

Abstract

Processes of regression and rudimentation are deeply involved in the evolution of life and are as important as constructive evolution. They occur in every taxonomic group and concern morphological, behavioural, as well as physiological traits. For example, whales have reduced their hind legs and the pelvic girdle. The ratite birds have convergently abandoned the ability to fly and exhibit reduced wings and sternal carina. In addition, the delicate feather structure is broken down. In the Pacific island of Tahiti, where no insectivore bats exist, noctuid moths have lost the acoustic startle response. Even the gustatory system may selectively lose taste components (e.g. sweet in cats; bitter, sweet, and umami in penguins; or umami in the giant panda after changing their diet during evolution). However, from the view of human beings relying on sight as the dominant sense, the most bizarre and striking examples for rudimentation—often also characterized as degeneration or regression of traits—are provided by the loss of eyes and dark pigmentation in species living in the continuous absolute darkness of subterranean habitats like caves.

Impressive examples of rudimentation and regression are provided by the rudimentary pelvic girdles or hip bones of whales. Their anlagen are completely developed during early ontogeny but are reduced to a size no more than three percent of the total body length in adult specimens. The pelvic girdle of whales is no longer linked to the vertebral column, but lies deeply sunken, embedded in body tissue. The rudimentary hind legs may still be extant as minute remnants of the former thighs and shanks and are characterized by great variability (Abel 1908; Deimer 1977; Thewissen and Bajpai 2001) (Figs 2.1 and 2.2).

Striking evidence for rudimentation is also delivered by a large number of bird species. With the loss of the ability to fly, they have not only reduced their wing size—some of them even totally—but have also lost the flight musculature as well as the keel of the sternum, which the flight muscles attach to, and the delicate wing

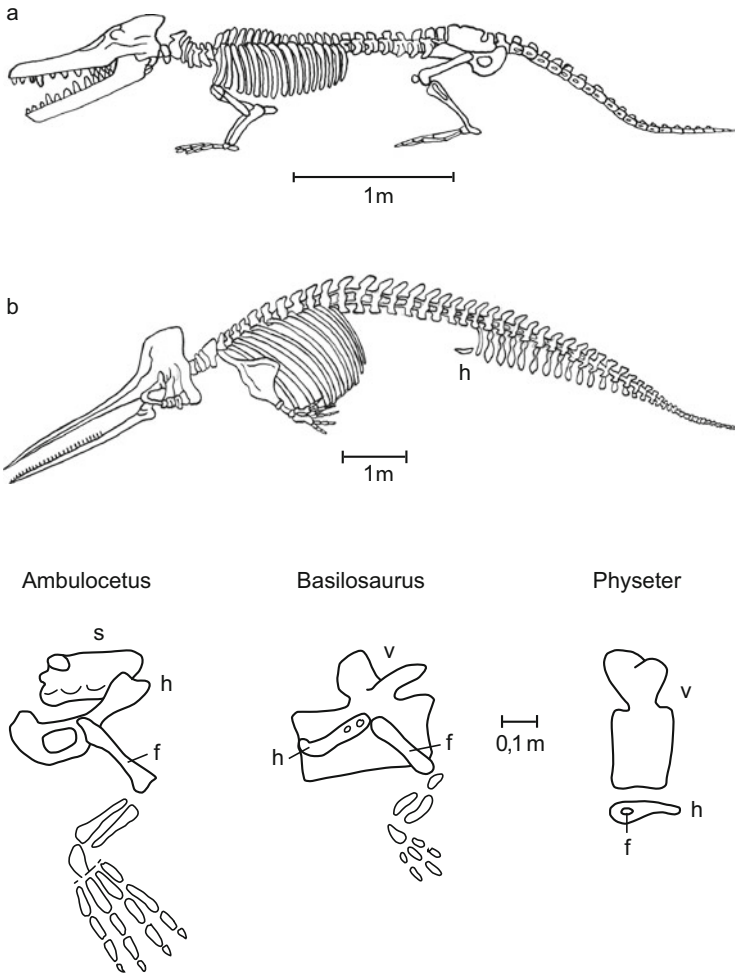


Fig. 2.1 Regressive evolution of hip bone and hind legs in ancestral (**a**: *Ambulocetus natans*) and modern whales (**b**: Sperm Whale, *Physeter macrocephalus*). In the archaic whale *Ambulocetus*, the sacrum (*s*) consisted of four fused vertebrae and there was a strong weight-bearing joint between sacrum and hipbone (*h*). In the extinct whale *Basilosaurus* and the recent Sperm Whale (*Physeter*), the sacrum consists of a single vertebra (*v*) and there is no contact between hip bone and sacrum. In both, hip bone and femur (*f*) lie on the ventral side, far removed from the spinal column. The rudimentary hind legs are no longer weight bearing (adapted from Thewissen et al. 2001)

