall brain size (see Fig. 5) and the size of most brain divisions is much greater than shown. From Northcutt (2002).

encephalization observed could simply be the result of random diffusion away from this bound.

#### Evolution of brain components

Although EQ is ‘the proper and best single number for expressing brain size in an allometric world’ (Gould 2001), it cannot replace a detailed analysis of brain structures because the unidimensional volumetric evolution of the brain is the result of the multidimensional evolution of its constituent parts (Thireau & Doré 2002, 2003). As fossil endocasts provide information only on overall brain size and features visible on their surface, more detailed investigations must rely on living species and tentative brain reconstruction of extinct species. The evolution of three types of brain components at increasingly finer resolutions (divisions, neural centres and neurons) has been analysed.

#### Size of brain divisions

All living vertebrates share the same major brain divisions, namely the hindbrain that includes the medulla, pons and cerebellum; the midbrain or mesencephalon (with the optic tectum); and the forebrain that includes the diencephalon (thalamus and hypothalamus) and the telencephalon (or cerebrum). The only exception is the cerebellum, a hindbrain

structure that governs balance, which is lacking in the agnathans (hagfishes and lampreys). In mammals, the largest division is the telencephalon, which is traditionally subdivided into olfactory bulb, basal ganglia (striatum, pallidum etc.), limbic system (hippocampus, septum etc.) and cerebral hemispheres. The neocortex (also called isocortex) is the outer layer of a variable part of the cerebral hemispheres. The conservative nature of major brain divisions suggests that this organization must have arisen with the origin of vertebrates or shortly thereafter, a conclusion compatible with fossil chordates from the Lower Cambrian in China (Northcutt 2002).

The size of some divisions, like the medulla, appears to change very little in vertebrate phylogeny whereas others, like the telencephalon, change a lot. In mammals, the cerebellum occupies a constant fraction ( $13.5 \pm 2.4\%$ ) of the total brain volume (the only exceptions are cetaceans and microbats with a fraction  $\sim 20\%$ ) (Clark *et al.* 2001; but see Rilling & Insel 1998). In contrast, the neocortex ranges from  $16 \pm 6\%$  in Soricomorpha (shrews and moles) to  $74 \pm 5\%$  in Hominoidea (apes and humans) (Clark *et al.* 2001). Expansion of the mammalian neocortex is the best known example of an evolutionary increase in the relative size of a particular brain structure. Comparison of humans and chimpanzees revealed no *qualitative* differences between them but many *quantitative*

differences, even after accounting for differences in body size. Expressed in relative volume, the olfactory bulb decreased, the medulla remained stable, whereas the corpus striatum, cerebellum and hippocampus doubled, and the neocortex tripled in humans with respect to chimpanzees (Baron *et al.* 1988).

Finlay and co-workers made an important contribution to the understanding of brain evolution when they showed in 10 orders of mammals (Finlay & Darlington 1995; Reep *et al.* 2007) and in chondrichthyans (sharks and related taxa; Yopak *et al.* 2010) that the relative sizes of most parts of the brain (except the olfactory cortex) are highly predictable from absolute brain size. Compared with total brain mass, each part scales with a characteristic slope, which is highest for the telencephalon (but also cerebellum, in contrast with Clark *et al.* 2001) so that large brains in absolute size become more and more composed of these elements, reaching >90% of total mass in mammals. Moreover, grade shifts (changes in parameter  $a$  of the allometric equation) between taxa concentrate in just those structures that enlarge disproportionately with total brain size. The order of neurogenesis in different brain areas is the same in all mammalian species and the areas that develop latest are largest, so the largest brain structures are the ones that spend the longest periods of time in the exponential cell division stage before terminal differentiation.

These observations have several consequences. First, the conserved pattern of brain scaling suggests that it appeared in early vertebrates and might have given the brain an 'evolvable' architecture where neural modules can be added and subtracted without compromising basic function. This important innovation would explain the extensive radiation of fish in the Devonian. Second, the simple allometric rules found support for the hypothesis that developmental constraints might play a greater role in brain evolution than adaptation. With these built-in rules, any selection pressure leading to increased brain size would result in the evolution of a brain with the same relative proportions of various areas as the human brain (a huge neocortex, a large corpus striatum and hippocampus, perhaps even a large Wernicke's area). In particular, the areas that increased in relative size across the ape-to-human transition need not be interpreted as the result of specific selective pressures. Nonetheless, this nonlinear model leaves room for selective modifications of the relative sizes, up to a factor of ~2.5-fold, which corresponds to the prediction error and is small with respect to the variations explained (>200-fold). According to this challenging view, the populations of initially uncommitted neurons would have been produced first and only subsequently requested for new functions (language, fine movements) subjected to natural selection (Nishikawa 1997).

#### Number and size of neural centres

Increases in brain size have frequently resulted in increases in the number of neural centres and the number of neuronal cell classes within a centre. This is best illustrated in the mammalian neocortex (Fig. 8). In all living mammals, the neocortex is a multilayered sheet 1–3 mm thick made of a

patchwork of discrete areas. The same cell density and the same basic set of primary sensory projections are found across all mammals, so the changes concern the overall surface area, the number of neurons, and the number and size of cortical modules (Rakic 1995; Nishikawa 1997). The more easily identified neocortical centres are sensory fields. Most investigated mammals appear to have primary (V1) and secondary (V2) visual areas, a somatosensory region with a primary area (S1) and three or four adjoining areas, a primary motor area (M1), a primary auditory region (A1) with possibly one or more additional fields. The neocortex of the first mammals was probably close to the neocortex of extant rodents (Fig. 8(A)) and contained relatively few areas, on the order of 10–20, including the sensory fields mentioned.

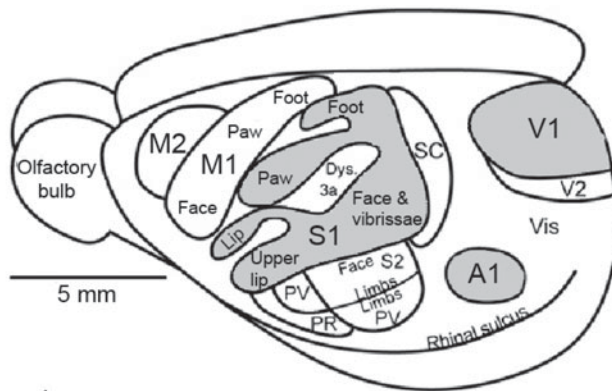
Comparison of the homologous cortical areas identified in rats and owl monkeys shows that several areas (>50% surface) in monkey brains are absent in rat brains (Northcutt & Kaas 1995; Kaas 2008). In visual cortex alone, the number of functional subdivisions is 3–8 in rats, >20 in owl monkeys and >32 in macaques. This increase in the number of functional subdivisions has occurred independently numerous times among mammals.

Various parts of the neocortex are relatively much larger in humans than in chimpanzees, in particular the thumb and finger areas of the motor cortex that are related to manual dexterity, and the Wernicke's and Broca's areas that are related to verbal communication (Northcutt & Kaas 1995).

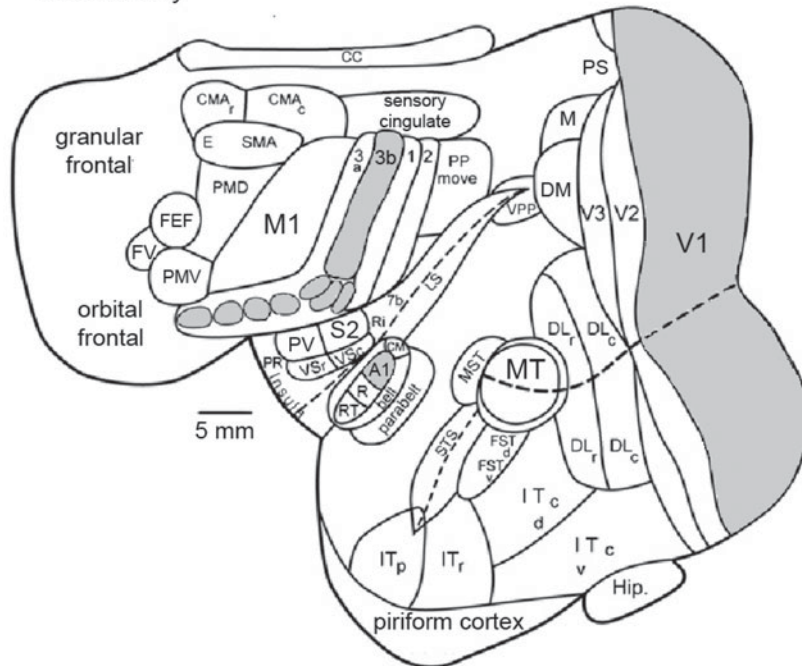
#### Number of cells in brain and brain divisions

A crucial characteristic is the number of brain cells. Counts of neuronal and non-neuronal cells were obtained recently in 19 species of mammals: six rodents (Herculano-Houzel *et al.* 2006, Herculano-Houzel 2007), five insectivores (Sarko *et al.* 2009), six primates and one Scandentia (Herculano-Houzel *et al.* 2007), orangutan, gorilla and man (Azevedo *et al.* 2009, Herculano-Houzel 2010, Herculano-Houzel & Kaas 2011). Cell membranes were mechanically disrupted and the free nuclei were counted after the neurons were marked with a specific antigen. The total number of neurons (in billions) varies from 0.11 (mouse) to 4.87 (capibara, the largest extant rodent) in rodents and from 0.64 (marmoset) to 86 (man) in primates. In rodents, the number of neurons increases faster than brain size ( $b \approx 1.6$ ), whereas in primates it grows isometrically ( $b = 1$ ). The scaling rule of rodents means that, to reach the number of neurons that humans have, the brain of a rodent would weigh >45 kg and its body >100 tonnes (Herculano-Houzel 2007) and the brain of a man (75 kg) would weigh 150 g and have only 3 billion neurons (Lent *et al.* 2012). In rodents ~60–75% of neurons are in the cerebellum, ~10–20% in the cerebral cortex and ~10–20% in the rest of the brain. In primates (except man), the proportions are 56–79, 16–42 and 2–9%, respectively, and in man, they are 80, 19 and 1%, respectively. These striking differences result from different neuron densities across orders and brain divisions. Neuronal densities are stable and independent of brain size in the primate brains, whereas they decrease in larger rodent brains. They are higher in all primate brain structures than in rodent brains of

(A) Rat



(B) Owl monkey



**Fig. 8.** Organization of the mammalian neocortex in rats (A) and owl monkeys (B). The owl monkey cortex has been flattened so that hidden areas can be shown. The primary sensory areas, visual (V1), auditory (A1) and somatosensory (S1 in rat, 3b in monkey) are shown in grey. In rats, the neocortex is small and a small number of cortical areas are identified. In owl monkeys, the cortical sheet is greatly expanded and many more areas are present. Despite differences in size and number of areas, homologous areas conserve their relative positions in both species. Modified from Kaas (2008).

equivalent size. Surprisingly, the cerebellum contains many more neurons than the cerebral cortex in a constant ratio of 3.6:1. This finding suggests that the increase in numbers of neurons as brain size increases is coordinated in cortex and cerebellum and reflects a general principle in mammalian brain evolution (Herculano-Houzel 2010). Another important finding is that non-neuronal cells, especially glial cells, make an important contribution to brain size, especially in the cerebral cortex where 3.7 non-neurons are associated with each neuron in man, whereas the proportion is inverse in the cerebellum (Azevedo *et al.* 2009).

