

REVIEW

Darwin, Haeckel, and the “Mikluskan gas organ theory”

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Abstract

A previously unknown reference to the Russian ethnologist, biologist, and traveler Nikolai N. Miklucho-Maclay (1846–1888) was discovered in correspondence between Charles Darwin (1809–1882) and Ernst Haeckel (1834–1919). This reference has remained unknown to science, even to Miklucho-Maclay's biographers, probably because Darwin used the Russian nickname “Mikluska” when alluding to this young scientist. Here, we briefly outline the story behind the short discussion between Darwin and his German counterpart Haeckel, and highlight its importance for the history of science. Miklucho-Maclay's discovery of a putative swim bladder anlage in sharks, published in 1867, was discussed in four letters between the great biologists. Whereas, Haeckel showed enthusiasm for the finding because it supported (his view on) evolutionary theory, Darwin was less interested, which highlights the conceptual differences between the two authorities. We discuss the scientific treatment of Miklucho-Maclay's observation in the literature and discuss the homology, origin, and destiny of gas organs—swim bladders and lungs—in vertebrate evolution, from an ontogenetic point of view. We show that the conclusions reached by Miklucho-Maclay and Haeckel were rather exaggerated, although they gave rise to fundamental insights, and we illustrate how tree-thinking may lead to differences in the conceptualization of evolutionary change.

KEYWORDS

ancestor, Chondrichthyes, embryogenesis, homology, respiratory system, swim bladder

1 | MIKLUCHO-MACLAY IN JENA AND THE CANARY ISLANDS

In October 1865, after spending time as a student at the universities of Heidelberg and Leipzig, the later famous ethnologist Nikolai N. Miklucho-Maclay moved to Jena in Germany. He enrolled in the Medical Faculty of Jena University and, between 1866 and 1868, studied zoology and anatomy under Ernst Haeckel and Haeckel's senior colleague Carl Gegenbaur (1826–

1903). During this time, Miklucho-Maclay became Haeckel's assistant^{1,2} and also attended lectures given by both Haeckel and Gegenbaur. His detailed and well-illustrated lecture notes are kept in the archive of the Russian Geographical Society (RGO) in St. Petersburg.^{3–6} This was exactly the time when Haeckel became a staunch defender and promoter of Darwinism, his public lectures and writings bringing the theory of evolution to the attention of other scientists in Germany and elsewhere on the continent. In

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particular, Haeckel's 1866 double-volume foundational opus, the *Generelle Morphologie*, presented his version of Darwinism, along with his own research methods, in explicit detail.⁷

Between November 1866 and April 1867, Miklucho-Maclay accompanied Haeckel on his research expedition to the Canary Islands (Figure 1). The main objective of the expedition was to study sponges and the brains of cartilaginous fishes from the island of Lanzarote.⁸ Remarkably, this expedition took place after Haeckel had visited Charles Darwin at Down House on October 21, 1866,⁹ and it is likely that Miklucho-Maclay was fully informed about this historical event. For Miklucho-Maclay, the Canary Island studies resulted in a publication in German on the comparative neurology of vertebrates, wherein he applied the descriptive techniques and research methods acquired in Jena.¹⁰

This joint expedition is of special importance because it brought Haeckel and Miklucho-Maclay into very close contact, making the latter into Haeckel's close associate for a while. In 1869, Miklucho-Maclay returned to Russia

and, in 1870, began preparing his first expedition to Polynesia.⁸ In 1871, however, Miklucho-Maclay broke all communication with Haeckel. One of the possible reasons for their alienation from each other was their growing disagreement over the nature of the human race.¹¹ The very last letter to Haeckel, signed with the name Miklucho-Maclay, was written by his Australian widow Margaret after he died in 1893. In this letter, written in English, she assured Haeckel that Miklucho-Maclay held "deepest feelings of esteem and regard" toward Haeckel and called him Haeckel's "old friend in science."¹¹

Back in St. Petersburg, in 1869, Miklucho-Maclay began the preparations for his expedition to New Guinea by submitting his initial plan to the Imperial RGO. In the same year, he received a research grant from the RGO and permission from Tsar Alexander II to join the corvette *Vitjaz* (Knight) to travel to New Guinea.⁸ Before his departure, Miklucho-Maclay visited Jena one more time (1869 to 1870) to finalize the publication of his anatomical monograph on shark brains.¹⁰ He also spent some time in Berlin, Leiden, Rotterdam, Brussels, and London

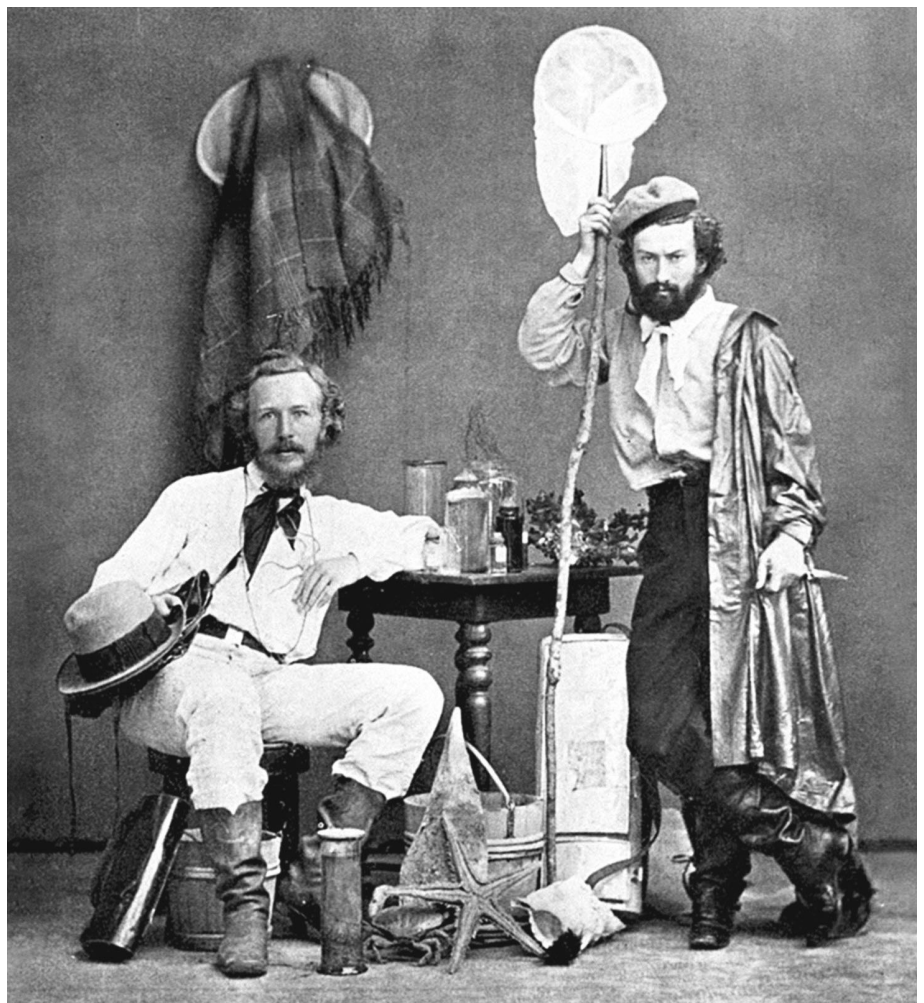


FIGURE 1 Ernst Haeckel (sitting) and Miklucho-Maclay before their trip to Canary Island (Lanzarote) in 1866 (Russian Geographical Society, RGO, St. Petersburg). Haeckel sent a copy of this photo to Darwin, who replied that "[t]he photograph is so good that it is like having you in the room" (see cited letters 5840 and 5841).

to strengthen scientific cooperation with leading scholars. In October 1870, he presented his detailed ethnological research program to the RGO, and at the end of the same month, he left for New Guinea.

2 | MIKLUCHO-MACLAY'S DISCOVERY OF THE SWIM BLADDER IN SHARKS

While on the Canary Islands, in 1867, Miklucho-Maclay dissected specimens from different chondrichthyan taxa.¹² Chondrichthyes, or cartilaginous fishes, are thought to represent a monophyletic clade that forms the sister group to all other jawed vertebrates (Gnathostomata). These fishes secondarily lost their bones in their evolutionary past¹³ and are subdivided into Holocephali (chimeras) and Elasmobranchii. The latter consists of sharks (Selachii) as well as rays, incl. skates and sawfish (Batoidea).¹⁴ Compared to all other living gnathostome fish, Chondrichthyes lack a swim bladder. While the swim bladder in other fish usually functions to control buoyancy, the Chondrichthyes are considered to use their large, oily liver as a buoyancy organ.¹⁴

For his famous study on the swim bladder, Miklucho-Maclay dissected shark (Selachii) specimens of the spiny dogfish *Squalus acanthias* (previously "*Acanthias vulgaris*"), the school shark *Galeorhinus galeus* (previously "*Galeus canis*"), and the smooth-hound shark *Mustelus*. He discovered "rudiments of a swim bladder" in embryos and also in adults of these sharks; this organ was previously unrecorded for these species (Figure 2).¹² In one unidentifiable "*Acanthias*" species native to the Canary Islands, he found only a thickening of the mucosa where the organ would be located. Among species of Batoidea, namely in the rays *Raja* (Rajidae), *Torpedo* (Torpedinidae), and *Dasyatis* (previously "*Trygon*," Dasyatidae), he did not find any such rudiments in embryos or adults.

The swim bladder is an unpaired organ formed dorsally in the posterior pharynx, which is only found in Actinopterygi [sic] (Figure 3), a group of bony fishes that includes sturgeons (Acipenseridae), paddlefish (Polyodontidae), gars (Lepisosteiformes), bowfins (Amiiformes), and teleosts (Teleostei). All other osteognathostomes, including bichirs (Polypteriformes), coelacanths (Coelacanthiformes), lungfishes (Dipnoi), and land vertebrates (Tetrapoda), have lungs, which are paired organs originating ventrally in the posterior pharynx. Compared to lungs, swim bladders rarely show a respiratory function and are mainly used for buoyancy and communication.¹⁵ Ontogenetically, the swim bladder forms dorsally from the posterior pharynx via a tube, the so-called ductus pneumaticus. This duct may persist into adulthood (physostome state;

Figure 3) or be reduced, leaving a discrete and separate gas bladder (physoclist state). Among Actinopterygi [sic], the swim bladder is reduced in taxa living in the deep sea where water pressure is high, and in highly pelagic taxa, where such an organ would have a perturbing effect.¹⁶ A pelagic lifestyle is also present in certain chondrichthyans.

The presence of the "swim bladder rudiment" in sharks was explained by Miklucho-Maclay along Darwinian lines. He related the organ to a "perfect state" (German: "*vollkommener Zustand*"), which could only be observed in the phylogenetically more advanced bony fishes (Osteognathostomata). There would be two possible ways of finding the "perfect state" of the organ in question¹⁷; it could either be found at a higher organizational level, that is, in the phylogenetic future, or it could be found in the ontogenetic or phylogenetic past of the individual, namely in embryos or the fossil record.

