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Opinion on the evolution of the Linnaean animal species concept, with discussion on his views on the Amphibia

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Abstract. While the Linnaean species has been assessed in depth for plants, a review of the development of the Linnaean animal species concept has never been performed. I review the application of his concept of animal species in a comparative assessment with his concept of plant species. The application of the animal species concept in practice is discussed in connection with his class Amphibia (in the Linnaean classification, the class included not only the presently known amphibians and reptiles, but additionally several groups of cartilaginous fishes, not covered in the present review). Linnaeus' species concept shifted from the fixist, creationist 'nulla species nova' concept in the first edition of 'Systema Naturae' in 1735, to a progressing species, a rudimental evolving species approach, by Edition 12 of the same work in 1766. Although rudimentary and naive, the concept applied by the mature and elderly Linnaeus was biological. He had a clear vision about the natural order within Amphibia as early as 'Systema Naturae' Ed. 6 in 1748, and in works that followed he only added species to the pre-existing genera created, retaining some, but keeping their number fixed, and additionally used variety as a placeholder for taxa worth investigating further.

Keywords: Carl Linnaeus, Carl von Linné, creationism, evolution, amphibians, reptiles, historical.

Introduction

Carl Linnaeus (1707–1778) or Carl von Linné after his ennoblement in 1761, is undoubtedly the most famous Swedish naturalist and is known as the father of taxonomy (Winsor 2001, Broberg 2023). His most important additions to science were the introduction of binomial nomenclature and his classification of plants and animals (Ramsbottom 1938, Broberg 1980, 2023). The magnitude of his classification work was perceived already during his lifetime; therefore, contemporary admirers honored him with the now-famous epigram 'Deus creavit, Linnaeus disposuit' (Fries 1903). Many modern taxonomic systems retain components of his original system by assigning categories in the Linnaean hierarchy (de Queiroz 1996). While his contributions to systematics are numerous and multiple elements of classifications survived the test of time, since they are still accepted close to three centuries after their publication, in the past decade his views and especially his species concept have been strongly criticized and recommended to be forgotten by evolutionary biologists Ernst Mayr (1904-2005) and Arthur James Cain (1921-1999).

Undoubtedly, the central concept of systematics, one of the oldest scientific disciplines, has been and is the concept of species (de Queiroz 2005, 2007). In the Linnaean system, the species was one of the most basic units and, to some extent, the key element (de Queiroz 1996), although as will be shown below, the genus played at least as important, if not a more crucial, role in the system.

While the Linnaean species concept and its application may no longer fit into our evolution-driven perspective of the world, understanding the origins and history of his animal species concept may support taxonomist assessing Linnaean type material to understand better the changes in the classification or nomenclatural acts, such as renaming, performed by Linnaeus in connection with the taxa they are investigating.

The Linnaean system, which still forms the basis of the classification of multiple classes, was the result of protracted development. Linnaeus strived to achieve the 'natural system' (i.e., the real classification), an approach he discussed in depth in connection with plants but not animals. For a review of the logic applied by Linnaeus, see Müller-Wille (2007). On account of his main interest in botany and the large number of publications in the field, he publicized his views and detailed his concept and approach in botanical works. Therefore, even if Linnaean publications dealing with the animal kingdom may have rather short summaries of his views, the development and evolution of the Linnaean animal species concept can only be understood if seen within the context of the complete publication activity of a certain period of his life.

Multiple authors have discussed the Linnaean species concept and its development from a botanical perspective (e.g., Greene 1909, Ramsbottom 1938, Engel 1953, Larson 1968, Müller-Wille 2007). However, assessments from the animal kingdom perspective are completely lacking. This might be attributable to the relatively scarce descriptions of the classification criteria and species classification logic applied in Linnaeus's zoological publications.

