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Evolution

Darwin, the amphibians, and the natural selection

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Abstract

A critical review of Darwin's publications shows that he did not dissert much about amphibians, in comparison with the other tetrapods. However, in "*A Naturalist's Voyage round the World*", Darwin described for the first time several amphibian species and was surprised by their peculiar way of life, terrestrial or euryhaline. These amphibian observations around the world led Darwin to discuss evolutionnary notions, like developmental heterochronies or evolving convergences, and later to illustrate his famous natural selection theory. This is confirmed, for example, by the publication of "*On the Origin of Species*" where Darwin ironically questioned creation theory, trying to explain the absence of amphibians on oceanic islands. Lamarck also considered amphibians as relevant material to illustrate his theory of acquired character heredity. These historical uses of lissamphibians as evolutionary models have been mostly realized before any amphibian fossil discovery, i.e. out of a palaeontological context. ***To cite this article: J.S. Steyer, C. R. Palevol 8 (2009).***

Résumé

Darwin, les amphibiens et la sélection naturelle. Une revue des travaux de Darwin montre qu'il n'a pas trop disserté sur les amphibiens par rapport aux autres tétrapodes. Cependant, dans « *Voyage d'un naturaliste autour du monde* », Darwin décrit pour la première fois plusieurs espèces d'amphibiens, il est surpris par le mode de vie particulier de certains, terrestres ou euryhalins. Ses observations sur les amphibiens l'amènent à discuter de notions évolutives comme les hétérochronies du développement ou les convergences évolutives et à illustrer sa célèbre théorie de la sélection naturelle. Cela est confirmé par l'ouvrage « *l'Origine des espèces* » dans lequel Darwin, tentant d'expliquer l'absence d'amphibiens sur les îles océaniques, remet en cause ironiquement la théorie des créations indépendantes. Lamarck considérait également les amphibiens comme matériel adéquat pour illustrer sa théorie de l'hérédité des caractères acquis. Ces utilisations historiques des lissamphibiens comme modèles évolutifs ont été principalement effectuées avant toute découverte d'amphibien fossile, c'est-à-dire hors contexte paléontologique. ***Pour citer cet article : J.S. Steyer, C. R. Palevol 8 (2009).***

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Mots clés : Histoire des sciences ; Lissamphibiens ; Évolution ; Stégocéphales ; Lamarck ; Ontogénie

The year 2009 is a double anniversary for Charles Darwin; the famous British naturalist was born in 1809 (i.e. 200 years ago) and published his major book "*On the Origin of Species*" in 1859 (i.e. 150 years ago). It is a

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priori not so easy to celebrate Darwin by speaking about amphibian evolution only, because he did not dissert a lot about this group in comparison with the other tetrapods: he did observe amphibians during his travel around the world, on the *H.M.S. Beagle* (from 27 December 1831 to 2 October 1836, cf. [13]), but these observations remain rare compared with those related to reptiles. He also described amphibian species (e.g., [7]), but few compared with reptile and especially bird species. However, considering the rare amphibians he crossed during his travel around the world, Darwin observed and described some of them for the first time: this is the case of the famous "Darwin's frog" (*Rhinoderma darwinii*), an amazing small (3 cm long) anuran which raises its tadpoles inside the vocal sac of the male. This taxon is indeed named after Darwin because he firstly discovered the species in Chile and Argentina.

Before developing further the relationships between Darwin and amphibians, it is interesting to note that there are, in the literature, at least 36 living and fossil species literally called *darwinii* (subspecies and amphibians excluded); two protists (*Coccodiscus*, *Pediastrum*), one mushroom (*Cyttaria*), 16 plants (*Berberis*, *Gossypium*, *Maihueniopsis*, *Hoya*, *Eustephia*, *Lecocarpus*, *Senecio*, *Abutilon*, *Opuntia*, *Bonatea*, *Chaetomorpha*, *Tephrocactus*, *Calceolaria*, *Hymenophyllum*, *Nassauvia*, *Neosparton*), eight "invertebrates" (*Sapphirina*, *Cosmocalanus*, *Orchestia*, *Alleloplasis*, *Camponotus*, *Spirifer*, *Parahelops*, *Nettastomella*), two "fish" (*Marylina*, *Gephyroberyx*), three reptiles (*Liolaemus*, *Amphisbaena*, *Gymnodactylus*), three birds (*Rhea*, *Nothura*, *Tanager*) and one mammal (*Mylodon*).