feather structure. The most spectacular examples are provided by the systematic group of ratite birds (Ratitae), which comprise species like the African ostrich, the Australian emu (*Dromaius novaehollandiae*; Fig. 2.3) and cassowaries, the South American nandu, the extinct elephant birds from Madagascar, and the kiwis and extinct moas from New Zealand (Fig. 2.4). Molecular genetic studies provide evidence that flightlessness in these species evolved independently and did not

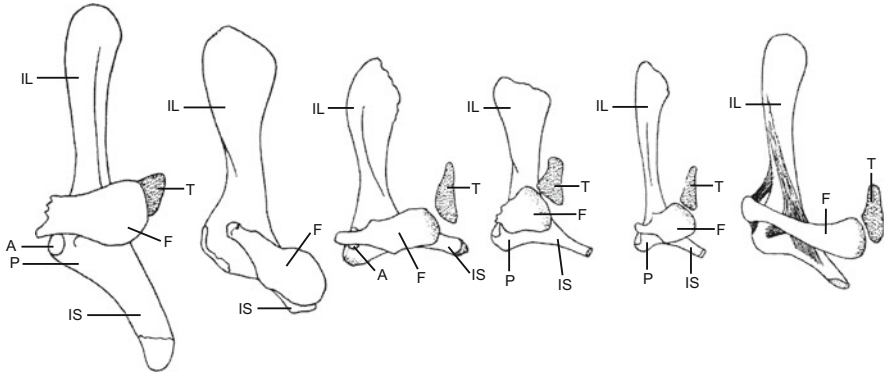


Fig. 2.2 Variability of the left hip bone and rudimentary hind leg of six female Bowhead whales (*Balaena mysticetus*). Body length 12–15 m, length of hip bones about 0.5 m (adapted from Abel 1908). IL ileum, P pubis, IS ischium, F femur, T tibia



Fig. 2.3 The ratite Australian emu (*Dromaius novaehollandiae*) exhibits reduced wings and disturbed feather structure (Photo Ulrike Strecker)

rely on common descent from a unique flightless ancestor but on convergence (Mitchell et al. 2014; Phillips et al. 2010). Flightlessness and the phenomenon of gigantism observed in most species of this group are assumed to have been facilitated by early Tertiary expansion into the diurnal herbivory niche after the extinction of the dinosaurs. Comparable evolutionary processes have also taken