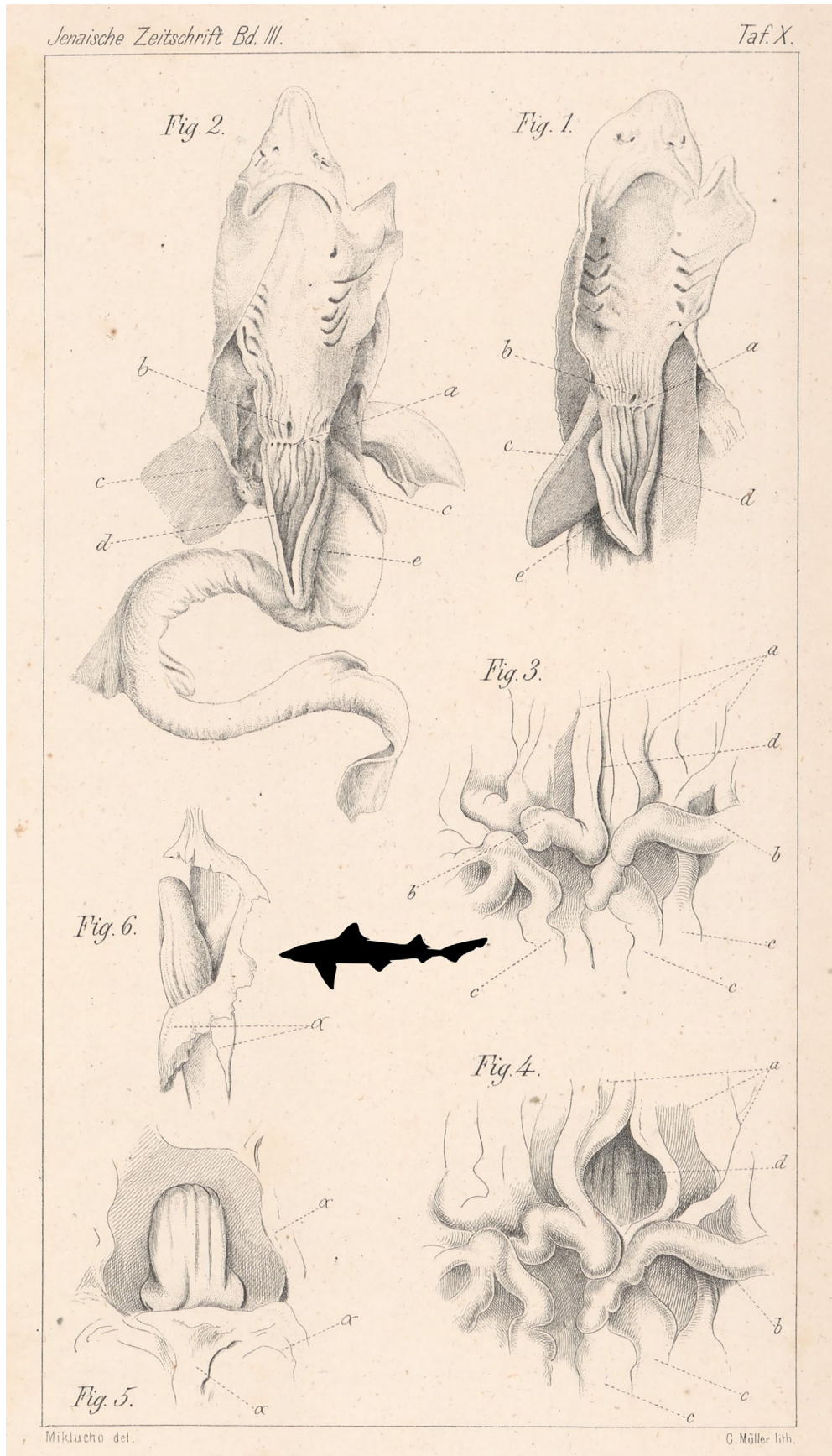
In the case of sharks, according to Miklucho-Maclay,¹² the presence of a swim bladder rudiment resulted from the phylogenetic past. It could be expected in sharks, because fully developed swim bladders would have existed in earlier gnathostome ancestors, further down the phylogenetic tree. It would be inherited but not develop fully, based on processes of partial formation and regression. In that sense, Miklucho-Maclay¹⁸ applied the Darwinian theory of rudiments to the special case of swim bladders in sharks. He hoped that his discovery would contribute to the understanding of phylogenetic history in general, as sharks play an important role in this history. Haeckel and Miklucho-Maclay believed that sharks were a perfect model for understanding the origin of gnathostomes, and the discovery of the putative swim bladder rudiment supported their view on unifying anatomy in which a swim bladder is part of the original vertebrate "*bauplan*." This has important consequences in the determination of character polarity, as discussed further below.

3 | A PROMINENT CORRESPONDENCE ON MIKLUCHO-MACLAY'S STUDY ON THE SWIM BLADDER

In an undated letter to Darwin (Darwin Correspondence Project, Letter 5840)* that was written before the reply on February 6, 1868, Haeckel referred to the discovery made by Miklucho-Maclay in 1867 during their joint expedition to the Canary Islands.¹² To our knowledge, this reference

*Darwin Correspondence Project, "Letter no. 5840," accessed on April 25 2023, <https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-5840.xml>

FIGURE 2 Figure plate of Miklucho-Maclay article in 1867.¹² Translated legend as follows: fig. 1: *Galeorhinus* (“*Galeus*”) *canis* embryo of a length of 15 cm (based on a photograph). Esophagus and stomach opened from the front. (A) Border between esophagus and stomach (cardia). (B) Opening of the swim bladder rudiment. (C) Liver. (D) Stomach. (E) Gut. The fig. 2: *Mustelus* (?) [sic!] embryo of a length of 18 cm (based on a photograph). Same labels as in fig. 1. The figs. 3 and 4: Swim bladder rudiment of *Galeorhinus* (“*Galeus*”) *canis* (youngest most specimen), much enlarged. (A) Fine elongated fold of the esophagus. (B) Bordering folds between the esophagus and the stomach. (C) Mucosa epidermal folds of the stomach. (D) Opening of the swim bladder rudiments, in fig. 4 showing the cleft in natural position, in fig. 5, the edges are stretched away from each other. The figs. 6–8: Posterior and lateral views of the same swim bladder (as in figs. 4 and 5). (A) Removed muscularis [layer] of the intestinal [gut] tube. Silhouette added (see Acknowledgments for reference).



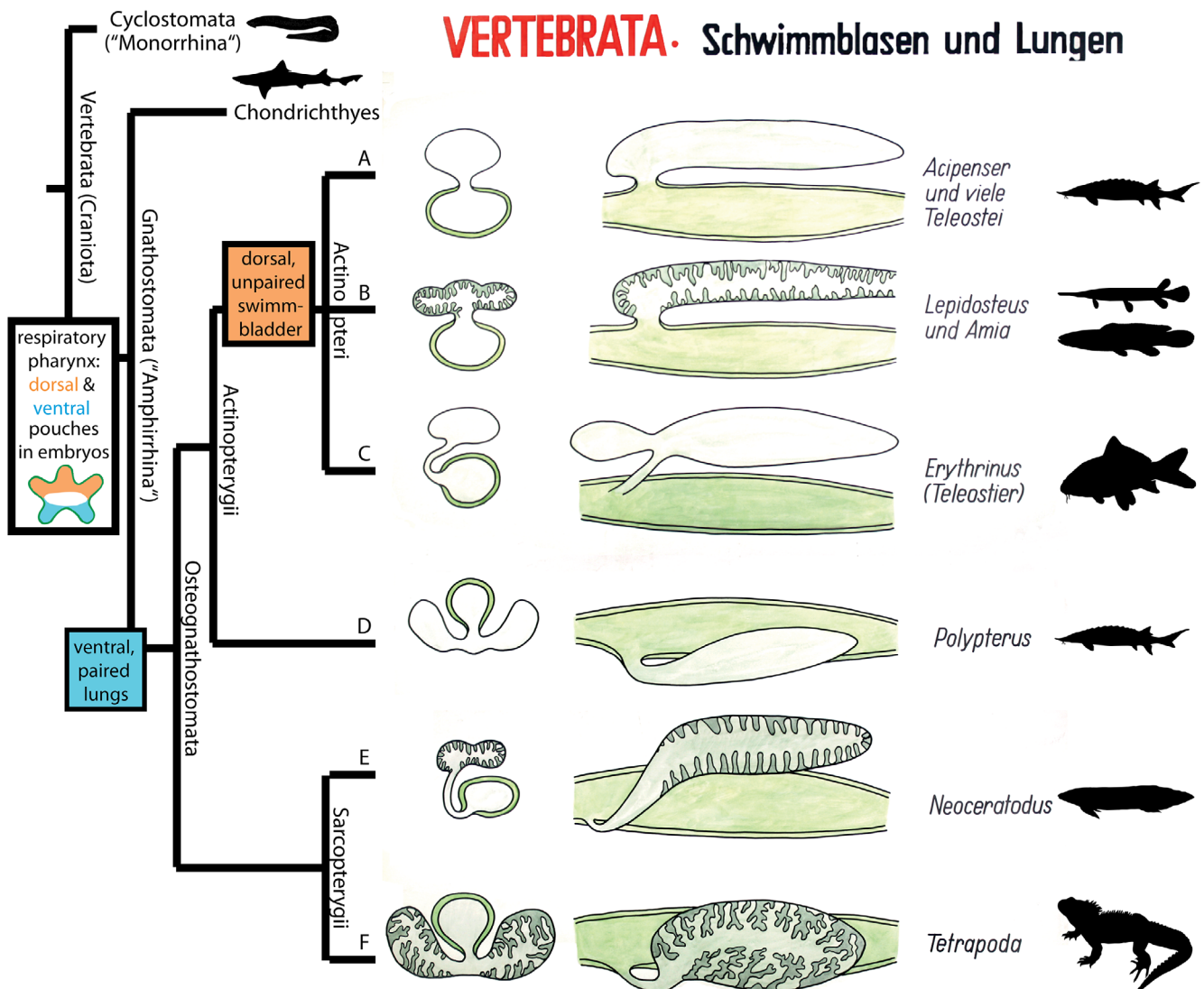


FIGURE 3 Evolution of the “swim bladders and lungs” [Schwimmblasen und Lungen] in Vertebrata with character distribution and modern phylogeny as argued by Lambertz and Perry in 2015.²¹ Anatomical diagrams of the respiratory apparatus are modified from wall chart “C 338” of Zoologisches Institut in Tübingen/Germany (drawn by artist Heiner Bauschert in the 1950s), with the institute’s permission. Cyclostomata is illustrated by the lamprey (*Petromyzon marinus*) and Chondrichthyes by Miklucho-Maclay’s smooth-hound *Mustella*. (A) The sturgeon *Acipenser* “and many teleosts [und viele Teleostei]”; (B) the gar *Lepidosteus* “and” [und] the bowfish *Amia calva*; (C) the trahira *Erythrinus* (silhouette shows the carp *Cyprinus caprio*); (D) the bichir *Polypterus*; (E) the Australian lungfish *Neoceratodus forsteri*; (F) terrestrial vertebrates (Tetrapoda) with a silhouette of the tuatara *Sphenodon punctatus*. The Haeckelian taxonomic terms are added in quotation marks. For silhouette credits see Acknowledgments.

was not recognized in the literature until now (see also below). Haeckel wrote: “My assistant and companion on the trip to the Canary Islands, [the] talented young Russian *Miklucho*, greatly works on the phylogeny of vertebrates. At Lanzarote, he made a nice discovery, namely that *selachians* have a rudiment of a *swim bladder*, which is very important for the phylogenetic tree of vertebrates and for the fact that the anlage of the lung emerged from the swim bladder [...]” (our translation, italics as in the Project’s webpage). Haeckel was excited about Miklucho-Maclay’s discovery as it supported his hypothesis that

Selachii were the ancient progenitors of the so-called Amphirrhina (German: “Paarnasen”), an idiosyncratic Haeckelian clade describing organisms possessing a sympathetic nervous system and a paired olfactory organ, and approximately corresponding to Gnathostomata (jawed vertebrates) in today’s terms—Monorrhina, in the opposite, would be the cyclostomes (hagfish and lamprey).¹⁹

Haeckel deemed Miklucho-Maclay’s discovery so important that, as mentioned in the letter, he asked the Darwinist Thomas Henry Huxley (1825–1895) to send a copy of Miklucho-Maclay’s publication to Darwin.