Darwin observed and collected amphibians (mainly frogs and toads), mostly in South America. He was very surprised about the peculiar way of life of some of them, which were living in very different environments than those he used to observe before, in Europe: for example, the famous "Darwin's toad" ("*Phryniscus nigricans*" or *Melanophryniscus stetcheri* or *M. montevidensis*) (Fig. 1, center) is a small buffonid found by Darwin himself in the dunes of the sandy shore of Maldonado (Uruguay). This subterrestrial species does not really like water. Darwin, surprised to find a living individual in a very dry environment, put it in a pond but, as it was unable to swim, he needed to take it back out... "*At Maldonado, I found one in a situation nearly as dry as at Bahia Blanca, and thinking to give it a great treat, carried it to a pool of water; not only was the little animal unable to swim, but I think without help it would soon have been drowned*." ([13] pp. 101–102). Darwin attributed this bizarre amphibian's "terrestriality" to the capacity it has to store water in the bladder: "*I believe it is well ascertained that the bladder of the frog acts as a reservoir for the moisture necessary to its existence...*" ([13] p. 409).

But beyond the terrestriality of some amphibians, Darwin was more surprised by the euryhalinity of some of them: "*Leiuperus salarius*" (today *Pleuroderma bufonina* or *P. buffoni*) (Fig. 2, upper left) is indeed one of the rare living amphibians supporting salty waters. This amazing frog was first observed by Darwin at Port Désiré, Patagonia. Again, Darwin was surprised by its euryhaline habits "*it is reproducing and living in waters too salted to be drunk*" [4](Fig. 2).

This euryhalinity is very rare among living amphibians (lissamphibians), but it was more common among the fossil forms (e.g., stegocephalians). The amphibians (as nonamniotic tetrapods) emerged during the Late Devonian (if not during the Middle Devonian, [26]). It is now generally admitted that the first amphibians (e.g., *Ichthyostega*, *Acanthostega*) were mostly aquatic and euryhaline (e.g., [1,23]). This capacity to support high variations of salt concentrations within the body (which does not mean an obligatory life in a marine environment) could have been linked initially with polydactyly [27]: every fossil tetrapod showing more than five (true) digits (i.e., the Devonian amphibians, the Jurassic ophthalmosaurian ichthyosaurs and a Triassic marine reptile [28]) is indeed euryhaline (Fig. 3).

In living tetrapods, polydactyly is today exceptional but could still occur in lissamphibians, for example, and especially anurans (cf. prehallux, prepollex, e.g., [15]). However, morphogenetically speaking, it is often a pseudopolydactyly, i.e. the surnumerary "digit" is not a true digit, but is formed initially by dichotomy of a phalanx or a tarsal or carpal (e.g., [30]). However, even if most of the polydactylous living amphibians do not show any true extra digit like their Devonian relatives, this phenomenon was puzzling generations of naturalists, and Darwin himself, of course: "*Additional digits have been observed in negroes as well as in other races of man, and in several of the lower animals. Six toes have been described on the hind feet of the newt* (Salamandra cristata)*, and, as it is said, of the frog. It deserves notice from what follows, that the six-toed newt, though adult, had preserved some of its larval characters; for part of the hyoidal apparatus, which is properly absorbed during the act of metamorphosis, was retained*." ([9] p. 14). Interestingly, Darwin associated the occurrence of polydactyly with retention of larval characters in adults, i.e. paedomorphosis. He was, of course, aware of the works of his colleague (and strong defender) Ernst Haeckel (1834–1919), German embryologist who firstly created the terms "Ontogeny" and "Phylogeny" [17] to better