These findings support the idea that a major innovation in primate brains may have been the packing of larger number of neurons per unit volume than in rodents. However, they do not confirm that the brain composition of humans stands out from

other primates and indicate that, as far as cell numbers are concerned, the human brain is an isometrically scaled-up primate brain. Finally, in agreement with Roth & Dicke (2005), they suggest that body size may not be a good reference for comparing brains and that the total number of neurons, irrespective of brain or body size, may be a better predictor of cognitive abilities (see below).

#### *Energy constraints*

All electric signals in neurons are created by the opening of channels selectively permeable to sodium, potassium and other small ions. The resulting passive ionic movements depolarize the neuron membrane yielding local post-synaptic potentials in dendrites and propagated action potentials in axons. These ion movements are compensated by active, energy consuming

processes. Most of the energy in nervous tissues serves to drive the sodium–potassium pumps that maintain constant the concentrations of sodium and potassium ions. The brain is an energetically very expensive organ that demands a large and continual supply of glucose and oxygen irrespective of whether the animal is awake or asleep, active or at rest. For example, the human brain, only 2% of body mass, consumes ~20% of the total energy at rest (basal metabolism). The energy constraints on brain help to understand several features of brain evolution.

The increase in body and brain sizes implies greater neuron number and axon length, especially to communicate between cerebral areas. For example, in the mammalian neocortex, the volume of the white matter that contains long axons increases faster than the volume of the gray matter that contains cell bodies, dendrites and short axons for local information processing ( $b=1.47$ ; Zhang & Sejnowski 2000). In order to decrease axonal energy consumption and increase conduction speed, long segments of insulating myelin sheath are wrapped around the axons that limit ionic movements to interval between segments (nodes) resulting in saltatory conduction of action potentials from one node to the next. The myelin sheath, made of tight helically wound glial membrane, have arisen independently several times in vertebrates, annelids and crustaceans (Hartline & Colman 2007).

Heart, liver, kidney and the gastrointestinal tract are also ‘expensive’ organs that consume ~50% of basal metabolism of the human body. An increase in brain size can be balanced by a reduction of these organs (‘expensive tissue hypothesis’, Aiello & Wheeler 1995). In the case of the human brain, the reduction of gut size had to be compensated by an increase in the quality of food (Aiello *et al.* 2001; Roth & Dicke 2005). Brain size and diet quality are positively correlated in most living primates and they changed together in their evolutionary history (Fish & Lockwood 2003). The fast growth of the human brain in prenatal and first post-natal years is especially demanding for both mother and infant (Aiello *et al.* 2001; ‘maternal energy hypothesis’, Martin 1996).

Another solution to the energy problem of producing and maintaining a brain is to reduce its size. Bats foraging in open space have small and narrow wings relative to body mass rendering them efficient flyers but poorly manoeuvrable, while the opposite is true for species foraging in complex environments. Relative to the ancestral state, brain size in bats has been reduced in fast flyers, while it has increased independently several times in agile flyers. These opposite evolutions correspond to two types of foraging. Fast flying bats are aerial insectivores which hunt by echolocation whereas agile bats must find energy rich food at locations unpredictable in time and space, and searching requires large brains (Eisenberg & Wilson 1978; Mace *et al.* 1980; Safi *et al.* 2005).

### Convergences

Several examples of convergences in brain evolution were mentioned above. Cladistics has revolutionized our understanding of brain evolution by demonstrating that many brain structures, traditionally thought to be homologous, had in fact

evolved several times independently in taxa whose common ancestors lacked these structures. It appears now that convergence is very frequent. Relatively few cortical areas appear to be homologous among all living species of mammals. Most of the non-primary cortical areas probably expanded independently among different lineages. For example, the neurons of the middle temporal (MT) area receive input from visual areas V1 and V2 and analyse the direction of movement (not colour). The MT area is present in all investigated primates and absent in all non-primates (Krubitzer, 2009). However, an MT-like area has been found in cats and in some members of the archontan radiation (which includes tree shrews, flying lemurs and bats), suggesting that they may have arisen independently in these taxa.

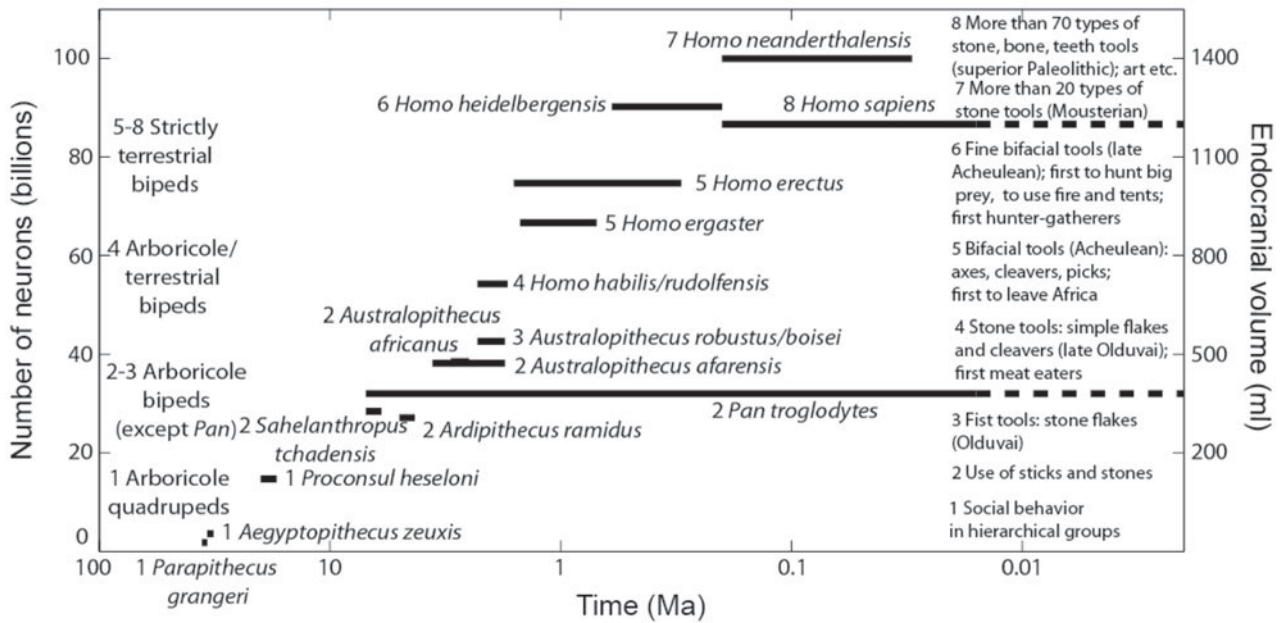
Many other examples concerning neural circuits are known. Hagfishes have independently evolved a highly laminated cerebral cortex, comparable in many ways to the cerebral cortex of mammals (Northcutt 2002). Similar (but not identical) circuits have evolved convergently in at least four frog lineages controlling precise coordination of tongue and jaw movements during prey capture and illustrate how small changes in neural pathways can lead to dramatic changes in an organism’s abilities (Nishikawa 1997, 2002). In electric fish that generate an electric field to sense their environment, jamming avoidance evolved independently in African and American fishes. This solution to avoid interference between the signals emitted by two individuals at close proximity was acquired through relatively small changes in the physiology (neurotransmitters, membrane properties) and interconnections of neurons used previously for a different purpose (Nishikawa 1997). An example of more global significance is parallel distributed processing and population coding in neural networks that have evolved convergently in distantly related species throughout the animal kingdom (Nishikawa 1997; Heinze & Homberg 2007).

### Trends in the evolution of intelligence

In Drake’s perspective, brain evolution is important only as far as it is a necessary condition for the apparition of intelligence. So, the next problem to study is the relationship between brain and intelligence. Many definitions of ‘intelligence’ have been proposed, most of them pointing to the ability to respond with an appropriate behaviour in a given context (e.g. Sternberg 2002). In principle, with this behavioural definition, intelligence can be measured, correlated with encephalization and its evolution on Earth empirically reconstructed.