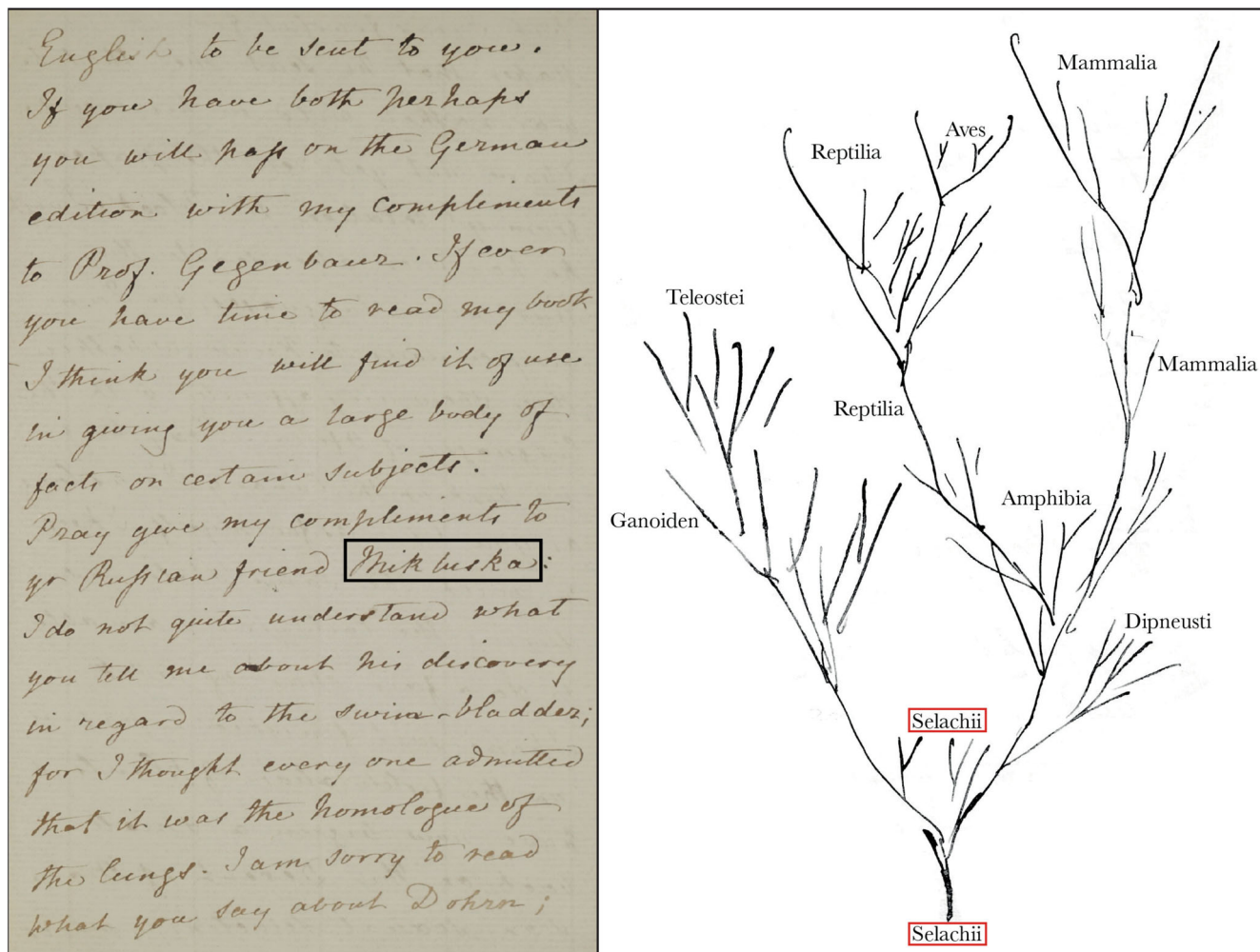


FIGURE 4 (A) A part of Darwin's letter to Haeckel dated February 6, 1868 (Darwin Correspondence Project, Letter 5841), where Darwin mentioned "Mikluska" (courtesy of Ernst-Haeckel-Haus Jena). The shown fragment of the letter is from a page which has an original width of 25.2 cm and a height of 20.2 cm. (B) Drawing of a tree referring to the origin of gnathostome vertebrates illustrating how Haeckel understood Selachii first as the ancestors to all gnathostomes (his "Amphirrhina") and second as extant taxon. Note the paraphyly of extant selachians. The tree is found in the response letter from Haeckel to Darwin dated March 23, 1868. Modified from: Darwin Correspondence Project, "Letter no. 6040".

Darwin was less excited about Miklucho-Maclay's discovery, as evidenced in his written reply to Haeckel on February 6, 1868 (Darwin Correspondence Project, Letter 5841),[†] which is stored in the Ernst Haeckel Archive in Jena, Germany (Figure 4A). He reduced its significance to just another additional proof that lungs and swim bladders would be homologous structures. Darwin wrote: "Pray give my compliments to y[ou]r Russian friend Mikluska: I do not quite understand what you tell me about his discovery in regard to the swim bladder; for I thought everyone admitted that it was the homologue of the lungs." This prominent mention of Miklucho-Maclay

was not even known to his biographers,²⁰ probably due to Darwin's friendly use of a Russian nickname.

The homology of the swim bladder and lungs was only disputed sometime after Miklucho-Maclay's discovery, which inspired numerous anatomical and ontogenetic observations.^{21,22} Historical arguments for the homology of both organs were critically summarized by W. Wassnetzov (also known as Wassnezow) in 1932²³ as follows:

1. There is a transient functionality of both organs with hydrostatic (e.g., some amphibians) as well as respiratory (e.g., some fish) characteristics.
2. Some intermediate forms are present in lungfishes (Dipnoi) and bichirs (*Polypterus*), meaning that the position of the gas organ is not strictly dorsomedial (swim bladder) or ventrolateral (lung).

[†]Darwin Correspondence Project, "Letter no. 5841," accessed on April 25 2023, <https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-5841.xml>

3. The ductus pneumaticus of the swim bladder does not always lie strictly dorsomedially on the posterior pharynx in many taxa.

The latter two observations on transient positioning can be explained easily by the spatial pressure of the yolk that secondarily, and only temporarily, pushes the dorsal swim bladder into a more lateral position (discussed in detail by Steven F. Perry²²). Also, the first observation of the transient functionality of both organs can be explained by secondary adaptations of existing organs to a new environment, such as a secondary aquatic milieu in tetrapods. As both organs derive from the posterior pharynx, which originally clearly has a respiratory function,²⁴ and there is a tube connecting the pharynx to the swim bladder (in the case of physostome taxa), a functional adaptation to gas exchange is not surprising.

Nevertheless, only recently has a certain consensus appeared in the literature thanks to a better understanding of the phylogenetic relationships between major vertebrate groups, the taxonomic distribution of these character complexes, and the physiology of both organs.²² In their review of the homology of both organs, Markus Lambertz and Steven F. Perry²¹ cautiously refrained from providing a conclusion about homology, given that the genetics of the development of these two organs still need to be understood—which is critical when considering different levels of homology.^{25,26} However, on a structural level, the original opinion that the lung and the swim bladder, which never occur at the same time in one individual, could transfer into each other either by dorsad or ventrad shift, has been discredited, mainly by developmental observations. Both organs are indeed ontogenetically related to each other, but they distinguish as one or the other organ early in development. Much of this was envisioned by Wassnetzov in the 1930s,^{23,27} as outlined below (see also Figures 5 and 6).

In contrast to Darwin's assessment, Miklucho-Maclay¹² never discussed the homology of lungs and swim bladders. He focused on the swim bladder and the possible homology between this organ and the dorsal evagination (tube, pocket) that he found in sharks. He discussed, and promptly rejected, possible objections against his hypothesis. First, the tube-like rudiment found in sharks points in a rostral direction, whereas the typical swim bladder has a predominantly caudal orientation. He argued, however, that the swim bladders also have a small anterior portion in relation to the ductus pneumaticus, which would indicate a secondary posterior expansion of the originally anteriorly oriented tube, resulting in the typical swim bladder. As a side note, this explanation of Miklucho-Maclay might be further

supported by the presence of the anterior, hence ancestral, position of the rete mirabile, the blood capillary network enabling gas supply to the swim bladder. Extensive blood support of the “rudiment” was described by Miklucho-Maclay.¹²

A second objection related to the structural embedding of the tube. Whereas the swim bladder is fully or partly separated from the pharynx, the tube is confluent with it. Although the tube does not have its own muscular support and originates from the mucosa, Miklucho-Maclay¹² argued that it is embedded in the pharynx musculature anteriorly and is continuous with the (muscular) wall of the esophagus posteriorly. Thus, the tube is not just a fold inside the mucosa. With the tube's muscular embedding as a precondition, an evolutionary emergence of a swim bladder with its own musculature would be possible.

4 | HISTORICAL DISCUSSIONS ON MIKLUCHO-MACLAY'S OBSERVATIONS

When Paul Mayer, in 1894,²⁸ discussed the historical treatment of the swim bladder in fish, he recognized that, until the end of the 19th century, nobody apart from Miklucho-Maclay¹² had studied this organ system in any detail. Mayer²⁸ summarized that standard anatomical textbooks actually cited the discoveries of Miklucho-Maclay¹² but were always skeptical about the scientist's interpretation of his results.^{29–31}

Mayer²⁸ made his own dissections of different shark species, including embryos, and in the first instance, agreed with Miklucho-Maclay¹² that there is a dorsal pocket in the pharynx of *Mustelus laevis*, that is, an evagination of the mucosa above which, externally, musculature would expand smoothly. He also, however, made other pertinent observations summarized below.