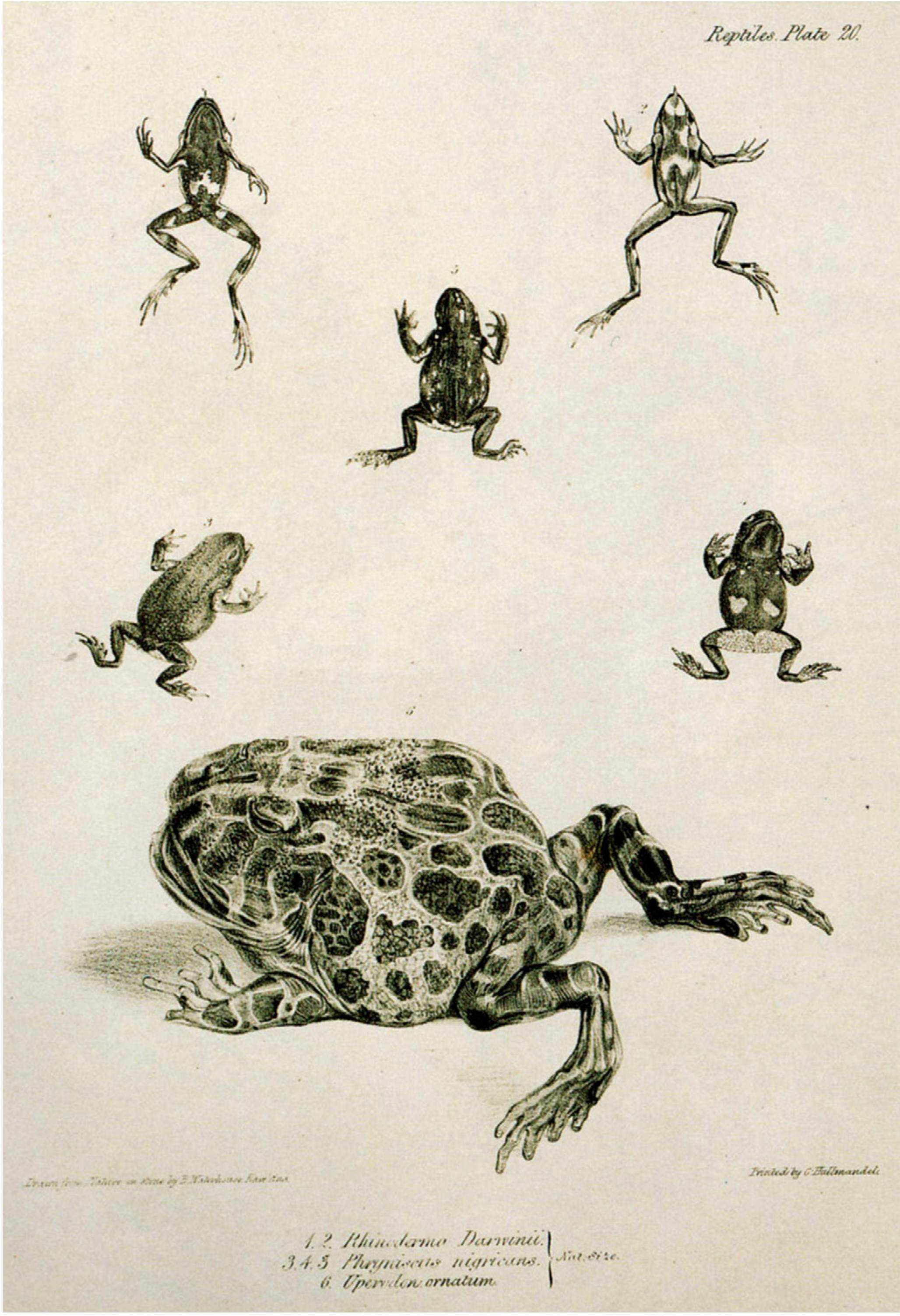

Fig. 1. Amphibian specimens collected by Darwin, [4] Plate 20, the "Darwin's toad" ("*Phryniscus nigricans*") center of the Plate. It is interesting to note that this Plate is titled "Reptiles" (upper right corner).