#### *Evolutionary trends in behaviour*

A suggestive illustration is provided by Cailleux (1971). He proposed a semi-quantitative method based on behavioral tests (simple reaction, T choice, labyrinth, detour, etc.). He asked two specialists of animal behaviour to list and rank these tests in order of increasing difficulty. He found the two independent scales to be in good agreement, ranging from simple directed response (level 1) to the notion of far future (level 55, end of scale). He plotted the various grades of behavioural



**Fig. 9.** Trend in the number of neurons in human ancestors (left axis) derived from endocranial volumes (right axis). The derivation is based on the isometric scaling law between brain volume and number of neurons in primates (Herculano-Houzel *et al.* 2007, 2011). Ancestral primates had less than 20 billion neurons, *Australopithecus*, had ~40 billion neurons, just above the chimpanzees (~30 billion neurons). In the genus *Homo*, the number of neurons grew from ~50 billion (*H. habilis*) to ~70 (*H. erectus*) and finally ~90 (*H. sapiens*) and even ~100 (*H. neanderthalensis*). The 15 species are numbered according to eight cognitive levels (on the right) and four motor behaviours (on the left). Redrawn from Lent *et al.* (2012).

performance of species or group of species versus their time of apparition. He found that successive equal levels were crossed in exponentially shorter times (see Fig. 2 in Rospars 2010). Although suggestive, this approach suffers from the obvious limitation that the behavioural scale is partly subjective and does not provide proof of the equivalence of equal intervals (is the jump from level 1 to level 11 equivalent to the jump from 21 to 31?).

Lent *et al.* (2012) illustrate a similar approach in human ancestors which links brain volume, number of cerebral neurons, main motor behaviours and cognitive achievements (Fig. 9). However, the link remains qualitative as the motor and cognitive scales are qualitative. Clearly, before cognitive trends can be studied, quantitative scales of cognition have to be established.

#### Relationship between intelligence and brain

Any brain is a compromise between costs and benefits. We have analysed energetic costs, what are the benefits? The main advantage hypothesized or even assumed of big brains is 'intelligence'. This raises three questions: how to measure intelligence? Does intelligence facilitate the survival and/or reproduction of animals in the wild? How is intelligence related to brain?

#### How to measure intelligence?

For a long time there has been no universally accepted definition of animal intelligence, or procedure to measure it. Making comparative estimates of cognitive capabilities present serious difficulties and fuel debates between animal

psychologists and ethologists. Traditional experimental tests have been criticized because they have little significance for the animal, are not fair to different species, and do not provide data on large numbers of species. Observations in natural conditions have been advocated because intelligence is well reflected in the appearance of novel solutions that are not part of the animal's normal repertoire (Gould 2004; Roth & Dicke 2005). This approach based on behavioural flexibility circumvents the aforementioned problems, because novel behaviours can be observed and measured; it is quantitative, ecologically relevant and non-anthropocentric, and can be used in the wild on hundreds of species.

Lefebvre *et al.* (1997) collated, in nine ornithological journals, all mentions of foraging innovations by birds in the British Isles and in North America. Foraging innovation was defined as the ingestion of a new food type or the use of a new foraging technique. A famous example of such an innovation involves British tit. In the 1920s, a few birds started opening milk bottles with foil tops delivered daily to front doors (this was before the generalization of refrigerators). The behaviour spread so rapidly that, within a few decades, thousands of tits had acquired the new feeding technique (Fisher & Hinde 1949; but see Gould 2004). Other examples include opening horsechestnuts by dropping them on pavement (jackdaw), using automatic sensor to open bus station door (house sparrow), systematic searching and entering of car radiator grilles for insects (house sparrow), using cars as nutcrackers for palm nuts (common crow), etc. Lefebvre and collaborators determined in this way the frequencies of innovation in 17 avian orders, absolute and corrected for the number of species per order.

Both frequencies were found to vary strongly between orders and consistently in the two geographical zones.

Similarly, Reader & Laland (2002) searched the literature for examples of the tendency to discover novel solutions to environmental or social problems ('innovation'), to learn skills and acquire information from others ('social learning'), and to use tools. The frequencies of the three variables were determined for 116 of the 203 known species of primates. The three variables showed large variations between species and were found to be positively correlated. To the extent that innovation is a measure of individual learning, these results suggest that individual and social learning are based on the same abilities.

Interestingly, Deaner *et al.* (2006) confirmed these results using traditional experimental tests. They collated all studies of cognition and intelligence in primate species and sorted them according to the experimental paradigms utilized, for example detour, tool use, object discrimination learning set, delayed response, etc. Based on this dataset (from 44 publications, eight paradigms and 24 genera), they found no indication that some genera excelled in particular paradigms. Instead, they showed that some genera performed consistently better than others across all of the paradigms, so giving evidence of global cognition and providing a way to measure it. They also found a good correspondence between this non-social cognitive ability and social cognition.

In summary, solutions have been found for quantitative comparisons of cognitive abilities in closely related species, but the problem of establishing valid comparisons among a broader array of species is still unsolved (for a suggestion, see below).

Is behavioural flexibility useful to survive in the wild?

Field observations and laboratory experiments suggest that flexibility can be advantageous in various contexts like tracking resource variation, using hard-to-eat foods, exploiting new ecological opportunities, dealing with environmental complexity (see the example of bats above), avoiding unfamiliar predators and learning from conspecifics (Sol 2009). Sol *et al.* (2002, 2005) examined the success of bird species when introduced in different regions of the world. They found that the degree of behavioural flexibility is a major determinant of invasion success. Innovative birds tend to be more successful at establishing themselves in novel environments.

Is behavioural flexibility related to brain features?

The previous studies provide the behavioural data whose absence prevented for so long a quantitative answer to this essential question. Lefebvre *et al.* (1997) used the ratio of forebrain volume (the equivalent of cortex in birds) over brainstem volume (medulla, pons and midbrain) and found that it was significantly related to both absolute and relative innovation frequency per order. Reader & Laland (2002) used three measures of brain size: the 'executive brain' volume (calculated as the sum of neocortex and striatum volumes), the 'executive brain ratio' (executive brain volume over brainstem volume, equivalent to EQ because brain stem volume is well

correlated to body mass), and residual executive brain volume, calculated by including brainstem in a multiple regression. All three measures of behavioural flexibility (innovation, social learning and tool use frequencies) were found to be significantly positively correlated with executive brain volume and executive brain ratio (but not with residual executive brain volume). These findings support the view that multiple factors have been important in the evolution of large brains, involving technical skills, as well as social and ecological factors, since most innovations are foraging innovations. However, these studies of birds and primates do not establish whether increased forebrain or neocortex size was directly selected because these brain regions facilitates complex behaviours, or if the improved information processing capacities resulting from an increase of these regions was used secondarily to cope in new ways with environmental challenges.

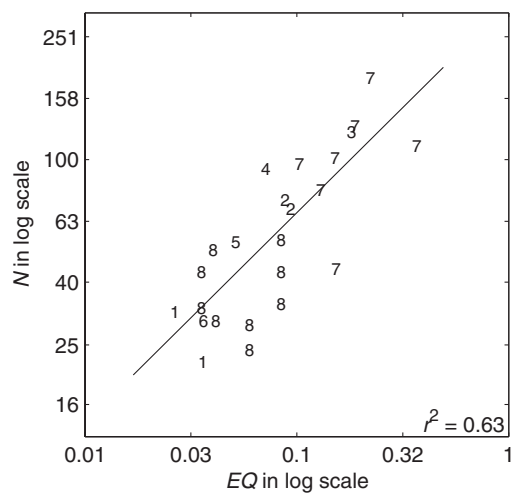
Other characteristics than innovation frequency and tool use are positively correlated with relative size of the brain or brain components (Morand-Ferron *et al.* 2007) – learning speed, capture of mobile prey, group size and/or social complexity, frugivory and kleptoparasitism, that is, the stealing of food items already procured by others. Collectively, they provide strong evidence that the cognitive skills of animals are limited by the size of the brain.

Deaner *et al.* (2007) studied the correlations between eight neuroanatomical measures and their quantitative estimate of global cognition for 24 non-human primate genera (see above). They found no significant correlation with measures based on EQ or brain size residuals that control for a possible effect of body size. The best two predictors of global cognitive ability were the logarithms of whole brain size and of neocortex size. These results call into question the hypothesis that the primate brain can be divided into somatic and cognitive parts and the usefulness of EQ in cognitive studies. They also provide an objective basis to convert the trend in brain size shown in Fig. 9 into a trend in global cognition.

Changizi (2003) showed in mammalian species from eight orders that behavioural repertoire size – the number of unique categories of behaviours displayed by a species – is significantly correlated with encephalization (Fig. 10). Although ethologists may have difficulties for delineating and counting behaviours (grooming, sitting, jumping, scratching ears, etc.), ethogram size appears as an informative measure related to behavioural flexibility. Further work in this direction is desirable as this measure holds the promise to be applicable across a wider array of species than other methods.

*Evidence for non-human 'high intelligence'*

It has long been thought that tool use, tool-making, syntactical-grammatical language, self-awareness, imitation, deception and 'theory of mind', that is, the ability to understand another individual's mental state and to take it into account in one's own behaviour, were unique properties of humans that required an exceptionally large brain. Both views have been undermined. A major contribution of ethology and animal psychology has been to demonstrate that man's abilities are not so unique. Although signs of imitation, theory of mind



**Fig. 10.** Number of behaviour types as a function of encephalization index in mammals. Behavioural repertoire size ( $N$ ) as determined by ethologists and encephalization index (EQ) defined as brain size after correcting for body size. Each point represents a different species (or a mean value for several species) from eight orders: Artiodactyla (1), Carnivora (2), Cetacea (3), Chiroptera (4), Insectivora (5), Lagomorpha (6), Primates (7) and Rodentia (8). Regression line of  $N$  on EQ is shown. Data from Table 1 in Changizi (2003).

and syntactical language were found in non-human animals, the evidence is still debated (Roth & Dicke 2005), but the other signs of ‘high intelligence’ are better established. Deception has been widely observed among monkeys (Bates & Byrne 2007). Tool use, defined as ‘the use of an external object as a functional extension of mouth, beak, hand, or claw, in the attainment of an immediate goal’ (van Lawick-Goodall 1970) has been observed in many primates, birds and other animals. For example, New Caledonian crows can craft hook tools that are used to poke out insect larvae from holes in trees and acquire otherwise unobtainable foods (Hunt 1996).

The understanding that one’s own mirror reflection does not represent another individual but oneself appears in humans at 18–24 months of age and marks the beginning of self-awareness. Until recently it was known only in great apes (Gallup 1970). Monkeys, other non-primate mammals and several bird species typically respond to a mirror by social behaviours, e.g. aggressive displays, quickly followed by disinterest. In a few ape species (chimpanzees, bonobos, orang-utans, some of gibbons and gorilla), however, behaviour changes over repeated presentations with a mirror. Social behaviour decreases and the mirror is used for exploration of the own body. Behaviours suggestive of self-recognition are observed in 75% of young adult chimpanzees.