1. The pocket is not a rudimentary organ in embryos and juveniles but is (at least in *Mustelus*) visible as a large and clearly recognizable organ in adults.
2. Moreover, in *Mustelus*, Mayer²⁸ found not only a dorsal pocket but also two ventral ones with similar specific anatomy (see Figure 5A).
3. As mentioned above, Miklucho-Maclay¹² stated that the rudiment was present in embryos and not in adults of what he called “*Acanthias vulgaris*,” but was preserved in adults of an unidentified “*Acanthias*” species from the Canary Islands. Mayer²⁸ dissected large and small specimens of Canary Island species, but never found such a pocket. Thus, he concluded

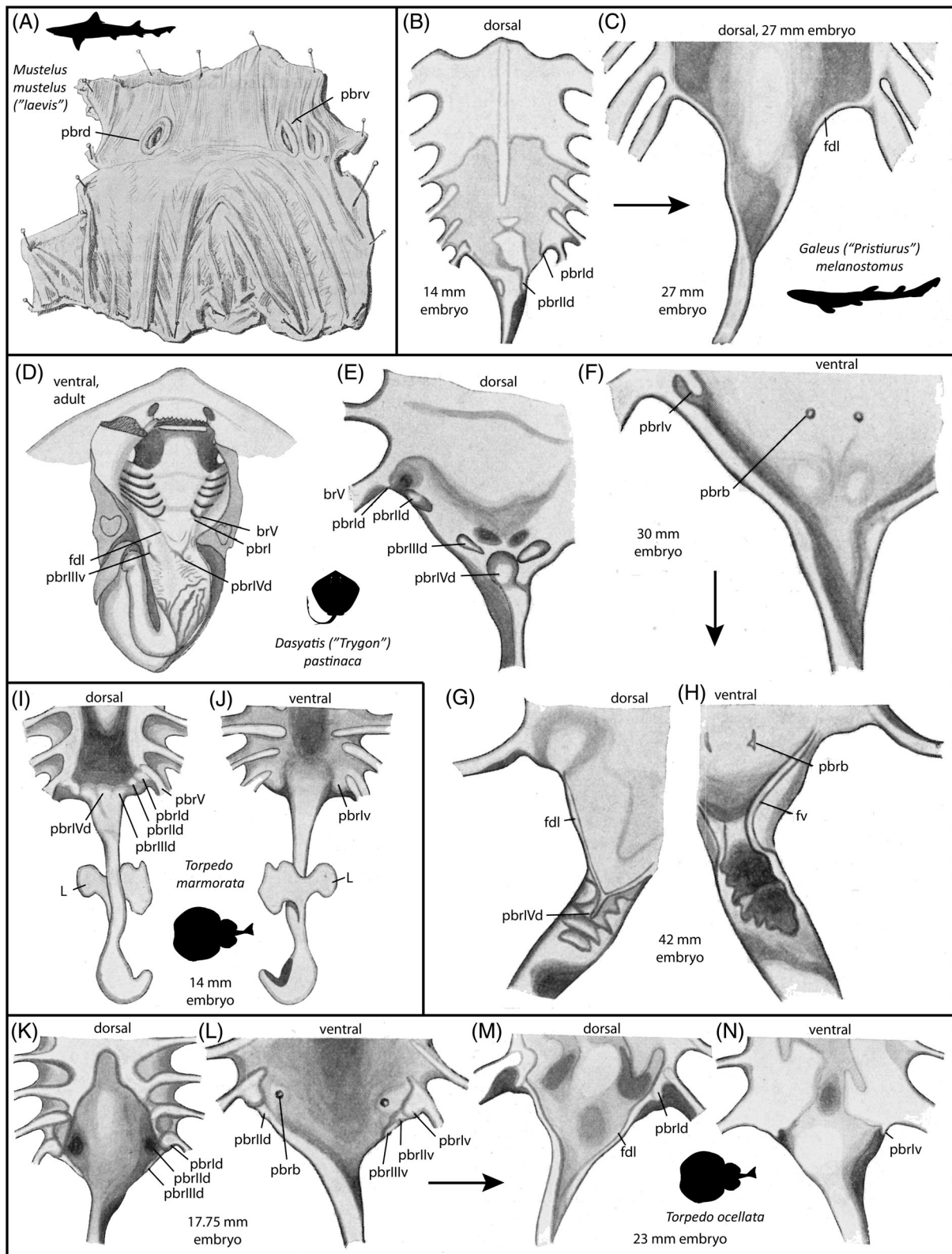


FIGURE 5 Embryogenesis of the swim bladder in Chondrichthyes. (A) after Mayer.²⁸ (B–N) after Wassnezow.²³ Arrows between ontogenetic stages. brV, fifth branchial pouch; fdl, dorsolateral fold of the posterior pharynx; pbrI, first postbranchial pouch; pbrId, dorsal part of the first postbranchial pouch; pbrIId, dorsal part of the second postbranchial pouch; pbrIIId, dorsal part of the third postbranchial pouch; pbrIVd, dorsal part of the fourth postbranchial pouch; pbrIV, ventral part of the first postbranchial pouch; pbrIIv, ventral part of the second postbranchial pouch; pbrIIIv, ventral part of the third postbranchial pouch; pbrb, postbranchial body; pbrd, dorsal part of a postbranchial pouch; pbrv, ventral part of a postbranchial pouch. For silhouette credits see Acknowledgments.

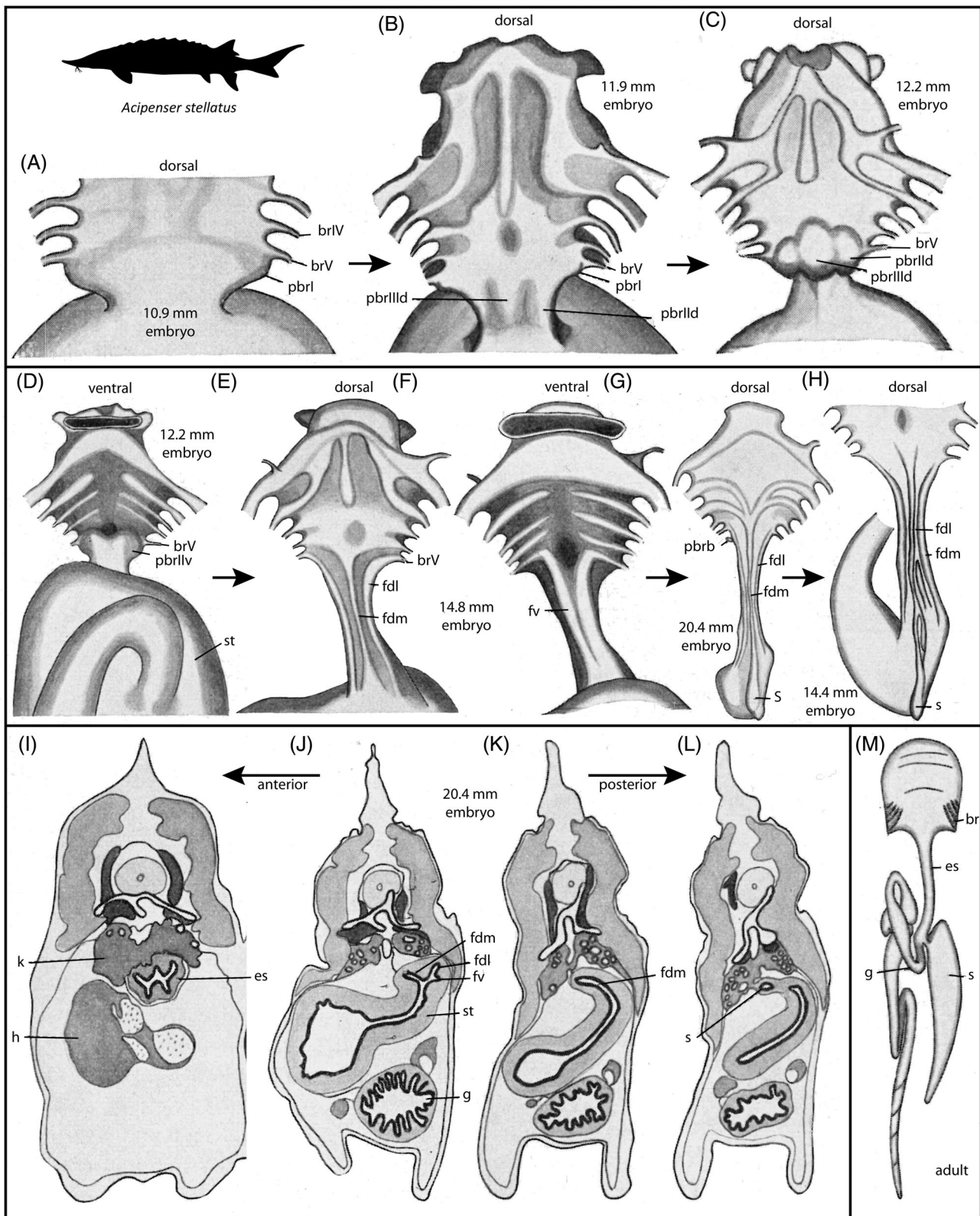


FIGURE 6 Embryogenesis of the swim bladder in *Acipenser stellatus*. (A–H) Ontogenetic stages are separated by arrows. (I–L) In this stage, arrows indicate the position of sections in the body. (M) Gut system of an adult specimen. Modified after Wassnezow.²³ br, branchial (gill) apparatus; brIV, fourth branchial pouch; brV, fifth branchial pouch; es, esophagus; h, heart and associated larger vessels; fdl, dorsolateral fold of the posterior pharynx; fdm, dorsomedian fold of the posterior pharynx; fv, ventral fold of the posterior pharynx; g, gut; pbrb, postbranchial body; pbrI, first postbranchial pouch; pbrIIv, ventral part of the second postbranchial pouch; pbrIIIId, dorsal part of the third postbranchial pouch; s, swim bladder; st, stomach. For silhouette credit see Acknowledgments.