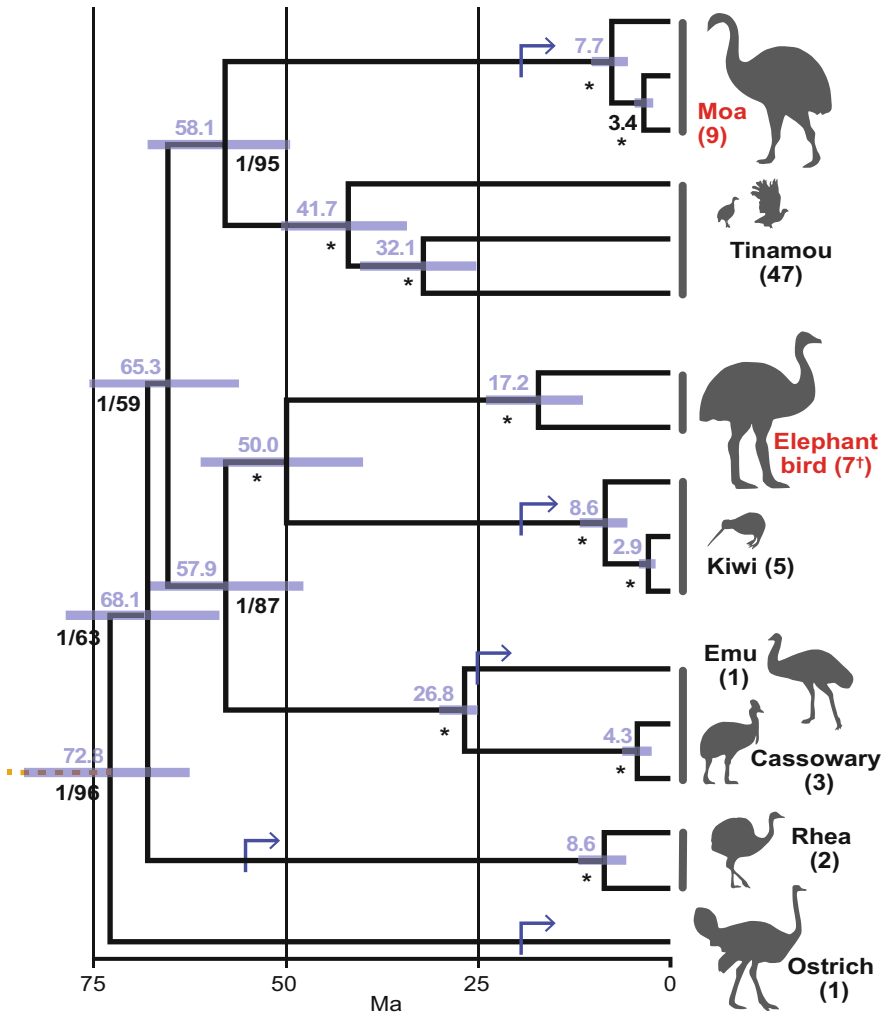


Fig. 2.4 Phylogeny of ratite birds from mitochondrial sequence data revealed convergent origins of flightlessness. Only the tinamous species from South America are able to fly. Numbers above branches indicate divergence dates. Arrows mark the minimum date for the evolution of flightlessness in lineages for which fossil evidence is available. The scale is given in millions of years before the present. Silhouettes indicate the relative size of representative taxa. Species diversity for each major clade is presented in parentheses, with extinct groups shown in red. The dagger symbol indicates that the number of elephant bird species is uncertain (adapted from Mitchell et al. 2014)

place in other systematic avian bird families like doves (Columbiformes) and cormorants (Phalacrocoracidae) on the isolated oceanic Mascarene and Galapagos Islands, respectively. These species evolved on islands without terrestrial predators,



Fig. 2.5 The flightless cormorant (*Phalacrocorax harrisi*) from Galapagos exhibits reduced wings and disorderly variable arrangement of primary and secondary wing feathers. This species provides an example of many birds reducing their flying abilities on isolated islands (Photo Harald Schliemann)

where the ability to escape by flight was no longer an advantage and the birds eventually became flightless (Fig. 2.5).

Fossorial mammals inhabit light-poor environments. In several species, the eyes are reduced to small size and may even be totally covered by skin (Emerling and Springer 2014; Nikitina et al. 2004). Traits like lens and retina may be subjected to structural regression. For example, in the naked mole rat (*Heterocephalus glaber*) the lens replaces the vitreous body and the retina is deformed but still consists of all sensitive layers. However, the eyes of these fossorial species cannot be completely reduced because they have still retained rudimentary biological functions like that of perceiving surface light for orientation or setting the biological clock. Analysis of the central visual system of the naked mole rat revealed that it appears to have selectively lost structures that mediate form vision while retaining those structures needed for minimal entrainment of circadian and seasonal rhythms (Crish et al. 2006).