Spécimens d'amphibiens récoltés par Darwin [4]. *Pl. 20, le «crapaud de Darwin» («Phryniscus nigricans») au centre de la planche. Il est intéressant de noter que cette planche est intitulée «Reptiles» (coin droit en haut).*

Fig. 2. Amphibian specimens collected by Darwin, [4] Plate 18, the euryhaline frog "*Leiuperus salarius*", up left of the Plate. It is interesting to note that this Plate is titled "Reptiles" (upper right corner).

Spécimens d'amphibiens récoltés par Darwin [4]*. Pl. 18, la grenouille euryaline* « *Leiuperus salarius* »*, en haut à gauche de la planche. Il est intéressant de noter que cette planche est intitulée* « *Reptiles* » *(coin droit en haut).*

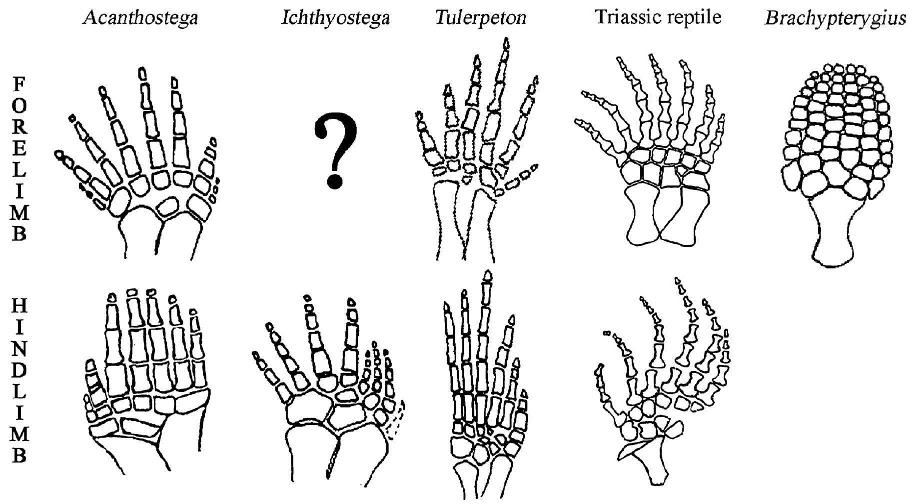

Fig. 3. Fore- and hindlimbs of the polydactylous fossil tetrapods; *Acanthostega* (Devonian of Greenland) has eight digits at the manus and seven at the pes [3]; *Ichthyostega* (Devonian of Greenland) has seven digits at the pes, its manus being unknown [1]; *Tulerpeton* (Devonian of Russia) has six digits at the manus and the pes [2]; a marine reptile (Triassic of China) has seven digits at the manus and six at the pes [28]; and the ophthalmosaurian ichthyosaur *Brachypterygius* (Jurassic of Germany) has six digits at the manus [24]. Only the polydactylous limbs are represented here (not to scale).
Membres antérieurs et postérieurs de tétrapodes polydactyles fossiles. Acanthostega (Dévonien du Groenland) a huit doigts à la main et sept au pied [3]*; Ichthyostega (Dévonien du Groenland) a sept doigts au pied, sa main étant inconnue* [1]*. Tulerpeton (Dévonien de Russie) a six doigts à la main et au pied* [2]*; un reptile marin (Trias de Chine) a sept doigts à la main et six au pied* [28]*; et l'ichthyosaure Brachypterygius (Jurassique d'Allemagne) a six doigts à la main* [24]*. Seuls les membres de polydactyles sont représentés ici (pas à l'échelle).*

study developmental heterochronies (reviewed in [16]). More importantly, the association made by Darwin of polydactyly (limb "supermorphology") and rentention of the hyoidal apparatus (cranial morphology) is very pionneering, because it is confirmed today by molecular genetics: it has, indeed, been shown recently that the limb and digit morphogenesis is controlled by the same *Hox gene* groups (of types *A* and *D*) as the craniofacial morphogenesis (e.g., [29]).