Attempts at demonstrating self-recognition in other primates and non-primates failed to provide convincing evidence, until two bottlenose dolphins were tested (Reiss & Marino 2001). Each dolphin studied was marked on its body with black ink and these marks were not visible to it without the use of a mirror. The subjects showed no social behaviours but engaged in mark-directed behaviours at mirrors and spent a significantly greater cumulative amount of time at mirrors when

marked than when sham-marked (i.e. when a water-filled marker was used). The main difference with chimpanzees is that dolphins did not attend to marks on companions, maybe because, unlike primates, they do not groom each other. Experiments with Asian elephants gave similar results. None of the elephants aimed social behaviour at the mirror. All, like the apes and dolphins, exhibited exploratory and mirror-testing behaviour before more explicitly self-directed activities (Plotnik *et al.* 2006). Finally, corvids were also tested and the European Magpie *Pica pica* was confronted with mirrors. The first time, the birds displayed similar sequences of behaviour as described in apes. Clear evidence for mirror-recognition was obtained in two of the five birds tested (Prior *et al.* 2008). Emery & Clayton (2004) suggest that complex cognition is based on four non-verbal cognitive ‘tools’ (causal reasoning, flexibility, imagination and prospection) that are shared by both apes and corvids. These findings show that elaborate cognitive skills arose independently in two vertebrate classes, birds and mammals that diverged ~300 Ma ago. ‘High intelligence’ appears also as a convergent feature of evolution.

#### *Is a big brain needed to be ‘intelligent’?*

This question arises because the brain of corvid birds is relatively small (~10 g). However, it can achieve many of the cognitive operations of apes, like tool making, tool use and self-recognition. Certainly, the crow has a large brain with respect to its body as shown by its EQ which is equal to that of chimpanzees (Jerison 1973), but this is not a sufficient explanation. Its small absolute brain size may be compensated in part by smaller neurons and higher neuronal density (Roth & Dicke 2005). Unfortunately, number of neurons in corvid brains is not known. Also, the relative size of the forebrain of crows (and parrots) is significantly larger than in other birds, particularly the areas thought to be analogous to the mammalian prefrontal cortex (Reiner *et al.* 2004). However, the evolution of these brain divisions has been divergent in mammals and birds; the ape neocortex is laminar, whereas the corvid nidopallium presents a nuclear organization. This gives evidence that a convergent cognitive evolution can be built on a divergent brain evolution (Emery & Clayton 2004). A neocortex is not a prerequisite for complex cognition.

A confirmation that the relationships between brain and cognition are intriguing and ill-understood is found in insects. Their cognitive functions have been well studied, especially in honeybee workers, and they far exceed simple hard-wired responses to specific configurations of sensory stimuli (Giurfa 2003). Yet, insects have very small brains. The 1.1 mg brain of honey bees (Strausfeld 1976) contains slightly less than  $10^6$  neurons. However, this is sufficient not only to provide them with sophisticated sensory systems, well-developed learning and memory capacities, some counting abilities (Gross *et al.* 2009), but also to endow them with the capacity to manipulate abstract notions (Chittka & Niven 2009). For example, bees have been trained to distinguish horizontal and vertical bands in a series of distinct patterns. When confronted with different patterns, they were able to transfer the learned discrimination and thus to generalize the first examples.

Similarly, bees can learn the concept of above/below. They have also been shown to learn the notions of symmetry and similarity and, simultaneously, of asymmetry and difference. Recently, they have been shown to master simultaneously a spatial concept (above/below and right/left) and a difference concept (same/different) (Avarguès-Weber *et al.* 2012). All these cognitive tools are useful for flower recognition and navigation. Chittka & Niven (2009) conclude that brain size is less related to cognitive capacity than generally assumed. They argue that a greater neuron number adds precision to perception and motor control and enlarges memory capacity, which is important for flexible behaviours, but is not necessary for qualitative shifts in behaviour.

These observations make clear that brains are intrinsically multidimensional objects. Intelligence also is multidimensional. Any attempt to reduce their multiple dimensions to a single one (brain size, EQ, number of neurons, etc.) is helpful but inevitably creates exceptions, especially when evolutionary distant brains, possibly built on different principles, are compared.

### Discussion: from biology to astrobiology

Several quantitative variables that describe important aspects of the evolution of living organisms—their hierarchical organization, size and biodiversity—and of brains—their overall size, the number and size of their components—were measured on dated fossils or reconstructed from extant animals, and related to behavioural flexibility. The evolution of the maximum value across species of these variables as a function of geological time was found to be increasing, often according to exponential-like functions and during long periods, sometimes up to the present. They offer reliable evidence of the reality and generality of evolutionary trends. From the examples studied a few general properties of these trends can be tentatively drawn. Summarizing what trends are, and what they are not, may prevent misinterpretations that obscure their objective assessment and underestimate their significance for the probability of apparition of intelligent life.

#### *Main properties of observed trends*

A trend is not necessarily indicative of a progress. All biologists have admitted till the 1960s or 1970s that a ‘progress’ had taken place during evolution because they believed that a steady increase in complexity was obvious. The notion of evolutionary progress has been criticized as loaded with value judgment. Whether the apparition of intelligence is a ‘progress’, can be debated. However, the notion was defended by Ayala (1988) because once a standard of progress has been chosen, decisions concerning whether progress has occurred can be made following the usual methods of science.

Trends are not a modern version of the long-abandoned misconception that all beings can be arranged in a linear progressive series—the chain of being, or *scala naturae*—as first advocated by Buffon, Goethe and Oken. Later, this series was termed the ‘phylogenetic scale’ and led, for example, to the

telencephalization theory in which the telencephalon (cerebral hemispheres and related structures) of living adult vertebrates was seen as representing the various stages of a unilinear increase in complexity. It is now realized that evolution is better described as a ‘bush’ than as a ‘scale’ or ‘ladder’ (Parent & Hazrati 1994) because all living species are the terminal results of distinct branches (clades) that have evolved independently after their divergence. As a result, organisms are mosaics of components with different rates of evolution that cannot be ranked by increasing anatomical or functional complexity (Hodos & Campbell 1969; Campbell & Hodos 1991). A simple organism is not ‘lower’ than a complicated one (Cailleux 1971), both may be equally fitted to their environment and, if contemporary, have evolved during the same time.

The trends observed do not give any evidence for the existence of some universal force acting on all living forms that would drive them uniformly towards higher complexity with time. The absence of overall trend presents two complementary aspects: (i) for a given characteristic not all lineages in a group show the same trend (brain size can increase or decrease) and (ii) for a given lineage, not all characteristics show the same trend (in primates, while cerebrum increases, olfactory bulb and digestive system decrease). In all examples reviewed here, different lineages showed different trends characterized by an increase, a stagnation or a decrease in complexity. Prokaryotes have not disappeared after the advent of eukaryotes, if only because bacteria are indispensable for the global functioning of the Earth ecosystem. The observed diversity of trends raises the question of whether, when a large sample of lineages of a given group is considered, the number of increases in complexity exceeds the number of decreases (biased changes). Although important for a proper understanding of evolutionary processes, a definite answer to this question is not essential for the present discussion. Biased changes do not seem necessary for the apparition of highly complex organisms. A few positive trends in different lineages appearing successively in time are a sufficient condition, especially if these lineages are evolutionary successful.

Many other variables than those chosen here might have been examined—means of reproduction, of locomotion, of nutrition, to name only a few—that might have led to different ranking of species. Lineweaver (2008) notes that if relative nose size was chosen instead of relative brain size, elephants would be on top. Similarly, McShea (1996) remarks that if the human brain is ‘extraordinarily complex, in some sense and at some scale’, this may be expected from any hypertrophied and specialized structure, for example the arborescent tentacles of sabellid annelids that are more complex than those of other annelids. So, ‘with all specializations taken into account, it is not at all obvious that humans are more complex than other species’ and the higher complexity of humans ‘is not warranted by any reliable evidence’. Although provocative the objection is judicious; it is an aspect of the difficulty to compare rigorously different species and calls for further quantitative studies. The fact that, for example, the insect *Locusta migratoria* has almost the same number of muscles (296)



than primates (316) and more than rodents (214) encourages caution (Changizi 2003; Chittka & Niven 2009). However, these remarks are misleading. The question addressed here is not to decide whether humans are more complex than other species. In a discussion of complex intelligent life it is merely more appropriate to study brain size rather than nose size and to give more weight to neural information processing than to mouth appendages. In short, complexity *per se* is not relevant.

The time range over which an increasing trend of a given characteristic can be observed, in a single lineage or in a wide group of lineages, is usually limited. The size of the largest animals (limited by mechanical forces) and the biodiversity of oceans (possibly limited by its carrying capacity) are examples of sigmoid trends apparently ending in a stasis. Another example of greater theoretical significance is the slowing down of the number of higher taxonomic levels with time. The mean doubling time of the number of genera was much shorter in the first half of existence of several groups than in their second half: 40 Ma in the first half then 250 Ma in the second half for fish, 25 then 100 for terrestrial tetrapods, 15 then 21 for birds and 60 then 100 for terrestrial plants (Cailleux 1971). The same slowing down, known for a long time, occurred for orders, classes and phyla. The number of phyla has increased by 2 or 3 units only in the last 500 Ma. The diversification of the living world through time has concerned first the overall body plans then the details. The hierarchical organization in time is apparently a general feature of evolution. It is observed also in the evolution of the brain and brain divisions, and likely finds its origin in developmental constraints. However, in the course of evolution, the stasis of the 'old' variables is taken over by 'new' variables, expanding complexity in other directions, at least in some lineages. Each innovation creates a set of new possibilities for qualitatively different forms of changes. So, positive trends seem to be associated with radiations, when a combinatorial explosion is made possible by innovations.