Studying two insectivores (*Condylura cristata* and *Chrysochloris asiatica*), two rodents (*Heterocephalus glaber* and *Spalax ehrenbergi*), and a marsupial (*Notoryctes typhlops*) revealed that the fossoriality of these mammals is intimately linked to eye regression (Fig. 2.6). It was shown that a decrease in the amount of light that reaches the retina is associated with increased regression of retinal genes and that the phototransduction and visual cycle pathways degrade. The timing of retinal gene loss is associated with the entrance of mammalian lineages into

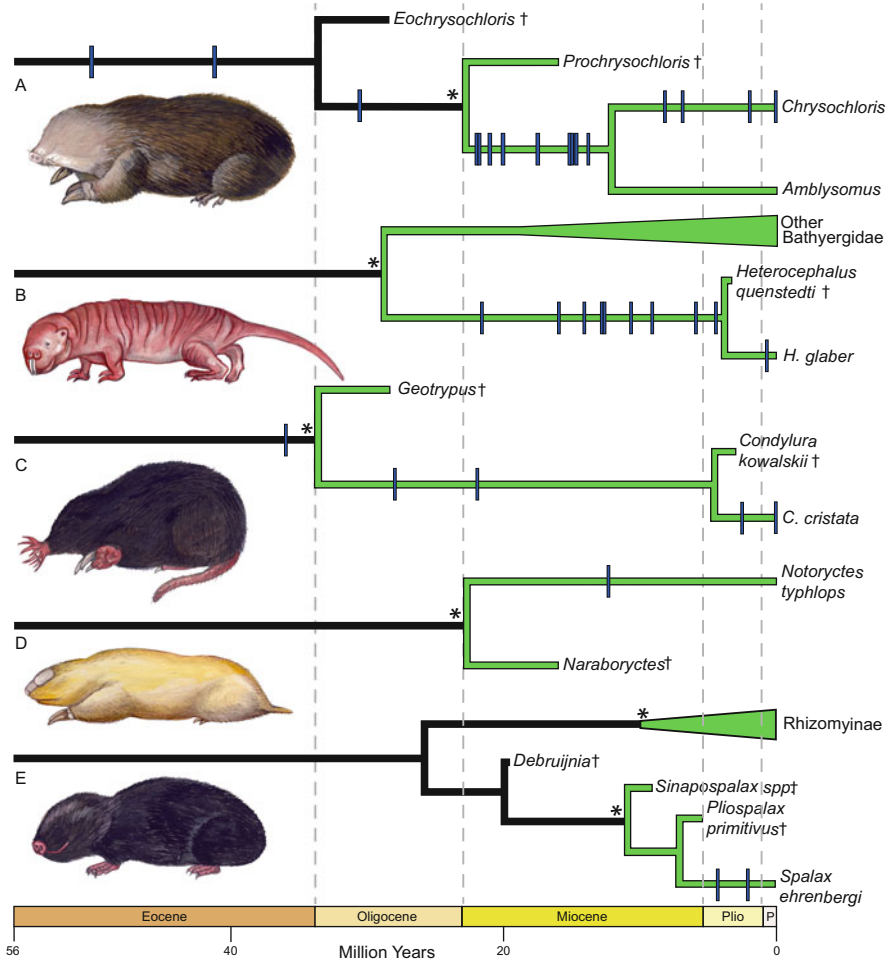


Fig. 2.6 Pseudogenization of retinal genes in fossorial mammals: Cape golden mole (*Chrysochloris asiatica* (a), Chrysochloridae), Naked mole rat (*Heterocephalus glaber* (b), Bathyergidae), Star-nosed mole (*Condylura cristata* (c), Talpidae), Marsupial mole (*Notoryctes typhlops* (d), Notoryctidae), Blind mole rat (*Spalax ehrenbergi* (e), Spalacidae). Vertical bars represent average estimates of pseudogenization and inactivation dates. Nodes with asterisks indicate inferred transitions to the underground habitat (adapted from Emerling and Springer (2014), paintings by Michelle S. Fabros, redrawn by Monika Hänel)

subterranean environments. The incidence of regressive mutations in retinal genes (pseudogenization) post-dates the inferred entrances into their subterranean habitat and increases with time (Emerling and Springer 2014).

Rudimentation is not only restricted to morphological traits. Noctuid moths endemic to the mountains of the South Pacific island of Tahiti have evolved in an environment without bats and have lost their defensive behaviour against these

predators, the acoustic startle response (Fullard et al. 2007). This response is activated by a single receptor neuron, which still exists, but exhibits a rudimentary reduced firing activity. Partial regression in the nervous control of a defensive behaviour is also observed in the Pacific field cricket *Teleogryllus oceanicus* (Orthoptera, Gryllidae), whose distribution ranges naturally across the South Pacific Ocean from Indonesia to French Polynesia, in those areas characterized by the absence of bats (Fullard et al. 2010).