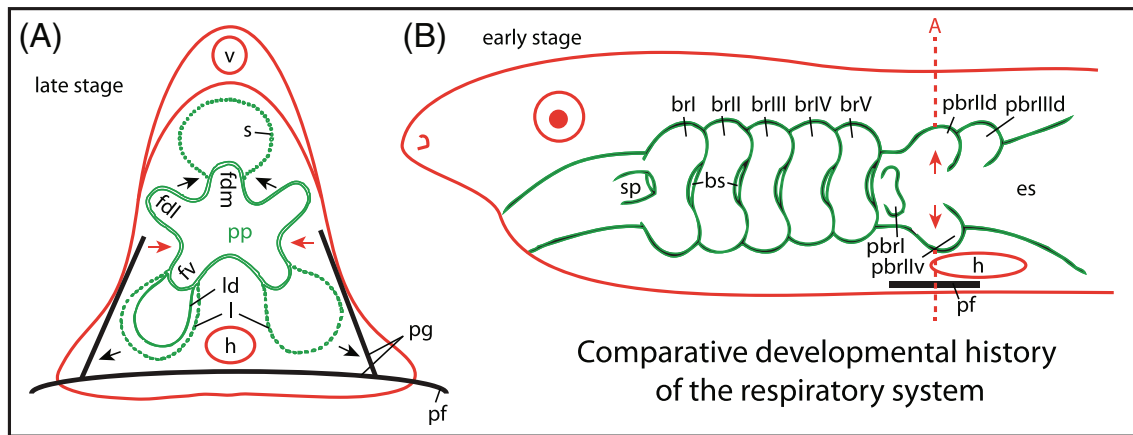


FIGURE 7 Comparative developmental history of the respiratory system, modified and expanded after Wassnetzov.²³ Cross section (A) through the posterior pharynx of a vertebrate. The section is indicated in (B). Based on spatial restrictions in the body flank (red arrows), the postbranchial pouches (pbrI) are separated into dorsal and ventral parts (shown for the second postbranchial pouch in B). Later in development (B), the dorsal and ventral pouches (evaginations) merge as elongated pouch folds (fdl and fv). Dorsally, the paired pouch folds (fdl) posteriorly merge to a dorsomedian fold (fdm). In Actinopteri [sic], this median fold may give rise to the swim bladder (s). The paired ventral pouch folds (fv) may expand to the lungs (l, ld) in non-actinopterygian gnathostomes. In the area of the pectoral girdle (pg), they can unfold on both body sides, whereas the swim bladder is spatially restricted dorsomedially. br, branchial (gill) apparatus; brII, second branchial pouch; brIII, third branchial pouch; brIV, fourth branchial pouch; brV, fifth branchial pouch; h, heart and associated larger vessels; l, lung; ld, lung of Dipnoi (lungfish) based on Wassnetzov (1032); pbrI, first postbranchial pouch; pbrId, dorsal part of the first postbranchial pouch; pbrIIId, dorsal part of the second postbranchial pouch; pbrIIIId, dorsal part of the third postbranchial pouch; pbrIVd, dorsal part of the fourth postbranchial pouch; pf, pectoral fin; pg, pectoral girfile (incl. shoulder); sp, spiracle.

that Miklucho-Maclay¹² must have misidentified the spaces between the papillae on the mucosa of the esophagus as evaginations.

- Mayer²⁸ could not confirm the presence of any evagination in embryos, young free-living larvae, or an adult female (1 m in length) of the school shark *Galeorhinus galeus* (previously called “*Galeus canis*”), a species also dissected by Miklucho-Maclay.¹²

Mayer²⁸ studied the histology of the dorsal and ventral pockets of *Mustelus laevis* in detail and found their cells to be more cubic than high and slender in shape when compared to the surrounding cells of the esophagus wall. He confirmed Miklucho-Maclay's¹² observation that the reddish coloration of their epithelia is similar to that of the stomach but has nothing else in common with that organ. The author acknowledged the acidic milieu found in the stomach and the esophagus but could not follow the argument, because he did not find any reasons why the secretions of the pocket cell mucosa should be any different from the secretions of other esophageal cells.

For these reasons, Mayer²⁸ concluded that the ventral pockets could be the “rudiments of anything,” and snappily formulated that, given the similarity of the dorsal and ventral pockets, one would, following Miklucho-Maclay's¹² argument, actually need to declare them all

as rudiments of the swim bladder (dorsal) as well as the lungs (ventral)—and that would be ridiculous to believe. He wrote,²⁸ “So it seems to me, following the saying: what is good for the goose is good for the gander, that there is no reason to consider only the dorsal pocket, not the two ventral ones as well, as rudimentary organs, and that is how the whole passage about it should soon disappear in the textbooks of comparative anatomy and developmental history. Unless one wanted to surpass MUKLUCHO [sic] and declare the ventral pockets as the two rudimentary lungs.”[‡]

In 1902, Fanny Moser,³² who studied the morphology and evolution of swim bladders and lungs across vertebrates (see also³³), principally agreed with Mayer²⁸ and concluded that this author rejected Miklucho-Maclay's hypothesis “with good reasons by highlighting the improbability that a swim bladder may appear in such a primitive animal group [like sharks]” (our translation). However, later in the same article,³² she contemplated

[‡]Our translation from: “Es scheint mir also nach dem Spruche: was dem Einen recht ist, ist dem Anderen billig, kein Grund dazu vorzuliegen, nur die dorsale Tasche, nicht auch die beiden ventralen als ein rudimentäres Organ zu betrachten, und so dürfte wohl der ganze Passus darüber aus den Lehrbüchern der vergleichenden Anatomie und Entwicklungsgeschichte bald verschwinden. Es sei denn, man wollte MUKLUCHO [sic] noch überbieten und die ventralen Taschen als die beiden rudimentären Lungen ansehen.“

that there might be a “certain hope” that such an organ—“maybe of gland-like constitution”—may be found once in a shark and, in that case, has to be declared as the “beginning of a swim bladder.” In this regard, she confusingly agreed with but also curiously rejected Miklucho-Maclay.

Two years later, in 1904, D. Deneika³⁴ was a bit more careful and concluded that “at least most selachians” do not have a swim bladder. This author highlighted the great anatomical and histological diversity of the swim bladder among fishes and called for more caution when interpreting the origin and evolution of the organ. This advice has been followed, and subsequent studies have provided comprehensive scenarios on the diversification, loss, and reacquisition of swim bladders in bony fishes (Osteognathostomata).^{16,21,22}

Among osteognathostomes, the lobe-finned vertebrates (i.e., Sarcopterygii: coelacanth, lungfishes, and tetrapods) are generally characterized by paired lungs that fold out ventrally from the posterior pharynx. In comparison, the ray-finned fishes (Actinopterygii; i.e., their sister group) either also have paired ventral lungs (Polypteriformes: bichirs and reedfish) or an unpaired swim bladder dorsally emerging from the posterior pharynx (Actinopteri: sturgeons, gars, bowfins, and teleosts; Figure 3).

Given the uncertain basal condition of this character complex, it is difficult to say whether the dorsal and ventralanlagen of the gas organs both originated only once, at the same time, with either the dorsal or the ventralanlagen being subsequently reduced (scenario 1), whether lungs originated twice (scenario 2), or whether lungs were originally present and then reduced or transformed to the dorsal swim bladder in Actinopteri (scenario 3) (sensu²¹). This last scenario would involve a complex relocation from two ventral organs (lungs) to one dorsal organ (swim bladder), for which there is no evidence in embryological research. It is also unknown why there are usually two lungs (only secondarily one lung can be reduced, such as in snakes) and only one swim bladder, and why both organs are never present in an individual at the same time. The original observations and considerations of Miklucho-Maclay¹² might be informative for these questions, and a further simple geometric observation might help to resolve this dilemma (see below).

5 | ONTOGENY OF THE POSTERIOR PHARYNX

In his handbook chapter, M. Rauther³⁵ summarized the discussions on the presence of swim bladders in early

gnathostomes. He favored Miklucho-Maclay's¹² hypothesis of early swim bladder origin in the Chondrichthyes and referred to the extended studies by the Russian researcher, Wassnezov on elasmobranchs (sharks and rays).^{23,27} This researcher described the ontogeny of the posterior pharynx in a shark [i.e., *Galeus* (“*Pristiurus*”) *melanostomus*] and in three ray species [i.e., *Dasyatis* (“*Trygon*”) *pastinaca*, *Torpedo marmorata*, and *T. ocellata*] (Figure 5). For comparison, he studied the ontogeny of this region in the sturgeon *Acipenser stellatus* (Figure 6) as a representative “basal” member of the Osteognathostomata (Figure 3A), in which a clearly defined swim bladder is present (Figure 6M). Wassnetzov²³ summarized his findings as follows:

In embryos of Elasmobranchia (sharks and rays), there are several evaginations in the posterior part of the pharynx. These evaginations likely evolved from the most posterior gill pouches of the caudally reduced gill apparatus of the gnathostome ancestors and are, as such, serially homologous (“homoserial”) to each other. Only the five most anterior gill pouches break through the skin as gill openings in most fishes today. These reduced posterior gill pouches are ontogenetically split, by spatial restrictions in the body cavity, into dorsal and ventral parts, and eventually align as separate evaginations—dorsal and ventral folds—through development (Figure 7). There are one to three evaginations in each row [three in *Torpedo* and *Dasyatis* (“*Trygon*”)]. The dorsal pair of rows unites posteriorly in an unpaired median evagination. This fusion can again be explained by the restricted space in the upper part of the body cavity (Figure 7A).

Later in development, the rows of separate, taxon-specific evaginations merge to form elongated folds, with one unpaired dorsal and two paired ventral folds. The former evaginations can persist as sac-like pouches into adulthood. In *Dasyatis* (“*Trygon*”), this condition is easily visible, whereas it is much modified in other elasmobranchs due to the formation of secondary folds in the esophagus that are related to the helical anatomy of the entire gut system.²³

Because in the sturgeon *A. stellatus* and other non-chondrichthyan fishes, very similar ontogenetic changes occur, Wassnetzov²³ concluded that it is possible that the unpaired dorsal fold provides the material for—and is, in this regard, homologous to—the swim bladder of other fishes (Actinopterygi [sic, see Figure 3], Figure 6). The observation by Neumayer³⁶ that the swim bladder of *A. stellatus* may form from the right dorsal fold, must be seen as an intraspecific variation dependent on individual yolk distribution. One may, thus, declare that all three dorsal folds provide the potential source material for the swim bladder in actinopterygian fishes (see fig. 1B in reference Perry²²).