Depending on the studied variables various functions of times have been reported to describe trends – linear, exponential, logistic, hyperbolic and others. However, logarithmic transformation, applied either to the time-dependent variables (Russell 1983) or to time (Cailleux 1971; Pettersson 1976), has been the most frequently used to linearize the curves. Using the later transformation, Cailleux (1971) and Pettersson (1976) showed that the anatomical and behavioural evolution, as well as the technical and social evolution in human societies, have accelerated through time (increasing growth rates with equal increments in exponentially shorter times). However, some evolutions, illustrated by the growth of the human population, are better described by hyperbolic functions that end as vertical asymptotes (Meyer & Vallée 1975). According to the interpretation of Chaline *et al.* (2009), based on non-linear dynamics and punctuated equilibria, the accelerated evolutions result from a series of discontinuous innovations (index  $i$ ) that appear with higher probability at successive times  $t_i$  according to a log-periodic function  $t_i = t_c + (t_0 - t_c)g^{-i}$ , where  $t_c$  is the critical time of the series and  $g$  a constant (scale factor). This function has been applied to the evolution of various clades, including the five successive cranial morphologies of primates

(Dambricourt-Malassé *et al.* 1999). The critical time may correspond in this case with the apparition of *H. sapiens* (Chaline *et al.* 1999). Although these independent studies support the idea that recent evolution is hyperexponential and suggest that innovations are cumulative, further research is needed to clarify and unify them. These quantitative studies are essential to model evolutionary trends and test hypotheses on their origin, notably the random diffusion hypothesis and the zero-force evolutionary law (McShea & Brandon 2010; Bogonovich 2011).

#### *Are evolutionary trends repeatable?*

The problem of repeatability of life on Earth, assuming the same initial conditions and the same planetary environment can serve as a simplified case before considering what could happen on different planets. If the tape of life were replayed, in what fraction of many independent repetitions will species with high intelligence appear? Many biologists have proposed pessimistic estimates: 'vanishingly small' (Simpson 1964), 'infinitely improbable' (Monod 1970), 'incredibly improbable' (Mayr 1985), the 'immense majority' of repetitions will not produce a conscious being (Gould 1996). Although dissenting views have also been expressed (e.g. Sagan 1995; de Duve 1998; Conway Morris, 2011), so that no consensus has been reached in the last 50 years or so, it is appropriate to take the pessimistic estimates as reference. Five main arguments have been proposed to support extremely small probability.

First, evolution shows no uniform trend. Evolution is not repeatable because 'there is no central line leading steadily, in a goal-directed way, from a protozoan to man' (Simpson 1964).

Counter-argument: This hypothesis of a global tendency for progress, now fallen in disrepute (Gould 1996), is unnecessarily strong. There is no evidence that the minimal 'random diffusion' hypothesis for trends would not lead to their repetition.

Second, exact repetitions are impossible. Evolution depends on many fortuitous events, both in reproduction (mutation and recombination are stochastic processes) and in the environment. 'If the causal chain had been different, *Homo sapiens* would not exist.' (Simpson 1964).

Counter-argument: This argument proves convincingly that *exact* repetitions are impossible but does not rule out approximate repetitions. Recognizing the existence of alternative evolutionary paths is not sufficient to exclude that some of these paths can lead to some form of high intelligence. If history had been different and if all known favourable events had never happened, then other events would have occurred and some of them might have been favourable. No sure conclusion can be drawn from the singularity of history and a probability cannot be calculated on this basis.

Third, the number of paths leading to high intelligence is small and contingent events can prevent evolution from following them. This central argument is supported by several observations. At least 40 different phyla of animals originated in the Cambrian explosion. Many of them were quickly eliminated (possibly at random) and only one, that of chordates, eventually gave rise to 'genuine intelligence'.

If this phylum would have been eliminated this form of intelligence would not have appeared (Mayr 1983; Gould 1989). Similarly, without the end Cretaceous extinction that wiped out the dinosaurs, mammals and primates would not have diversified.

Counter-argument: Although contingency certainly decreases the probability of similar repetitions, the eliminated alternative evolutionary paths might have been equally or more favourable paths for the apparition of intelligence. For example, the mammalian reptiles with their bipedal walk, thumb-like finger, frontal eyes and enlarged cerebral hemispheres might have led to highly intelligent beings with reptilian reproduction (Russell 1979). Is the number of solutions to develop a brain providing high flexibility and creativity large or small? It is difficult to answer this question in the present state of knowledge, although the diversity of solutions observed (insects, cephalopods, birds, primates, etc.) suggests but does not prove that this number is relatively large. The greater the number of possible paths to a given level, the higher is the probability that it is reached. The argument that bacteria are the dominant form of life on Earth, not mammals and still less human, is another form of this argument (Gould 1996). Similarly, the dominant forms of metazoan life are insects, the body plan of which are not compatible with large size and large brain, and therefore could not support human-like intelligence. The weight of this argument is difficult to assess because acknowledging that bacteria-like (or insect-like) organisms will be found in most or all repetitions does not prove that man-like beings will almost never be found.

Fourth, the paths leading to high intelligence have slow evolutionary rates. In this interpretation of the failure of repetitions the favourable paths are not necessarily rare but their evolutionary rates are very slow or null. Along many paths further development would be prevented at some point or would evolve at too low rates to give birth to highly complex metazoans during the ~10 Ga of the stable circumsolar habitable zone.

Counter-argument: On the one hand, admittedly, lines of slow evolution and dead ends have been frequent, likely even more frequent than innovative paths. Lethal mutations and short-lived lineages leave no trace in the fossil record. One can imagine cells that cannot aggregate, or could aggregate but not support the development of multiple organs, or would lead to animals but with no possibility to evolve complex brains. It is easy to imagine oceans where the 'highest' life forms are very slowly evolving dolphin-like animals (Lineweaver 2008).

On the other hand, it is equally difficult to identify clear biological obstacles preventing lineages to evolve at the rates actually observed. It seems likely that physical and chemical processes are dominant in the early phases of life. All chemical processes on which terrestrial life is based, including amino acids, nucleic acids, the cellular organization and even the genetic code (Freeland *et al.* 2000) may be universal because they depend on universal laws (de Duve 1998; Rospars 2010). Under these conditions, it is expected that the mutation rates would be similar as would the diversity of observed evolution

rates. For all variables examined here that describe important features for the apparition of high intelligence, positive trends have been found; this general property suggests that the hypothesized stasis is not the rule.

Slow evolution might also result from more frequent or more severe catastrophes than in the actual Earth history, possibly resulting from the coincidence in time of several factors and destroying all life (Erwin 2006). Raup (1991) estimated that severe catastrophes would have a periodicity greater than 2 Ga. This estimate indicates that actual life may have been lucky but not extremely lucky. Conversely, the idea that a world with less frequent catastrophes would evolve more slowly can be advocated (Conway Morris 2011).

Fifth, convergent evolution of high intelligence is improbable. Convergences have been presented as evidence for repeatability (Conway Morris, 2003, 2010). However, Lineweaver (2008) pointed out that all convergent species shared a long common history before they diverged and that the extent of convergence cannot be larger than the extent of divergence from the common ancestor. For the species which converged on eyes, the divergence could only take place during the relatively brief fraction of their existence as independent organisms.

Counter-argument: Clearly, new structures must evolve from pre-existing structures. Any brain presupposes the existence of a nervous system. However, this objection must not be overstated because if historical (contingent) constraints play a role, biophysical constraints cannot be ignored. Biophysical constraints play a dominant role to mould the shape and organization of animals as illustrated previously by the ubiquitous allometric relationships, the consequences of size increase, the lesser mobility in water than on land, brain energetics, etc. Optimum solutions for swimming, walking or flying are not so many. Sensory organs are constrained by the physical nature of stimuli on the sensor side and the processing of raw sensory signals on the neural side. These constraints are the major determinant of the convergences and contingency can play only a secondary role. Constraints explain the most general features of animals, like bilateral symmetry and the presence of a head housing a brain at close proximity of many cephalic sensory organs. There is little doubt that eyes are useful in the Earth environment. They can be expected to arise with similar organizations in any repetition of the evolutionary experiment where the coordinated growth of specialized cell types is possible, even if it is now known that eyes in different phyla have evolved by means of very similar changes in the same developmental genes (Shubin *et al.* 2009). It is difficult to imagine solutions very different from nervous systems to conduct and process information. Even if many designs are conceivable, general principles resulting in glomeruli, retinotopic maps, population coding etc., can be expected that owe little to history and much to optimization. Although the genetic background inherited from their common ancestor channels the evolution of convergent species (Losos 2011), in some convergences like placental and marsupial wolves, the morphologies reached are so similar that they seem to go much beyond this channelling. Convergences suggest that the

possible solutions are not so many and that they can be reached repeatedly through many different paths (Conway Morris 2003, 2010).

Mayr (1985) confirms that highly complicated organs like eyes ‘can evolve repeatedly and convergently when advantageous’ but adds ‘provided such evolution is at all probable’. This restriction is important because eyes are probable, as indicated by the fact that it evolved several times, but not ‘genuine intelligence’ that evolved only once. Lineweaver (2005) gives a vivid illustration of Mayr’s argument. He observes that five continents, South America, Australia, North America, Madagascar and Indonesia, drifted independently of each other for 50–200 Ma without evolving a species with human-like intelligence.

Counter-argument: If the failure of these five natural tests is a clear proof that the probability of high intelligence is less than 1, it does not prove that it is close to 0. A paradoxical weakness of the argument is that it stresses the singularity of man. The overall lesson of biology is that man is much closer to animals and his separation from them less profound than he used to believe. His brain is an enlarged primate brain and most of his features traditionally considered as unique are shared at various degrees by other species. There is no strong reason to believe that the path leading to an abstract thinking and tool-making creature is so exceptional that it would appear only rarely or never when the tape is replayed. Admittedly, the probability that all desirable features are found in the same species is lower than the probability of the features taken separately, but because these features are found with relatively high frequency, as evidenced by independent convergences on most man attributes (Conway Morris 2003), their product does not seem to be vanishingly small. *H. sapiens* is merely the first species who reached the proper level. Four human species close to or above the ‘high intelligence’ line were co-existing in East Africa between 2 and 1.5 Ma, *Paranthropus boisei*, *Homo* (or *Kenyanthropus*) *rudolfensis*, *Homo habilis* and *H. erectus*, and, as we have seen, several other extant species are not so far from the line. The implicit contention that many more species should be close to the line to make the transition to high intelligence less improbable is acceptable but not unquestionable.