Another example is provided by the penguins, all of which have lost the sweet, umami, and bitter tastes and only the genes responsible for salty and sour are intact (Zhao et al. 2015). It is suggested that a key component of taste transduction in the gustatory system of bitter, sweet, and umami but not of sour or salty taste, the cation channel *Trpm5*, is temperature sensitive, with lower activities at lower temperatures. It may have been effectively non-functional in the taste buds of ancestral penguins, which radiated after the formation of the large Antarctic ice sheet about 30 million years ago, rendering the tastes relying on this channel unusable and gradually lost. For the giant panda, it was shown that the functional constraint of the umami taste receptor gene *Tas1r1* relaxed leading to pseudogenization at about 4.2 Ma with its dietary switch from a carnivorous to a vegetarian diet (Zhao et al. 2010). Similarly, the pseudogenization of a sweet-receptor gene was found to account for the indifference of cats to detecting sweetness (Li et al. 2005). This molecular change detected in tigers, cheetahs, and the domestic cat was probably a loss due to the carnivorous type of feeding of Felidae, in which sweetness has no importance.

From the view of a human being relying on sight as the dominant sense, the most bizarre and striking examples for rudimentation—often also characterized as degeneration or regression of traits—are provided by the most conspicuous loss of eyes or dark pigmentation in species living in the continuous absolute darkness of subterranean habitats like caves (Juberthie 2000; Juberthie and Decu 1994; Culver and Wilkens 2000). Such so-called troglobites are found in almost every taxonomic group distributed over all continents except Antarctica. The outer appearance of these blind and white animals seems mysterious and has fascinated scientists for a long time. Even Darwin found explaining regressive evolution difficult.

Such continuously dark habitats are usually denominated as caves, which are big enough for humans to enter. However, these are not the only places where cave species may evolve. Smaller animals inhabit narrower fissures; for example, those found in lava rocks in large numbers. The majority of such habitats originated by hydrological erosion in karstic limestone (Culver and Pipan 2009; Mitchell et al. 1977) or formed in the lava fields of volcanic eruptions (Juan et al. 2010). Caves may even exist at the bottom of the oceans as demonstrated by some marine lava tubes (Wilkens et al. 2009). A specific type of cave exists close to marine coasts and is termed anchialine (Iliffe 2000; Pérez-Moreno et al. 2016). Such habitats are landlocked with a subterranean connection to the sea and fresh and salt water may be stratified. They are colonized by marine cave animals. The cave species living here may actively invade the inland freshwater parts of such habitats or, after the