What Mayer²⁸ found as paired ventral evaginations in *Mustelus* (Figure 5A) must be interpreted as

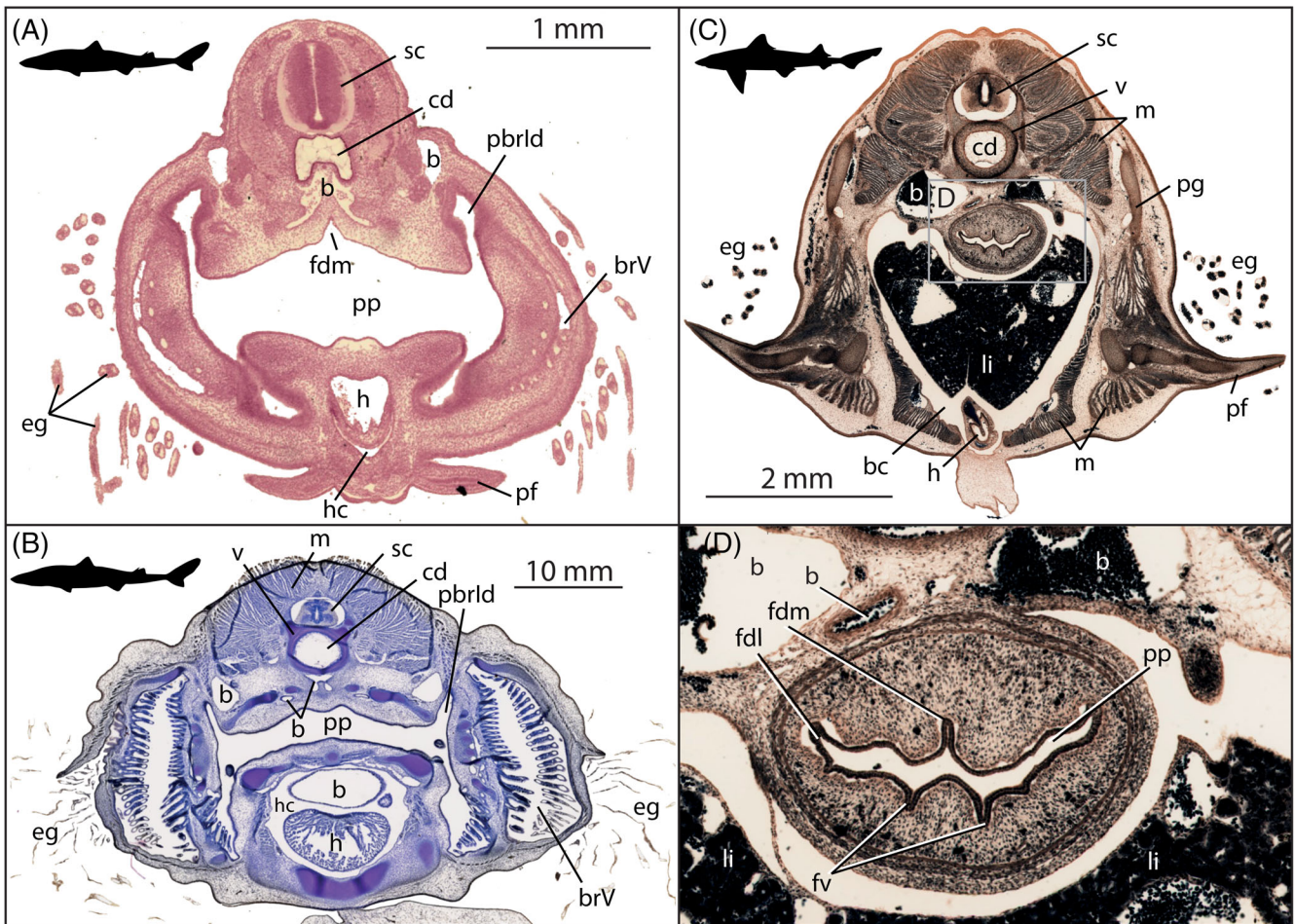


FIGURE 8 Embryogenesis of chondrichthyans 1/2. (A) *Squalus acanthias*, 28 mm embryo, MCZ:SC:677, slide G, section 12–6 (section numeration: starting in the left upper corner of the slide, with column 12, and section 6). (B) *Squalus acanthias*, 55 mm embryo, MCZ:SC:3779, slide 43, section 1–1. (C,D) *Mustelus mustelus*, 40 mm embryo, MCZ:SC:2387, slide Q, section 1–1, with D focusing on the posterior pharynx (width of D is 2 mm). Sections of Figures 8 and 9 originate from Harvard University, Special Collections (SC) and regular collection of the Museum of Comparative Zoology Collection (MCZ), CC-BY-NC-SA 4.0. b, blood vessel; bc, body cavity; brV, fifth branchial pouch; cd, chorda chordalis; eg, external, i.e. embryonic gills; fdl, dorsolateral fold of the posterior pharynx; fdm, dorsomedian fold of the posterior pharynx; fv, ventral fold of the posterior pharynx; h, heart and associated larger vessels; hc, heart cavity (pericard); li, liver; m, musculature; pbrld, dorsal part of the first postbranchial pouch; pf, pectoral fin; pg, pectoral girdle (incl. shoulder); pp, posterior (postbranchial) pharynx; sc, spinal cord; v, vertebra. For silhouette credits see Acknowledgments.

developing from the paired ventral folds of embryos and—on the material level—as being homologous to the paired ventral lungs of non-Actinopterygi [sic] fishes and tetrapods.

Using histological sections of elasmobranch species, we could generally confirm the anatomical observations of Miklucho-Maclay,¹² Mayer,²⁸ and Wassnezov.^{23,27} In early *Squalus acanthias* development, dorsal (and perhaps ventral) postbranchial pouches are formed (Figure 8A), with only the dorsal ones persisting to a later stage (Figure 8B). These could eventually fuse into an unpaired organ during further development (Figures 2 and 9C,D). In a *Mustelus mustelus* embryo, a separation of the posterior pharynx into five evaginations

(Figure 8C,D) is clearly visible and reminiscent of the anatomy found in the sturgeon embryo (Figure 6I)—this is the condition that inspired Wassnezov²³ to his hypothesis on the original configuration of the posterior pharynx in vertebrates (Figure 7).

Miklucho-Maclay¹² was not sure whether he actually dissected a *Mustelus* specimen and put a “(?)” in the caption of his figure 2 (see caption of our Figure 2). We can confirm that a swim bladder anlage is present in *Mustelus*, although with *M. mustelus* we perhaps studied a different species of this genus from the one he studied. Furthermore, we can confirm the observation of Mayer,²⁸ who found two paired ventral evaginations in the posterior pharynx of *M. mustelus*

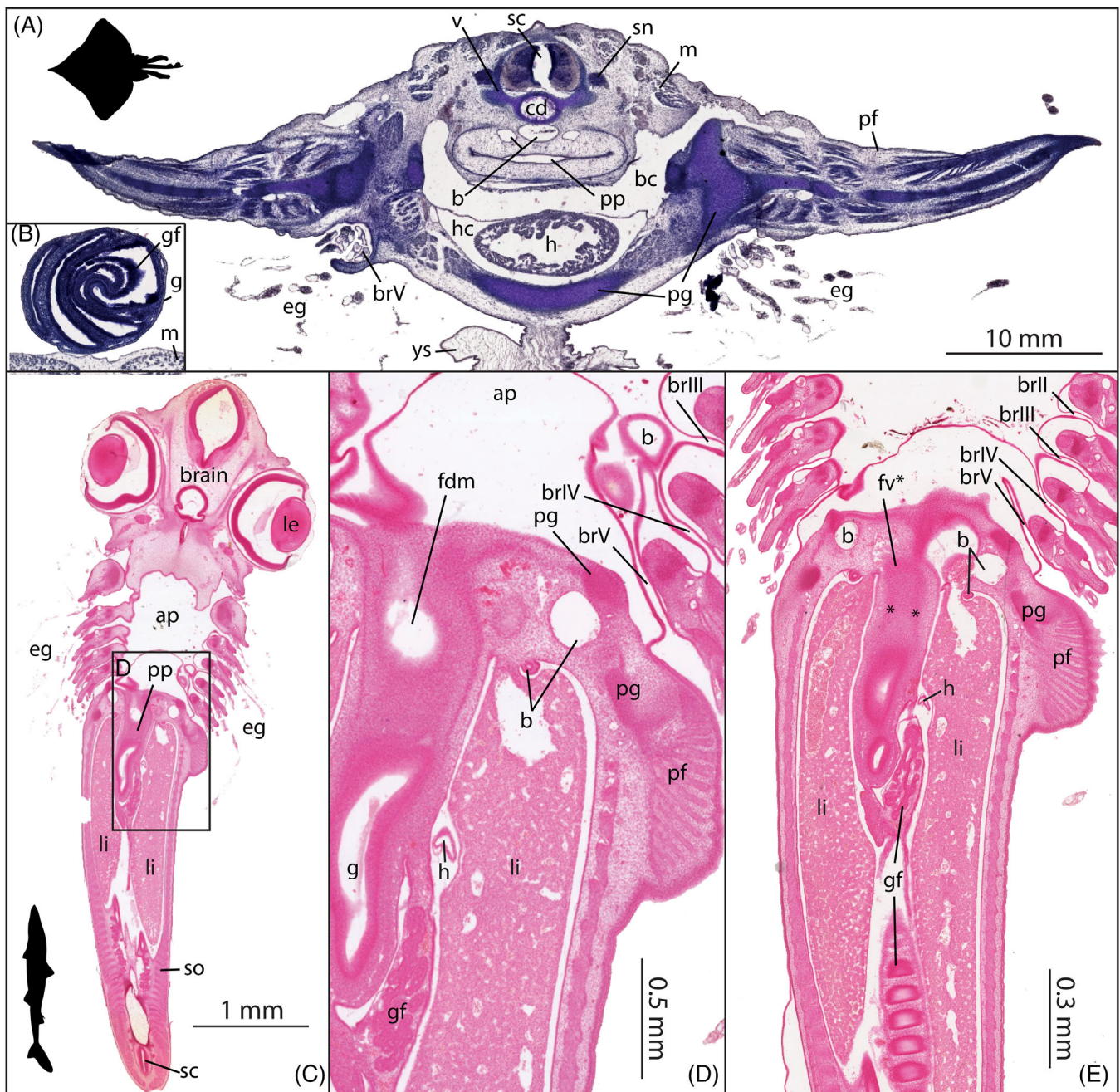


FIGURE 9 Embryogenesis of chondrichthyans 2/2. (A,B) *Raja eglanteria*, 32-day old embryo, MCZ:SC:3789, with (A) slide 20, section 3–2, and (B) slide 27, section 2–7 (box has a width of ca. 4 mm). (C–E) *Squalus acanthias*, 23 mm embryo, MCZ:SC:633, slide L, 1–3. (C) showing the whole specimen sectioned along the upper border of the posterior pharynx, which is in focus in (D). (E) Same specimen as in (C,D), with slide M, section 1–2, at the lower level of the posterior pharynx. ap, anterior (branchial) pharynx; b, blood vessel; bc, body cavity; brII, second branchial pouch; brIII, third branchial pouch; brIV, fourth branchial pouch; brV, fifth branchial pouch; cd, chorda chordalis; eg, external, i.e. embryonic gills; fdm, dorsomedian fold of the posterior pharynx; g, gut; gf, helical gut fold; h, heart and associated larger vessels; hc, heart cavity (pericard); li, liver; m, musculature; pf, pectoral fin; pg, pectoral girdle (incl. shoulder); pp, posterior (postbranchial) pharynx; sc, spinal cord; so, somites (already differentiating); sn, spinal nerve; v, vertebra; ys, yolk sac. For silhouette credits see Acknowledgments.

(Figures 5A and 8C,D). A paired cell condensation is also present in the ventral aspect of the posterior pharynx of *S. acanthias*, which might correspond to fused ventral postbranchial pouch anlagen (indicated with asterisks in Figure 9E).