After South America, the *Beagle* took cape toward the West and reached the Galápagos Archipelago, the 15 September 1835. The Galápagos visit of Darwin (until October 1835) is very famous for his "discovery" of the very endemic fauna composed of marine iguanas (*Amblyrhynchus cristatus*), giant turtles (*Geochelone elephantopus*) and numerous finches (again, the famous "Darwin's finches" such as *Geospiza conirostris*). However, Darwin was also surprised by the total absence of amphibians, despite humid and temperate upland forests on the Archipelago which could have well suited them. He opposed this amphibian absence with the reptile abundance on the oceanic islands, particularly of lizards that he considered a priori as similar morphotypes occupying the same ecological niches. Darwin indeed wrote (1890, p. 408): "*The absence of the frog family in the oceanic islands is the more remarkable, when contrasted with the case of lizards, which swarm on most of the smallest islands. May this difference not be caused by the greater facility with which the eggs of lizards, protected by calcareous shells, might be transported through salt-water, than could the slimy spawn of frogs*?" His ecological hypothesis, therefore, suggests that reptiles, thanks to their amniotic reproduction mode, benefit from a higher capacity of oceanic spreading than that of amphibians (as nonamniotic tetrapods). Following the systematic distinction between the classes Reptilia and Amphibia proposed by De Blainville [14], Darwin therefore put forward this higher spreading capacity of the reptiles which a priori involved a strong competition pressure on this poor amphibian oceanic distribution. Speaking about pressure, it is therefore possible that amphibians also correspond, for Darwin, to an inspiration source which might help him to write, later, his natural selection theory [8].

Darwin was therefore surprised by the wonderful amphibian world he discovered around the globe: he mentioned, for example, the extreme climbing hability of some specimens (Fig. 4) he collected in Rio de Janeiro from May to June 1832: "*I had some difficulty in catching a specimen of this frog. The genus* Hyla *has its toes terminated by small suckers; and I found this animal could crawl up a pane of glass, when placed absolutely perpendicular*." ([6] footnote p. 33). He also enjoyed lis-

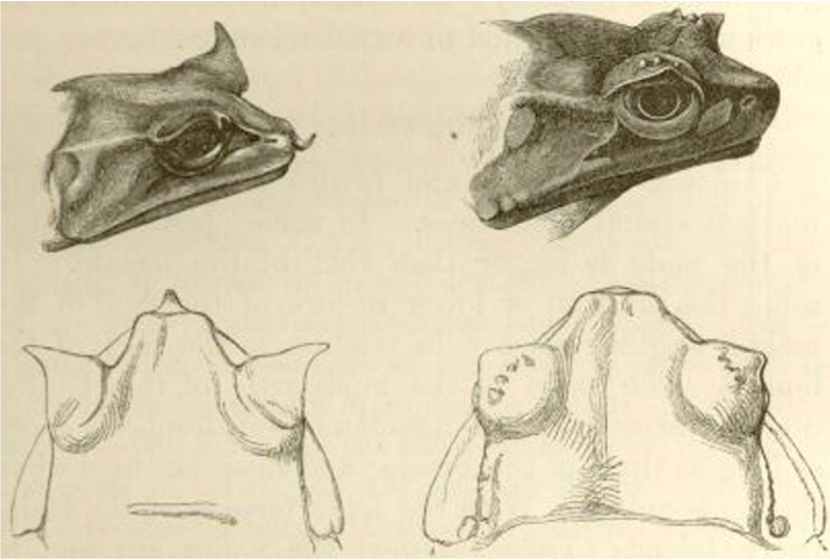

Fig. 4. *Megalophrys montana*, head of the male (left) compared with the female (right), observed by Darwin (from [6] p.27, fig. 32).
Megalophrys montana, tête de mâle (à gauche) comparée à celle de la femelle (à droite), observée par Darwin (d'après [6]*, p.27, fig. 32).*

tening to the songs of the males during the reproduction period and even discussed later, in his second major book entitled "*The descent of man, and selection in relation to sex*" (1871), about this sexual communication between males and females: "*These animals, however, offer one interesting sexual difference, namely in the musical powers possessed by the males [. . .]; certain frogs sing in a decidedly pleasing manner. Near Rio de Janeiro I used often to sit in the evening to listen to a number of little* Hylæ, *which, perched on blades of grass close to the water, sent forth sweet chirping notes in harmony.*" ([10] p.27) (Fig. 4).