#### *Astrobiological significance*

The problem of the apparition of intelligent life on exoplanets more or less similar to Earth is a variant of the repeatability problem on Earth with a greater number of degrees of freedom. The environmental conditions (gravity, pressure, temperature, atmospheric composition, duration of day and year, continental masses, etc.) can all be different. As mentioned above, strong physical and chemical constraints exist that favour the hypothesis of universal biochemical processes at the origin of life and of universal rules limiting the number and range of possible life forms. Then, it seems reasonable to believe that, if environmental conditions are not too different from those known on Earth and sufficiently stable through geologic times, life forms might evolve in hierarchical organization, size, diversity and information-processing skills. Our present

understanding of biology does not permit us to describe the space of all possible life forms or even phyla and still less to estimate their probabilities of apparition, survival or expansion.

In the most common view, probability  $f_1$  in Drakes’ equation that a highly intelligent organism appears on a planet endowed with life, is considered to be exceedingly small,  $f_1 = \varepsilon > 0$  ( $f_1 = 0$  is excluded because man evolved on Earth). In the view presented here that builds on the existence of accelerated trends, and takes into account the strong physical and chemical constraints on organisms, the branching (exploratory) properties of evolution and fundamental limitations in our present understanding of evolutionary processes (Conway Morris, 2010), it seems premature to dismiss  $f_1 > \varepsilon$ , and no compelling argument forbids  $f_1 \gg \varepsilon$ .

#### Acknowledgements

I thank Marc Bogonovich, Jean Chaline, Richard Delécolle, Jean-François Lambert, Nicole Meyer-Vernet and Dale Russell for their helpful comments on the manuscript.

#### Author disclosure statements

No competing financial interests exist.

#### References

- Aiello, L.C. & Wheeler, P. (1995). The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Curr. Anthropol.* **36**, 199–221.
- Aiello, L.C., Bates, N. & Joffe, T. (2001). In defense of the expensive tissue hypothesis. In *Evolutionary Anatomy of the Primate Cerebral Cortex*, ed. Falk, D. & Gibson, K.R., pp. 57–78. Cambridge University Press, Cambridge, UK.
- Aloy, J. *et al.* (2001). Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proc. Natl. Acad. Sci. U.S.A.* **98**(11), 6261–6266.
- Aloy, J. *et al.* (2008). Phanerozoic trends in the global diversity of marine invertebrates. *Science* **321**, 97–100.
- Avarguès-Weber, A., Dyer, A.G., Combe, M. & Giurfa, M. (2012). Simultaneous mastering of two abstract concepts by the miniature brain of bees. *Proc. Natl. Acad. Sci. U.S.A.* **109**(19), 7481–7486.
- Ayala, F.J. (1974). The concept of biological progress. In *Studies in the Philosophy of Biology*, ed. Ayala, F.J. & Dobzhansky, T., pp. 357–376. University of California Press, Berkeley and Los Angeles.
- Ayala, F.J. (1988). Can ‘progress’ be defined as a biological concept? In *Evolutionary Progress*, ed. Nitecki, M.H., pp. 75–96. The University of Chicago Press, Chicago, IL.
- Azevedo, F.A., Carvalho, L.R., Grinberg, L.T., Farfel, J.M., Ferretti, R.E.L., Leite, R.E.P., Filho, J.W., Lent, R., Herculano-Houzel, S. (2009). Equal numbers of neuronal and nonneuronal cells make the human brain an isometrically scaled-up primate brain. *J. Comp. Neurol.* **513**, 532–541.
- Baron, G., Frahm, H.D. & Stephan, H. (1988). Comparison of brain structure volumes in insectivora and primates. VIII. Vestibular complex. *J. für Hirnforschung* **29**, 509–523.
- Bates, L.A. & Byrne, R.W. (2007). Creative or created: using anecdotes to investigate animal cognition. *Methods* **42**, 12–21.
- Bauchot, R. & Platel, R. (1972). L’encéphalisation. *La Recherche* **4**, 1069–1077.
- Bell, G. & Mooers, A.O. (1997). Size and complexity among multicellular organisms. *Biol. J. Linn. Soc.* **60**, 345–363.

- Benton, M.J. (1985). Mass extinction among non-marine tetrapods. *Nature* **316**, 811–814.
- Benton, M.J. (2009). The Red Queen and the court jester: species diversity and the role of biotic and abiotic factors through time. *Science* **323**, 728–732.
- Benton, M.J. (2010). The origins of modern biodiversity on land. *Phil. Trans. R. Soc. B* **365**, 3667–3679.
- Benton, M.J. & Emerson, B.C. (2007). How did life become so diverse? The dynamics of diversification according to the fossil record and molecular phylogenetics. *Palaeontology* **50**, 23–40.
- Bogonovich, M. (2011). Intelligence's likelihood and evolutionary time frame. *Int. J. Astrobiol.* **10**(2), 113–122.
- Bonner, J.T. (1965). *Size and Cycle*. Princeton University Press, Princeton.
- Bonner, J.T. (1998). The origins of multicellularity. *Integr. Biol.* **1**, 27–36.
- Bonner, J.T. (2004). The size-complexity rule. *Evolution* **58**, 1883–1890.
- Bonner, J.T. (2006). *Why Size Matters. From Bacteria to Blue Whales*. Princeton University Press, Princeton and Oxford.
- Cailleux, A. (1971). Le temps et les échelons de l'évolution. In *Time in Science and Philosophy*, ed. Zeman, J., pp. 135–145. Elsevier, Amsterdam and Academia, Prague.
- Campbell, C.B. & Hodos, W. (1991). The Scala Naturae revisited: evolutionary scales and anagenesis in comparative psychology. *J. Comp. Psychol.* **105**(3), 211–221.
- Carroll, S. (2001). Chance and necessity: the evolution of morphological complexity and diversity. *Nature* **409**, 1102–1109.
- Chaline, J. & Marchand, D. (2002). *Les merveilles de l'évolution*. Editions Universitaires de Dijon, Dijon.
- Chaline, J., Nottale, L. & Grou, P. (1999). Is the evolutionary tree a fractal structure? *C.R. Acad. Sci. Paris, Sci. Terre Planètes* **328**, 717–726.
- Chaline, J., Nottale, L. & Grou, P. (2009). *Des fleurs pour Schrödinger. La relativité d'échelle et ses applications*. Ellipses, Paris.
- Changizi, M.A. (2003). Relationship between number of muscles, behavioral repertoire size, and encephalization in mammals. *J. Theor. Biol.* **220**, 157–168.
- Chittka, L. & Niven, J. (2009). Are bigger brains better? *Curr. Biol.* **19**, R995–R1008.
- Clark, D.A., Mitra, P.P. & Wang, S.S.-H. (2001). Scalable architecture in mammalian brains. *Nature* **411**, 189–193.
- Conway Morris, S. (2003). *Life's Solution: Inevitable Humans in a Lonely Universe*. Cambridge University Press, Cambridge, UK.
- Conway Morris, S. (2010). Evolution: like any other science is predictable. *Phil. Trans. Royal Soc. B* **365**, 133–145.
- Conway Morris, S. (2011). Predicting what extra-terrestrials will be like: and preparing for the worst. *Phil. Trans. Royal Soc. A* **369**, 555–571.
- Dambriocourt Malassé, A., Deshayes, M.J., Marchand, D., Magniez-Jannin, F. & Chaline, J. (1999). A solution to the human paradox: fundamental ontogenies and heterochronies. *Hum. Evol.* **14**(4), 277–300.
- de Duve, C. (1995). *Vital Dust. Life as a Cosmic Imperative*. Basic Books, New York.
- de Duve, C. (1998). Réflexions sur l'origine et l'évolution de la vie. *C. R. Soc. Biol.* **192**, 893–901.
- de Duve, C. (2011). Life as a cosmic imperative. *Phil. Trans. R. Soc. A* **369**, 620–623.
- de Miguel, C. & Henneberg, M. (2001). Variation in hominid brain size: how much is due to method? *Homo* **52**, 3–58.
- Deaner, R.O., van Schaik, C.P. & Johnson, V.E. (2006). Do some taxa have better domain-general cognition than others? A meta-analysis of nonhuman primate studies. *Evol. Psychol.* **4**, 149–196.
- Deaner, R.O., Isler, K., Burkart, J. & van Schaik, C. (2007). Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain Behav. Evol.* **70**, 115–124.
- Donoghue, M.J. (2005). Key innovations, convergence, and success: macroevolutionary lessons from plant phylogeny. *Paleobiology* **31**: 77–93.
- Eisenberg, J.F. & Wilson, D.E. (1978). Relative brain size and feeding strategies in the Chiroptera. *Evolution* **32**, 740–751.
- Elton, S., Bishop, L.C. & Wood, B. (2001). Comparative context of Pliocene hominin brain evolution. *J. Hum. Evol.* **41**, 1–27.
- Emery, N.J. & Clayton, N.S. (2004). The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science* **306**, 1903–1907.
- Erwin, D.H. (2006). *Extinction. How Life on Earth Nearly Ended 250 Million Years Ago*. Princeton University Press, Princeton and Oxford.
- Falk, D., Redmond, J.C. Jr., Guyer, J., Conroy, G.C., Recheis, W., Weber, G.W. & Seidler, H. (2000). Early hominid brain evolution: a new look at old endocasts. *J. Hum. Evol.* **38**, 695–717.
- Falk, D., Hildebolt, C., Smith, K., Morwood, M.J., Sutikna, T., Brown, P., Jatmiko, Wayhu Saptomo, E., Brunnsden, B. & Prior, F. (2005). The brain of *Homo floresiensis*. *Science* **308**, 242–245.
- Falk, D., Hildebolt, C., Smith, K., Morwood, M.J., Sutikna, Jatmiko, T., Saptomod, E.W. & Prior, F. (2009). LB1's virtual endocast, microcephaly, and hominin brain evolution. *J. Hum. Evol.* **57**, 597–607.
- Finarelli, J.A. & Flynn, J.J. (2006). Ancestral state reconstruction of body size in the Caniformia (Carnivora, Mammalia): the effects of incorporating data from the fossil record. *Syst. Biol.* **55**, 301–313.
- Finarelli, J.A. & Flynn, J.J. (2007). The evolution of encephalization in caniform carnivores. *Evolution* **61**(7), 1758–1772.
- Finlay, B.L. & Darlington, R.B. (1995). Linked regularities in the development and evolution of mammalian brains. *Science* **268**, 1578–1584.
- Fisher, J. & Hinde, R.A. (1949). The opening of milk bottles in birds. *Br. Birds* **42**, 347–357.
- Fish, J.L. & Lockwood, C.A. (2003). Dietary constraints on encephalization in primates. *Am. J. Phys. Anthropol.* **120**, 171–181.
- Freeland, S.J., Knight, R.D., Landweber, L.F. & Hurst, L.D. (2000). Early fixation of an optimal genetic code. *Mol. Biol. Evol.* **17**, 511–518.
- Gallup, G.G. (1970). Chimpanzees: self-recognition. *Science* **167**, 86–87.
- Giurfa, M. (2003). Cognitive neuroethology: dissecting non-elemental learning in a honeybee brain. *Curr. Opin. Neurobiol.* **13**, 726–735.
- Gittleman, J.L. (1986). Carnivore brain size, behavioral ecology, and phylogeny. *J. Mamm.* **67**, 23–36.
- Gross, H.J., Pahl, M., Si, A., Zhu, H., Tautz, J. & Zhang, S. (2009). Number-based visual generalisation in the honeybee. *PLoS ONE* **4**(1), e4263.
- Gould, J.L. (2004). Animal cognition. *Curr. Biol.* **14**(10), R372–R375.
- Gould, S.J. (1989). *Wonderful Life*. W.W. Norton & Co., New York.
- Gould, S.J. (1996). *Full House*. Harmony Books, New York.
- Gould, S.J. (2001). Size matters and function counts. In *Evolutionary Anatomy of the Primate Cerebral Cortex*, ed. Falk, D. & Gibson, K.R., pp. xiii–xvii. Cambridge University Press, Cambridge, UK.
- Gould, S.J., Gilinsky, N.L., German, R.Z. (1987). Asymmetry of lineages and the direction of evolutionary time. *Science* **236**, 1437–1441.
- Hartline, D.K. & Colman, D.R. (2007). Rapid conduction and the evolution of giant axons and myelinated fibers. *Curr. Biol.* **17**, R29–R35.
- Heinze, S. & Homberg, U. (2007). Maplike representation of celestial E-vector orientations in the brain of an insect. *Science* **315**, 995–997.
- Herculano-Houzel, S. (2007). Encephalization, neuronal excess, and neuronal index in rodents. *Anat. Rec.* **290**, 1280–1287.
- Herculano-Houzel, S. (2010). Coordinated scaling of cortical and cerebellar numbers of neurons. *Front. Neuroanat.* **4**(12), 1–8.
- Herculano-Houzel, S. (2011). Brains matter, bodies maybe not: the case for examining neuron numbers irrespective of body size. *Ann. N.Y. Acad. Sci.* **1225**, 191–199.
- Herculano-Houzel, S. & Kaas, J.H. (2011). Gorilla and orangutan brains conform to the primate cellular scaling rules: Implications for human evolution. *Brain Behav. Evol.* **77**, 33–44.
- Herculano-Houzel, S., Collins, C.E., Wong, P. & Kaas, J.H. (2007). Cellular scaling rules for primate brains. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 3562–3567.
- Herculano-Houzel, S., Mota, B. & Lent, R. (2006). Cellular scaling rules for rodent brains. *Proc. Natl. Acad. Sci. U.S.A.* **103**(32), 12138–12143.
- Hodos, W. & Campbell, C.B.G. (1969). *Scala naturae*: why there is no theory in comparative psychology. *Psychol. Rev.* **76**, 337–350.
- Hunt, G.R. (1996). Manufacture and use of hook-tools by new Caledonian crows. *Nature* **379**, 249–251.
- Huxley, J.S. (1932). *Problem of Relative Growth*. Methuen, London.
- Jerison, H.J. (1973). *Evolution of the Brain and Intelligence*. Academic Press, New York and London.