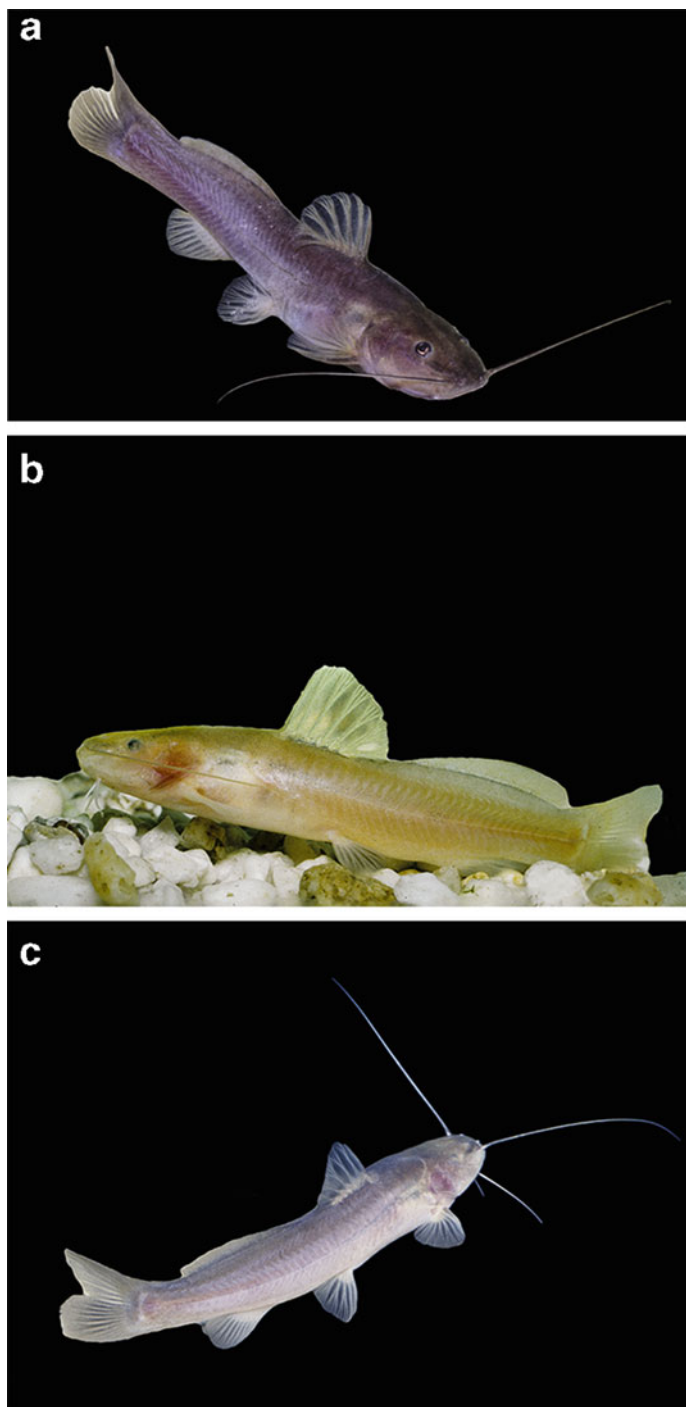


Fig. 2.7 The night-active troglophile surface catfish *Rhamdia laticauda* (a), and specimens of its eye- and pigment-reduced cave sister species *R. zongolicensis*. Cave specimens kept in permanent darkness (b) or in light (c), when dark pigmentation reappears

sea has regressed, adapt to live in the fresh water now filling the former anchialine caves. Fossil coast lines of no-longer extant oceans are still detectable today because of the geographical position of such caves.

Cave animals are completely cut off from light as a mode of energy and information. Unlike in fossorial mammals, cave animal evolution proceeds in continuous absolute darkness and is for several reasons extraordinary. In addition to the regression of eyes and black body pigmentation, many other traits including behavioural ones may get reduced. Simultaneously, adaptive traits are constructively improved.

In general, the common ancestors of cave species are night-active forms, so-called troglaphiles, which are preadapted to cave life because of already having acquired and improved traits necessary to live in light-poor environments or to be active at night. For example, whereas among teleosts the diurnal characid fish (Characiformes) are only represented by three cave species, the mostly nocturnal catfish (Siluriformes) contain at least one third of the 151 cave fish species in total known today (Fig. 2.7) (Proudlove 2010). For such troglaphiles, life in light-poor or lightless environments is not extreme. They exhibit morphological, physiological, and behavioural adaptations by which they are able to find food and propagate. They are even active cave invaders. Thus, the process of rudimentation may start immediately after cave colonization and may proceed comparatively quickly because there is no need for constructive functional compensation. In cave colonizing species, usually no gradual substitution of function exists as, for example, can be assumed for locomotion between the regressing hind legs and the constructive tail fin in the evolution of whales. This is an almost unique characteristic of cave animals and might accelerate the tempo of eye or pigment regression in them. This may explain why cave descendants and their surface ancestors are often closely related sister species or forms that are still interfertile.

Cave-living species have evolved in almost every systematic group of animals and in almost every type of lightless habitat (Culver and Pipan 2009; Juberthie and Decu 1994; Culver and Wilkens 2000). They occur in marine or fresh water as well as in terrestrial environments. The only common abiotic factor they are submitted to is continuous absolute darkness. In the temperate zones, low energy supply very often plays a role as a second cave characteristic, but is often overestimated as an important requisite in the evolution of cave animals because many caves (in particular, tropical ones) are, as a rule, food abundant (Gnaspini and Trajano 2000; Fernandes et al. 2016).

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Evolution in the Dark

Darwin's Loss Without Selection

Wilkens, H.; Strecker, U.

2017, IX, 217 p. 107 illus., 59 illus. in color., Hardcover

ISBN: 978-3-662-54510-2