Observing the terrestrial habit of *Melanophryniscus* (see above), he was also very surprised by its very colorful, flashy skin, black with flams of vermilion. Darwin ([13], p. 101) wrote, almost poetically: "*If it had been an unnamed species, surely it ought to have been called* Diabolicus, *for it is a fit toad to preach in the ear of Eve*." Beyond poetry, Darwin pointed out the repulsive look of this amphibian and therefore the ecotrophic notion of passive defense. . . As for the active defense of the amphibians, Darwin made interesting observations (and experiments) on these animals once he had returned to Great-Britain, in the Zoological Gardens, from October 1836: the capacity of some frogs and toads to inflate their body in front of predators is carefully reported in his book "*The expression of the emotions in man and animals*" (1872): "*When frogs are seized by snakes, which are their chief enemies, they enlarge themselves wonderfully; so that if the snake be of small size [. . .], it cannot swallow the frog, which thus escapes being devoured*." ([11] p. 105). Whether passive or active, this self-defense notion in animals which represent possible prey for others, is therefore related in the natural selection theory of Darwin.

Darwin made also interesting comparisons during his stay at Maldonado (Uruguay), from July 26, 1832, where he collected many mammals and compared the blindness rodent *Ctenomys brasiliensis* ("tuco-tuco") with the *Spalax* (the "mole rat") and with the famous urodel called *Proteus*. He wrote: "*Considering the strictly subterranean habits of the tuco-tuco, the blindness, though so common, cannot be a very serious evil; yet it appears strange that any animal should possess an organ frequently subject to be injured. Lamarck would have been delighted with this fact, had he known it, when speculating (probably with more truth than usual with him) on the gradually*-acquired *blindness of the Aspalax [as* Spalax], *a Gnawer living under ground, and of the* Proteus, *a reptile living in dark caverns filled with water; in both of which animals the eye is in an almost rudimentary state, and is covered by a tendinous membrane and skin*." ([13] p. 53). It is interesting to note that:

- Darwin cited Lamarck and his "*Philosophie Zoologique*" (see below), but he also strongly criticized him (cf. the parentheses): Darwin deliberately put the word "acquired" in italics in his text, by reference to the evolutionnary theory of the acquired character heredity of Lamarck he questioned (see also [12] for a discussion about progressive reduction of structures);

- the urodels were still classified among reptiles, and not among amphibians (*contra* the anurans, as mentioned above). However, beyond this systematical consideration, the comparison of Darwin between tetrapods being phylogenetically very distant (two mammals and one urodel) and showing a similar way of life (underground and blindness) is relatively precursor because it announced the notion of evolving convergence (but see also the Lamarck literature below). In consequence, it seems more and more that amphibians, as study material for Darwin, could have played a major role in the emergence of his evolutionnary theory. This idea is confirmed later, in "*On the Origin of Species*", in which Darwin ([8], p.411) ironically asked why the theory of independant creation does not allow to explain the absence of living amphibians on oceanic islands: "*This general absence of frogs, toads, and newts on so many oceanic islands cannot be accounted for by their physical conditions; indeed it seems that islands are peculiarly well fitted for these animals [. . .]. But as these animals and their spawn are known to be immediately killed by sea-water, on my view we can see that there would be great difficulty in their transportal across the sea, and therefore why they do not exist on any oceanic island. But why, on the theory of creation, they should not have been created there, it would be very difficult to explain*."

As mentioned above, Darwin ([13], p. 53) cited Lamarck. This allows me an interesting transition to discuss now about the relationships between Jean-Baptiste Lamarck (1744–1829) and amphibians. We are all aware that the year 2009 is a double anniversary for Darwin: everybody (especially the English speaking world) is celebrating the British naturalist, but one also need to celebrate the French one, who never read "*On the Origin of the Species*" but who published his major book "*Philosophie Zoologique*" in 1809 (Darwin's year of birth), two centuries ago.