- Jerison, H.J. (1991). *Brain Size and the Evolution of Mind*. American Museum of Natural History, New York.
- Kaas, J.H. (2008). The evolution of the complex sensory and motor systems of the human brain. *Brain Res. Bull.*, **75**, 384–390.
- Kappelman, J. (1996). The evolution of body mass and relative brain size in fossil hominids. *J. Hum. Evol.*, **30**, 243–276.
- Kerr, R.A. (2008). Life's innovations let it diversify, at least up to a point. *Science* **321**, 24–25.
- Knoll, A.H. (2003). *Life on a Young Planet*. Princeton University Press, Princeton and Oxford.
- Krubitzer, L. (2009). In search of a unifying theory of complex brain evolution. *Ann. N.Y. Acad. Sci.* **1156**, 44–67.
- Krubitzer, L. & Kaas, J. (2005) The evolution of the neocortex in mammals: how is phenotypic diversity generated? *Curr. Opin. Neurobiol.* **15**, 444–453.
- Labandeira, C.C. & Sepkoski, J.J. Jr. (1993). Insect diversity in the fossil record. *Science* **261**, 310–315.
- Lefebvre, L., Whittle, P., Lascaris, E. & Finkelstein, A. (1997). Feeding innovations and forebrain size in birds. *Anim. Behav.* **53**, 549–560.
- Lent, R., Azevedo, F.A.C., Andrade-Moraes, C.H. & Pinto, A.V.O. (2012). How many neurons do you have? Some dogmas of quantitative neuroscience under revision. *Eur. J. Neurosci.* **35**, 1–9.
- Leonard, W.R., Robertson, M.L., Snodgrass, J.J. & Kuzawa, C.W. (2003). Metabolic correlates of hominid brain evolution. *Comp. Biochem. Physiol. A: Mol. Integr. Physiol.* **136**, 5–15.
- Lineweaver, C.H. (2005). Book review of 'Intelligent Life in the Universe' by P. Ulmschneider. *Astrobiology* **5**(5), 658–661.
- Lineweaver, C.H. (2008). Paleontological tests: human-like intelligence is not a convergent feature of evolution. In *From Fossils to Astrobiology*, ed. Seckbach, J. & Walsh, M., pp. 353–368, Springer, New York.
- Lindstedt, S.L. & Calder, W.A. (1981). Body size, physiological time, and longevity of homeothermic animals. *Q. Rev. Biol.* **56**, 1–16.
- Losos, J.B. (2011). Convergence, adaptation, and constraint. *Evolution* **65**(7), 1827–1840.
- Losos, J.B., Jackman, T., Larson, A., de Queiroz, K. & Rogriquet-Schettino, L. (1998). Contingency and determinism in replicated adaptive radiations of island lizards. *Science* **279**, 2115–2118.
- Mace, G.M., Harvey, P.H. & Clutton-Brock, T.H. (1980). Is brain size an ecological variable? *Trends Neurosci.* **3**(8), 193–196.
- Marcot, J.D. & McShea, D.W. (2007). Increasing hierarchical complexity throughout the history of life: phylogenetic tests of trend mechanisms. *Paleobiology* **33**, 182–200.
- Marino, L., Uhen, M.D., Pyenson, N.D. & Frohlich, B. (2003). Reconstructing cetacean brain evolution using computed tomography. *Anat. Rec. B: New Anat.* **272**, 107–117.
- Marino, L., McShea, D.W. & Uhen, M.D. (2004). Origin and evolution of large brains in toothed whales. *Anat. Record A*, **281A**, 1247–1255.
- Martin, R.D. (1996). Scaling of the mammalian brain: the maternal energy hypothesis. *News Physiol. Sci.* **11**, 149–156.
- May, R.M. (1990). How many species? *Phil. Trans. R. Soc. Lond. B* **330**, 293–304.
- May, R.M. (1994). Biological diversity: differences between land and sea. *Phil. Trans. R. Soc. Lond. B* **343**, 105–111.
- Mayhew, P.J. (2007). Why are there so many insect species? Perspectives from fossils and phylogenies. *Biol. Rev.* **82**, 425–454.
- Maynard Smith, J. & Szathmáry, E. (1995). *The Major Transitions in Evolution*. Freeman, Oxford.
- Mayr, E. (1985). The probability of extraterrestrial intelligent life. In *Extraterrestrials. Science and Alien Intelligence*, ed. Regis, E., pp. 23–30. Cambridge University Press, Cambridge, UK.
- Melville, J., Harmon, L.L. & Losos, J.B. (2005). Intercontinental community convergence of ecology and morphology in desert lizards. *Proc. Royal Soc. London B*, **273**: 557–563.
- McHenry, H.M. (1994). Tempo and mode in human evolution. *Proc. Natl. Acad. Sci. U.S.A.* **91**, 6780–6786.
- McShea, D.W. (1991). Complexity and evolution: what everybody knows. *Biol. Philos.* **6**, 303–324.
- McShea, D.W. (1996). Metazoan complexity and evolution: is there a trend? *Evolution* **50**, 477–492.
- McShea, D.W. (2001a). The hierarchical structure of organisms: a scale and documentation of a trend in the maximum. *Paleobiology* **27**, 405–423.
- McShea, D.W. (2001b). The minor transitions in hierarchical evolution and the question of a directional bias. *J. Evol. Biol.* **14**, 502–518.
- McShea, D.W. & Brandon, R.N. (2010). *Biology's First Law: the Tendency for Diversity and Complexity to Increase in Evolutionary Systems*. The University of Chicago Press, Chicago, IL.
- McShea, D.W. & Changizi, M.A. (2003). Three puzzles in hierarchical evolution. *Integr. Comp. Biol.* **43**, 74–81.
- Meyer, F. (1954). *Problématique de l'évolution*. Presses Universitaires de France, Paris.
- Meyer, F. & Vallée, J. (1975). The dynamics of long-term growth. *Technol. Forecast. Soc. Change* **7**, 285–300.
- Monod, J. (1970). *Le hasard et la nécessité: Essai sur la philosophie naturelle de la biologie moderne*. Seuil, Paris.
- Morand-Ferron, J., Sol, D. & Lefebvre, L. (2007). Food stealing in birds: brain or brawn? *Anim. Behav.* **74**, 1725–1734.
- Neill, D. (2007). Cortical evolution and human behavior. *Brain Res. Bull.* **74**, 191–205.
- Niklas, K.J., Tiffney, B.H. & Knoll, A.H. (1985). Patterns in vascular land plant diversification: a factor analysis at the species level. In *Phanerozoic Diversity Patterns*, ed. Valentine, J.W., pp. 97–128. Princeton University Press, Princeton, NJ.
- Nishikawa, K.C. (1997). Emergence of novel functions during brain evolution. *BioScience* **47**(6), 341–354.
- Nishikawa, K.C. (2002). Evolutionary convergence in nervous systems: insights from comparative phylogenetic studies. *Brain Behav. Evol.* **59**, 240–249.
- Northcutt, R.G. (2002). Understanding vertebrate brain evolution. *Integr. Comp. Biol.* **42**, 743–756.
- Northcutt, R.G. & Kaas, J.H. (1995). The emergence and evolution of mammalian neocortex. *Trends Neurosci.* **18**, 373–379.
- Parent, A. & Hazrati, L.N. (1994). The ladder of progress in neuroscience. Reply C.G. Gross. *Trends Neurosci.* **17**(6), 227–228.
- Pettersson, M. (1976). *Complexity and Evolution*. Cambridge University Press, Cambridge, UK.
- Plotnik, J., de Waal, F.M.B. & Reiss, D. (2006). Self-recognition in an Asian elephant. *Proc. Natl. Acad. Sci. U.S.A.* **103**, 17053–17057.
- Prior, H., Schwarz, A. & Güntürkün, O. (2008). Mirror-induced behavior in the magpie (*Pica pica*): Evidence of self-recognition. *PLoS Biol.* **6**, 1642–1650.
- Rakic, P. (1995). A small step for the cell, a giant leap for mankind: a hypothesis of neocortical expansion during evolution. *Trends Neurosci.* **18**, 383–388.
- Rapoport, S.I. (1999). How did the human brain evolve? A proposal based on new evidence from *in vivo* brain imaging during attention and ideation. *Brain Res. Bull.* **50**, 149–165.
- Raup, D.M. (1976). Species diversity in the Phanerozoic: an interpretation. *Paleobiology* **2**, 289–297.
- Raup, D.M. (1991). *Extinction. Bad Genes or Bad Luck?* W.W. Norton, New York.
- Reader, S.M. & Laland, K.N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proc. Natl. Acad. Sci. U.S.A.* **99**, 4436–4441.
- Reep, R.L., Finlay, B.L. & Darlington, R.B. (2007). The limbic system in mammalian brain evolution. *Brain Behav. Evol.* **70**, 57–70.
- Reiner, A., Perkel, D.J., Bruce, L.L., Butler, A.B., Csillag, A., Kuenzel, W., Medina, L., Paxinos, G., Smimizu, T., Striedter, G. (2004). Revised nomenclature for avian telencephalon and some related brainstem nuclei. *J. Comp. Neurol.* **473**, 377–414.
- Reiss, D. & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: a case of cognitive convergence. *Proc. Natl. Acad. Sci. U.S.A.* **98**, 5937–5942.
- Rilling, J.K. & Insel, T.R. (1998). Evolution of the cerebellum in primates: differences in relative volume among monkeys, apes and humans. *Brain Behav. Evol.* **52**, 308–314.
- Rospars, J.-P. (2010). Terrestrial biological evolution and its implication for SETI. *Acta Astronaut.* **67**, 1361–1365.