As discussed above, the anatomy of the esophagus might largely alter the ancestral condition of the postbranchial pouch folds. Whereas the whiptail ray *Dasyatis* (“Trygon”) showed the anticipated arrangement of postbranchial pouch folds, this was less obvious in the clearnose skate

Raja eglanteria. Reference to the section (Figure 9A) reveals that this may relate to the flattened general anatomy of this species. This should, logically, also be the case in the flat whiptail ray, but—as is found in many other elasmobranchs (sensu Wassnetzov²³ and as visible starting at slide 25 of our section series; Figure 9B)—extensive curling of the esophagus is present.

6 | CONSIDERING EPIGENETIC BASES FOR INTEGRATIVE FUNCTIONAL MORPHOLOGY

Although early analysis of the Devonian placoderm *Bothriolepis canadensis* indicated evidence of paired, lung-like structures,^{37–39} subsequent material has brought this interpretation into question. It has been proposed, instead, that the fossilized structures in question represent the liver and that no gas organs were present in earliest jawed vertebrates (Gnathostomata).⁴⁰

It is worth noting that a shark's liver may make up to 25% of the body content, and that the liver may be composed of up to 80% fat. This fat serves not only as an energy reservoir but also as a buoyancy and balancing organ.⁴¹ As such, a swim bladder is not needed in these animals. Whether this high fat content in the liver is an original feature remains an open question for now, although the current fossil evidence supports such an idea. If the dorsal tube of the pharynx found in some chondrichthyan species actually represented a reduced rudimentary swim bladder (Miklucho-Maclay¹²; sensu Haeckel: Darwin Correspondence Project, Letter 5840), it may indicate a secondary acquisition of the fatty liver to serve these functions.

As discussed above, the swim bladder may be completely lost among certain benthic, deep-sea, and highly pelagic teleosts,¹⁶ which indicate that the presence of a swim bladder or fatty liver in a fish is dependent largely on the environmental setting. This would have relevance when considering the living conditions of the earliest crown gnathostomes (i.e., excluding agnathans and placoderms) and is supported by the great diversity of gas organs found among fishes.²¹ The presence of a possible secondary fatty liver in extant Chondrichthyes is, finally, not proof that their close ancestors might have had different living conditions or had gas organs at all.

The dorsal and ventral embryonic anlagen discovered by Miklucho-Maclay¹² (unintentionally further supported by Mayer²⁸) and Wassnetzov^{23,27} in Chondrichthyes (chimeras were not studied to our knowledge and were not even available to us) reinforce the idea that the earliest crown gnathostomes (also including chondrichthyan ancestors) had the capacity to form gas organs. Depending on lifestyle requirements, swimming,

and foraging behavior, either ventral lungs or a dorsal swim bladder were formed, modified, or even lost independently during subsequent gnathostome evolution. In this regard, again, the presence of dorsal and ventral anlagen clearly shows that there is no reason to believe that a vertical transposition from ventral lungs to a dorsal swim bladder took place.²²

The fact that either a dorsal or a ventral gas organ is present and they are never found together in an individual, remains a curiosity. In this context, we wish to refer to a recent study on the origin of vertebrae in early craniate evolution, with hagfish and lampreys showing either dorsal or ventral vertebral anlagen. Based on molecular evidence, their hypothetical common ancestor should have had both, like gnathostomes do.⁴² Similarly, the gnathostome ground pattern might have contained dorsal and ventral gas organs, which might even have served different functions compared to those in present-day animals. Perry²² highlighted the ancestral “respiratory” function of the posterior pharynx, which evidences a wide spectrum of physiological functions, not necessarily related to atmospheric air, but likely still related to receiving oxygen from water. Finally, either the lung or the swim bladder was established in the respective gnathostome groups. The physiological functions of gas bladders range from predominantly respiratory to just buoyancy in Actinopteri, and evolutionary changes can occur.^{15,16} As such, the environmental requirements at the time of their origin favored either air-breathing or buoyancy adaptations in the respective taxa. However, once a dorsal swim bladder had evolved, it was easier to change this organ's physiology than to overcome the anatomical constraints of evolving a new gas organ.

This discussion, however, does not answer *why* only *one* gas organ—lung or swim bladder—is present in extant forms. As outlined by Wassnetzov,²³ this question might simply be related to spatial, i.e., epigenetic conditions (Figure 7). Gas organs need to occupy a large amount of space in the body cavity, and even more volume can be accessed with just one organ because the space between several gas organs cannot be filled with gas. A further question relates to *why* there is only *one dorsal swim bladder* and usually *two ventral lungs*. This might also be related to simple spatial conditions related to the body wall (Figure 7). Toward the vertebral column, the width of the body cavity naturally decreases, whereas ventrally, toward the pectoral girdle, there is more space available (Figure 7). Therefore, dorsally, there might only be room for one gas organ, whereas ventrally more space is available for lateral expansion. Given the ventromedial position of the heart within the body, a spatial separation between the two lungs is further supported. A paired lung is biomechanically advantageous in taxa inhabiting

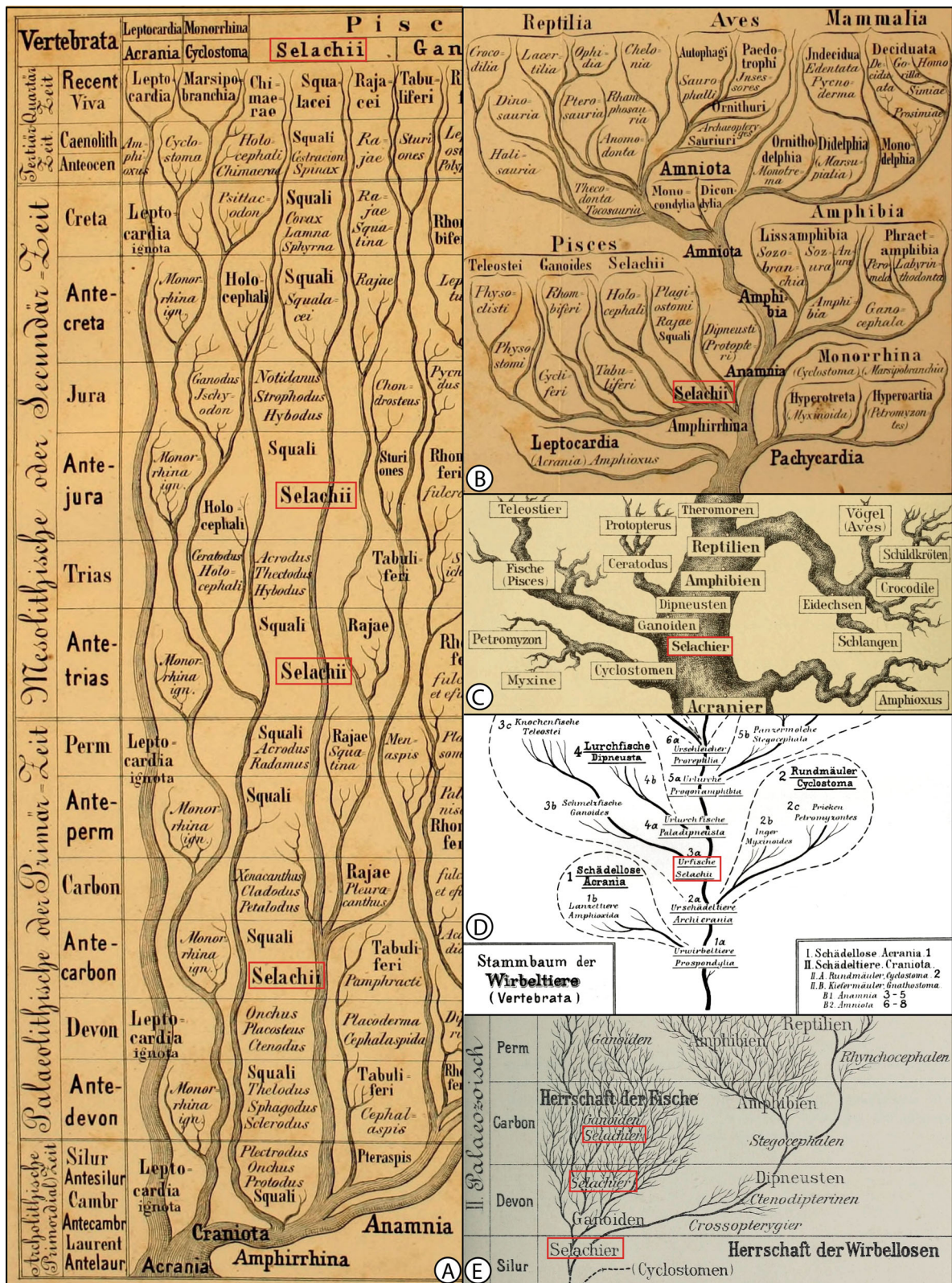


FIGURE 10 Fragments of different phylogenetic trees on vertebrate evolution published by Ernst Haeckel. “Selachii” highlighted by us. (A,B) Trees from Haeckel (1866, plate VII).⁷ Note that the term Selachii (sharks) only refers to the branch of fishes (“Pisces”) that split of the branch leading to Anamnia (i.e., Osteichthyes, bony fishes). In (B) an overview of all vertebrates is presented (from the right lower corner of the same plate). (C) Tree from Haeckel’s “Anthropogenie” (here sixth edition: 1905, plate XX)⁵⁴ showing the label of selachians only as the ancestor. The same is true for (D), which is from Haeckel (1905, plate 1).⁵⁵ In (E), from Haeckel (1910, plate XXI),⁵⁴ selachians are shown as ancestors as well as taxa nested within the fish-branch. Note, only first paleontological appearances of taxa are shown in this tree. This tree most closely corresponds to the sketch from 1868 (Figure 4B).

shallow waters or rugged and vegetated shorelines, particularly in species with paddle-like appendages, to allow buoyancy as well as maximum maneuverability.²² Considering such epigenetic factors is a promising approach to understanding gross morphological conditions in organismic research in the future (*sensu* Nuño de la Rosa et al.⁴³).

7 | ON THE EVOLUTIONARY ORIGIN OF THE SWIM BLADDER: A QUESTION OF PERSPECTIVE

The aggressive account of Mayer²⁸ against Miklucho-Maclay¹² was merely based on the latter's assumptions that swim bladders were reduced in elasmobranchs and were present in gnathostome ancestors. This idea primarily appears to correspond with an archaic, *Scala Naturae*-like understanding of evolution, in which chondrichthyans would form the direct ancestors of other gnathostomes (Figures 4B and 10), a common misunderstanding of evolution that persisted until the mid-20th century.^{44,45}

Some aspects of this outdated view of step-like evolutionary progression can still be recognized in the works of Haeckel and his close friend and colleague in Jena, Carl Gegenbaur, who was an expert on shark anatomy,^{46,47} and was also one of Miklucho-Maclay's teachers.⁴ Another important proponent of step-wise evolutionary thinking was Ernst Gaupp (1865–1916), who saw lizards, monotremes, and marsupials in a direct line toward placental mammals.^{48,49} This obvious misconception of evolution⁵⁰ was only resolved in 1950 by Hennig's concept of phylogenetic systematics,⁵¹ which takes terminal taxa as descendants of hypothetically reconstructable ancestors.⁵² We acknowledge that the Hennigian approach also has its difficulties. For example, individual fossils could represent the biological ancestors of later clades but are still handled as terminal taxa by this method; nevertheless, the largely misleading *Scala Naturae* approach is clearly avoided. Mayer²⁸ was thus apparently correct when criticizing a derivation from swim bladder-bearing gnathostome ancestors, but at the same time he underestimated the great importance of Miklucho-Maclay's¹² discovery in understanding the origin of gas organs from a morphogenetic perspective.