Before Darwin, and thanks to amphibians (which were classified among reptiles at that time), Lamarck already had observed in 1802 that characteristics (i.e., gills and lungs) used in systematics to define two classes (Fish and Reptiles, respectively) are also visible during an anuran life: « *Ainsi, non seulement la nature passe des branchies aux poumons dans des classes et dans des familles voisines comme l'indique la considération des poissons et des reptiles mais elle y passe même pendant l'existence d'un même individu, qui jouit successivement de l'un et de l'autre système. On sait que la grenouille dans l'état imparfait de têtard, respire par des branchies, tandis que dans son état plus parfait de grenouille elle respire par des poumons*. » ([21] p. 43) ("In this manner, nature is passing from gills to lungs in classes and in families which are close, as indicated by the consideration of fish and reptiles, but it is also passing even during the life of a single individual, which benefits successively to one and to the other system. One knows that the frog, in the imperfect stage of the tadpole, is breathing with gills, whereas, in its more perfect stage of the frog, is breathing with lungs."). In other words, amphibian development, according to Lamarck, summarizes the tetrapod classification. This very interesting "evo-devo" remark was developed later by Lamarck himself in "*Philosophie Zoologique*" ([22], p. 245) but also by Haeckel [17] in his famous "*biogenetic law*" or his recapitulation theory ("ontogeny is a [. . .] recapitulation of the phylogeny [. . .]").

Lamarck based his theory of acquired character heredity partly on amphibians: he illustrated his adaptationism by morphological characteristics such as the interdigital membranes of frogs: « *Les mêmes efforts faits pour nager, c'est-à-dire, pour pousser l'eau, afin d'avancer et de se mouvoir dans ce liquide, ont étendu de même les membranes qui sont entre les doigts des grenouilles, des tortues de mer, de la loutre, du castor, etc.* » ([22] p.249). ("The same efforts made to swim, that is to say, to push water, in order to go forward and to move in this liquid, have extended as identical the membranes which are between the digits of frogs, of sea turtles, of the otter, of the beaver, etc."). Interestingly, Lamarck compared different and distant aquatic tetrapods showing the same swimming structure. This comparison is very pioneering, because it announced the notion of evolving convergence, as Darwin did later (see above). In his multiple comparisons, Lamarck was also aware of the ectothermism versus the endothermism which marks the difference between reptiles (incl. the "amphibious" – for the amphibians – at that time) and birds. He wrote: « *[. . .] et on verra, par exemple, que dans les amphibies où l'action organique est lente et pénible, puisque ces animaux, comme le crapaud, les serpents, etc., digèrent avec beaucoup de lenteur, la tendance à la décomposition s'effectue aussi très lentement ; de sorte que ces êtres animés font peu de pertes : aussi ont-ils peu de besoins. Les oiseaux offrent des faits très différens [. . .]* » ([20] p.218) ("[. . .] and one shall see, for example, that in the amphibious where the organic action is slow and difficult, as these animals, such the toads, the snakes, etc., are digesting with a lot of slowness, the tendency to the decomposition is also made very slowly; in consequence these animated beings are making few losses:

they have also few needs. Birds show very different traits [...]").

At the time of Lamarck (1744–1829), almost no fossil amphibian (stegocephalian) record was published. In fact, the first stegocephalian to be described was the large temnospondyl *Mastodonsaurus* from the Triassic of Germany, published by Jaeger in 1828 ([19], p.35), the year before the death of Lamarck (although Damiani [5], mentioned a possible previous reference; [18]). The fossil specimens of *Mastodonsaurus* described by Jaeger were considered as fossil reptiles but were also compared (cf. *Salamandroides* [19] p.38) with *Salamandra* Daudin, 1803 (as *Cryptobranchus*), the giant salamander living in North America. *Mastodonsaurus* is no longer considered as ancestor of the (giant) urodels, it belongs to the stereospondyls, an extinct group of advanced temnospondyls mostly known in the Mesozoic, until the Cretaceous. However, some Palaeozoic representatives of temnospodyls could be more related to lissamphibians (as modern or living amphibians) but this is still much debated (e.g. [25])... Whatever their origin, since Lamarck and Darwin, the lissamphibians, therefore, played a major role in the conceptualization of evolutionary models.

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