- Roth, G. & Dicke, U. (2005). Evolution of the brain and intelligence. *Trends Cogn. Sci.* **9**(5), 250–257.
- Roth, G., Nishikawa, K.C., Naujoks-Manteuffel, C., Schmidt, A. & Wake, D.B. (1993). Paedomorphosis and simplification in the nervous system of salamanders. *Brain Behav. Evol.* **42**, 137–170.
- Russell, D.A. (1979). Speculations on the evolution of intelligence in multicellular organisms. In *Life in the Universe*, ed. Billingham, J., pp. 259–275. MIT Press, Cambridge, MA.
- Russell, D.A. (1983). Exponential evolution: implications for intelligent extraterrestrial life. *Adv. Space Res.* **3**, 95–103.
- Russell, D.A. (2009). *Islands in the Cosmos. The Evolution of Life on Land*. Indiana University Press, Bloomington and Indianapolis.
- Safi, K., Seid, M.A. & Dechmann, D.K.N. (2005). Bigger is not always better: when brains get smaller. *Biol. Lett.* **1**, 283–286.
- Sagan, C. (1995). The abundance of life-bearing planets. *Bioastron. News* **7**(4), 1–4.
- Sahney, S., Benton, M.J. & Ferry, P.A. (2010). Links between global taxonomic diversity, ecological diversity, and the expansion of vertebrates on land. *Biol. Lett.* **6**, 544–547.
- Salvini-Plawen, L.v. & Mayr, E. (1977). On the evolution of photoreceptors and eyes. *Evol. Biol.* **10**, 207–263.
- Sarko, D.K., Catania, K.C., Leitch, D.B., Kaas, J.H. & Herculano-Houzel, S. (2009). Cellular scaling rules of insectivore brains. *Front. Neuroanat.* **3**, article 8, pp. 1–12.
- Schmidt-Nielsen, K. (1984). *Scaling. Why is animal size so important?* Cambridge University Press, Cambridge, UK.
- Sepkoski, J.J. Jr. (1984). A kinetic model of phanerozoic taxonomic diversity. III. Post-paleozoic families and mass extinctions. *Paleobiology* **10**, 246–267.
- Sepkoski, J.J. Jr. (1996). Patterns of Phanerozoic extinction: a perspective from global data bases. In *Global events and event stratigraphy*, ed. Walliser, O.H., pp. 35–51. Springer, Berlin.
- Shubin, N., Tabin, C. & Carroll, S. (2009). Deep homology and the origins of evolutionary novelty. *Nature* **457**, 818–823.
- Simpson, G.G. (1964). The nonprevalence of humanoids. *Science* **143**, 769–775. (Also published as Chapter 13 in *This View of Life: The World of an Evolutionist*, Harcourt, Brace & World, New York.)
- Simpson, G.G. & Beck, W.S. (1965). *Life*, 2nd edn. Harcourt, Brace and World, New York.
- Sol, D. (2009). Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biol. Lett.* **5**, 130–133.
- Sol, D., Timmermans, S. & Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Anim. Behav.* **63**, 495–502.
- Sol, D., Duncan, R.P., Blackburn, T.M., Casset, P. & Lefebvre, L. (2005). Big brains, enhanced cognition and response of birds to novel environments. *Proc. Natl. Acad. Sci. U.S.A.* **102**, 5460–5465.
- Stebbins, G.L. (1969). *The Basis of Progressive Evolution*, University of North Carolina Press, Chapel Hill.
- Sternberg, R.J. (2002). The search for criteria: why study the evolution of intelligence. In *The Evolution of Intelligence*, ed. Sternberg, R.J. & Kaufman, J.C., pp. 1–7. Lawrence Erlbaum Associates, Publishers, Mahwah, NJ.
- Strausfeld, N.J. (1976) *Atlas of an insect brain*. Springer, Berlin, Heidelberg.
- Teissier, G. (1936). Croissance comparée des formes d'une même espèce. *Mem. Mus. R. Hist. Nat. Belg.* **3**, 627–634.
- Thireau, M. & Doré, J.-C. (2002). Liens phylogénétiques dégagés entre Tenrecinés, Insectivores, Prosimiens, Simiens non humanoïdes, Homme et Chiroptères (Méga- ou Micro-), au moyen d'analyses multivariées du volume des étages encéphaliques et de quelques macro-structures télencéphaliques. *Bull. Soc. Zool. France* **127**(2), 181–204.
- Thireau, M. & Doré, J.-C. (2003). Evolutionary anatomy of the primate cerebral cortex, 2001 et S.J. Gould: regards croisés. *C. R. Palevol* **2**, 373–381.
- Valentine, J., Collins, A.G. & Meyer, C.P. (1994). Morphological complexity increase in metazoans. *Paleobiology* **20**, 131–142.
- van Dongen, P.A.M. (1998). Brain size in vertebrates. In *The Central Nervous System of Vertebrates* (Vol. 3), ed. Nieuwenhuys, R. *et al.*, pp. 2099–2134. Springer, Berlin.
- van Lawick-Goodall, J. (1970). Tool-using in primates and other vertebrates. *Adv. Study Behav.* **3**, 195–249.
- Vermeij, G.J. & Grosberg, R.K. (2010). The Great Divergence: when did diversity on land exceed that in the sea? *Integr. Comp. Biol.* **50**(4), 675–682.
- Ward, P.D., Brownlee, D. (2000). *Rare Earth. Why complex life is uncommon in the universe*. Copernicus, NY, 333 pp.
- Williams, G.C. (1966). *Adaptation and Natural Selection*. Princeton University Press, Princeton.
- Wilson, E.O. (1992). *The diversity of life*, pp. 424. Harvard University Press, Cambridge, MA.
- Yopak, K.E., Lisney, T.J., Darlington, R.B., Collin, S.P., Montgomery, J.C. & Finlay, B.L. (2010). A conserved pattern of brain scaling from sharks to primates. *Proc. Natl. Acad. Sci. U.S.A.* **107**(29), 12945–12951.
- Zhang, K. & Sejnowski, T.J. (2000). A universal scaling law between gray matter and white matter of cerebral cortex. *Proc. Natl. Acad. Sci. U.S.A.* **97**(10), 5621–5626.