In his above-mentioned letter, dated February 6, 1868 (Darwin Correspondence Project, Letter no. 5841), Darwin saw a different value in this study, related to the possible homology of lungs and swim bladders—which was not considered in Miklucho-Maclay's¹² study at all. Darwin was very interested in this question, as proven by correspondences in other letters (e.g., Darwin

Correspondence Project, Letters no. # 7464, 2713, 2647, 1929, 7425, 2503, including letters to Arthur Russel Wallace, Asa Gray, Charles Lyell, John Richardson, and Francis Darwin). One has to acknowledge that the general value of ontogenetic variation and transitional formations might not have been as well understood in the late 1860s beyond some erratic exceptions known and recognized by Darwin himself. Only by the end of the 19th century, with the evidence from advanced histology and three-dimensional reconstructions, did a new cosmos of morphological evidence for evolutionary changes emerge.

In his reply to Darwin, dated March 23, 1868, Haeckel still insisted on the value of Miklucho-Maclay's¹² study and wrote (Darwin Correspondence Project, Letter no. 6040)[§]: “As for the treatise on the rudimentary swim bladder of the selachians which was recently sent to you, I consider it very important because I believe, with Gegenbaur, that the *selachians are the ancestors of the rest of the fish, consequently, of the amphibians, and therefore of the higher vertebrates.*” (Italics as in the Project webpage.) At this point in the letter, a phylogenetic tree was drawn by Haeckel, which we reproduce in Figure 4B. Haeckel continued: “If this is correct, the selachians *must have of necessity* already possessed a swim bladder, which remained a swim bladder in the ganoid and teleost fishes, but became a lung in the amphibians. Since no selachian was known so far to have a swim bladder, that rudiment seems very important to me.”

When comparing phylogenetic trees published by Haeckel, it becomes obvious that his concept of gnathostome origin developed very early in his career and manifested over the decades. In his 1866 *Generelle Morphologie* (Figure 10A,B), Haeckel⁷ recognized all chondrichthyans as paraphyletic, with chimeras (Holocephali) originating more rootward, while sharks (Haeckel's “Squali”) and subsequently rays (Haeckel's “Rajae”) are more closely related to all other “Pisces” (i.e., Actinopterygii). In his opinion, sharks, rays, and actinopterygians together form the sister taxon to Anamnia (i.e., lungfish and tetrapods; note: extant

[§]Darwin Correspondence Project, “Letter no. 6040,” accessed on 25 April 2023, <https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-6040.xml>; our translation from: “Was die neulich Ihnen übersandte Abhandlung über die rudimentäre Schwimmblase der Selachier betrifft, so halte ich sie deshalb für sehr wichtig, weil ich mit Gegenbaur glaube, dass die Selachier die gemeinsamen Stammformen der übrigen Fische einerseits, der Amphibien und dadurch der höheren Wirbelthiere andererseits sind. Wenn dies richtig ist, mussten nothwendig die Selachier bereits eine Schwimmblase besitzen, welche bei den Ganoiden und Teleostiern Schwimmblase blieb, bei den Amphibien aber Lunge wurde. Da nun bisher bei keinem Selachier eine Schwimmblase bekannt war, scheint mir jenes Rudiment sehr wichtig.”

coelacanths had not been discovered by this time⁵³). Haeckel's view of chondrichthyans (his "Selachier"/"Selachii") being paraphyletic with a subsequent evolution along the phylogenetic tree will have influenced his understanding of early gnathostome anatomical conditions.

In his book *Anthropogenie*, where Haeckel⁵⁴ focused on the heredity of man, he placed the term "Selachii" only on the stem of the vertebrate tree from which the jawed fishes ("Pisces") and Anamnia emerged—but one has to acknowledge the intentionally minimalistic labeling of the tree "toward" man in this particular figure (Figure 10C). In a later study, elsewhere Haeckel⁵⁵ synonymized Selachii with ancestral fishes in the category "Urfische" (primordial fishes; i.e., Gnathostomata) on the stem of his tree, but did not show extant sharks, although ganoid and teleost fishes were explicitly depicted (Figure 10D). Finally, as in the mentioned tree illustration in the letter dated March 23, 1868 (Figure 4B), Haeckel⁵⁴ used the term "Selachier" to label both the stem of gnathostomes as well as the origin of extant selachians (Figure 10E; in the text, p. 585, he calls sharks "Notidanides"). The latter two figures best help to understand Haeckel's scientific approach.

By comparing all these trees (Figures 4B and 10), it becomes obvious that Haeckel saw chondrichthyans (his "Selachii") as a paraphyletic group of extant fishes, with chimeras falling outside all other gnathostomes. Only along the evolutionary history of this paraphyletic "Selachii" group, would the original anatomical construction of gnathostomes have been established. In his later trees, Haeckel did not concentrate much on early vertebrate history, and his later simplifications from the original tree of 1866⁷ might confuse the interpretation. Nevertheless, neither sharks and rays, nor chimeras show swim bladders in adults today, and the likely incorrect paraphyletic view still does not indicate the presence a swim bladder in the origin of gnathostomes.

To our knowledge, there is only one further mention of this topic in the correspondence between Haeckel and Darwin. On March 30, 1868, Darwin responded to Haeckel again (Darwin Correspondence Project, Letter no. 6070) and wrote⁴: "I am much obliged for your interesting letter with its genealogical tree [Figure 4B]. I now understand, to a certain extent, the importance of the swim bladder in the Selachians. I shall be curious to see whether the organ ought not to be considered rather in a "nascent" than in a "rudimentary" state. I had always imagined that some animal like the [lungfish] *Lepidosiren* was the parent-form of the Vertebrata" (italics for the genus by us).

Apparently, Darwin was unsure about the phylogenetic position of chondrichthyans, which might have influenced his skepticism on the meaning of the "Mikluskan organ." Still, in the sixth edition of *On the Origin of Species*,⁵⁶ he wrote: "But we shall see how obscure this subject is if we look, for instance, to fishes, amongst which some naturalists rank those as highest which, like the sharks, approach nearest to amphibians; whilst other naturalists rank the common bony or teleostean fishes as the highest, inasmuch as they are most strictly fish-like, and differ most from the other vertebrate classes."

Darwin was convinced that the swim bladders converted into lungs and that these two organs were homologous. His view of lungfishes (Dipnoi: e.g., *Lepidosiren* and *Protopterus*) as being ancestral, with their transient anatomical position of the lung (Figure 3E, *Neoceratodus*), might have influenced his opinion. "Again, an organ may become rudimentary for its proper purpose, and be used for a distinct one: in certain fishes, the swim bladder seems to be rudimentary for its proper function of giving buoyancy, but has become converted into a nascent breathing organ or lung," Darwin wrote.¹⁷ For Darwin, rudimentary organs were defined as remnants of a former state that served no present function, while nascent organs were the early stages of organs that would later attain functional status (see the fourth edition of *Origin of Species*⁵⁷). Roberts⁵⁸ summarized that: "Darwin realized a need to distinguish between anatomical parts that appeared to be vestiges of once functional structures and »nascent« parts that were in fact very useful and perhaps even likely to become more complex over time." As for the case of the "Mikluskan organs," following Darwin's definition and opinion on this topic, an ancestral swim bladder would have become rudimentary before becoming a nascent organ for lung evolution.

We have illustrated, citing embryological evidence from the later literature and our own observations, that the "Mikluskan organs" are developed in chondrichthyans as rudiments of the posterior pharyngeal pouches derived from the gnathostome ancestors. These rudiments served as nascent organs to form the swim bladder dorsally in Actinopterygi [sic, see Figure 3] and the lungs ventrolaterally in all other osteognathostomes. Thus, only at a certain ontogenetic level (i.e., as early posterior gill pouch derivatives), are lungs and swim bladders homologous. The long-lasting debate on the organs' identities could only be solved using the new material, methodology, and technology that emerged in the second half of the 19th century. Current phylogenetic inference on extant adult anatomy would suggest lungs to have evolved first and swim bladders secondarily (Figure 3). However, our case study demonstrates that adult anatomical characters need to be understood from their ontogenetic (and phylogenetic)

⁴Darwin Correspondence Project, "Letter no. 6070," accessed on 25 April 2023, <https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-6070.xml>

origin. As such, the reconstruction of a respiratory pharynx with dorsal and ventral anlagen of gas organs, as provided by Lambertz and Perry,²¹ is the most appropriate way to deal with these morphological characters in phylogenetic research. Given the twofold potential of the respiratory pharynx and a potentially rapid early diversification of osteognathostomes, combined with a supportive epigenetic condition in a potentially vaulted body cavity, we cannot deny that both lungs and swim bladders could have been present in the evolutionary history of early gnathostomes at some point.

8 | CONCLUSIONS

1. The mention of Miklucho-Maclay in the letter exchange between Haeckel and Darwin is a small episode in the history of science, but it teaches us a great deal about both scientists' personalities and their approach to evolutionary biology. First of all, it is striking that Haeckel was so attentive to the achievements of his junior and inexperienced students. At the time that Miklucho-Maclay made what Haeckel regarded as a "lovely discovery" (Haeckel's expression in the cited letter, No. 5840), Miklucho-Maclay was only a foreign student in the medical faculty at the University of Jena, while Haeckel was already recognized worldwide as a Darwinian evolutionist.
2. Darwin's reaction to the brief mention of Miklucho-Maclay by Haeckel, in turn, demonstrates how attentive Darwin was to Haeckel's letters, and how he considered carefully even the smallest details Haeckel communicated in these letters.
3. Third, this episode shows the differences between Haeckel's and Darwin's approaches to evolutionary research. Haeckel was preoccupied with the exact reconstruction of his "genealogic trees", and Miklucho-Maclay's discovery¹² from 1867 primarily induced his thinking in that direction. Darwin designed no graphs presenting "real" phylogenies, his major focus was on the mechanisms of evolution and the very fact of evolution and, as a consequence, he saw in Miklucho-Maclay's discovery¹² what he was looking for: one more proof of evolution.
4. The observation by Miklucho-Maclay¹² on shark anatomy has inspired many embryological studies, some of which we have discussed herein. We provide additional evidence for the "rudiments," but highlight their evolutionary significance as derivatives of the reduced post-branchial pouches in the posterior pharynx (sensu Wassnetzov²³) that might have given rise—as nascent organs in Darwin's terminology—to lungs and swim bladders already in early gnathostome evolution.

5. Finally, we show that epigenetic space restrictions help shape the distribution of gas organs in living bony fishes.

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