My aim is to analyse how his views on species from the standpoint of animals changed over time. Comparing the evolution of the Linnaean plant and animal species is difficult, which may lead to hiccups in the logic applied. Hopefully, I have succeeded in properly assessing the change in his views of what a species is and accurately describing the evolution of his concept, which, as will be shown below, was not simultaneous and parallel among the two kingdoms. In addition to a general review of the development of the Linnaean animal species concept, within the framework of surveys investigating the origins of Linnaean Amphibia (Krecsák & Bauer 2025, Krecsák & Wahlgren 2007, 2008, Krecsák et al. 2024, in press), I have assessed the application of the concept in connection with his class Amphibia (in the Linnaean classification the class included not only the presently known amphibians and reptiles, but additionally several groups of cartilaginous fishes – not covered in the present review). Linnaeus's attitude towards Amphibia was predominantly negative, dominated by aversion and most probably religious fear of snakes (Wahlgren 2012, Krecsák &

Bauer 2025).

This class was the least preferred by Linnaeus, therefore when he required a model class to write about, he would not, or very rarely did, select Amphibia (Lindell 2012, Krecsák & Bauer 2025), but the species within it captivated him and he approached them with the same zealous and minute commitment as any other group of animals (or his beloved plants) and discussed them in dozens of papers and dissertations (for a review see Krecsák & Bauer 2025). Linnaeus even decided to omit the group from general descriptions in his main systematic works (e.g., 'Animalia per Sveciam observata' (Linnaeus 1742 [1736]), 'Systema Naturae' Ed. 6 (Linnaeus 1748)) while in other publications (e.g., Linnaeus 1754) the Amphibia take the lead.

We have recently assessed (Krecsák & Bauer 2025) all Linnaean publications to locate those with herpetological content. The findings of this survey provided a solid basis to use Amphibia as a suitable test class for the species concept assessment, since, despite Linnaeus's limited interest in the group, by analyzing all of his 89 publications with herpetological content, I could review a substantial pool of evidence. Krecsák et al. (in press) documented 222 available Amphibia names published by Linnaeus in 'Systema Naturae' Ed. 10 (Linnaeus 1758) and post 1758. Although the class may not be the typical animal example, it shows at least to a certain extent how the theory was applied in practice.

Materials and methods

The complete published output (i.e., travelogues, individual encyclopaedic works, publications in scientific journals, dissertations co-authored with his students, revised dissertations included in 'Amœnitates Academicæ', orations) of Carl Linnaeus/Carl von Linné was reviewed for information on his animal species concept.

Findings have been compared with the Linnaean plant species concept, documented from the same literature sources as above, and extensive historical assessments published by various scholars of Linnaean botany.

Results

The fixed species concept: views of the young Carl Linnaeus (period between 1735–1744)

Very early in his scientific career (Linnaeus was only 28 when the first edition of 'Systema Naturae' (Linnaeus 1735) was published), we can trace clearly defined ideas about species and their origin. Early in his publishing history, Linnaeus stated his views about species and how they developed, and rendered detailed arguments on the various elements of his concept. Considering the quality and level of detail provided, we can conclude that the ideas put into print were the result of lengthy consideration and not simple repetitions of creation-linked concepts the young student would have been acquainted with during his childhood and early student years.

The species concept of the young Linnaeus was a fixist one, or in Broberg's (1980) denotation, 'almost fundamentalistic', namely, as a result of divine creation, only a defined and finite number of species exist.

Linnaeus discussed his view on the origin and number of species in the first edition of 'Systema Naturae' (Linnaeus 1735: [i] Observationes in Regna III. Naturae, Aph. 4), stating that God created one male and one female of every sexual species (namely animals) and one individual of every hermaphroditic species (namely plants). As the species reproduced, the number of individuals multiplied with every generation; therefore, we have more individuals than there were in the beginning. The key element of the concept was applicable to the three kingdoms of nature. 'Hinc nullae species novae hodienum producuntur.' ("Hence, no new species are produced nowadays.") (translation by Engel-Ledeboer & Engel 1964), therefore the progenitorial unity must be attributed to God, and the process must be called Creation. His first major botanical work, 'Fundamenta Botanica' (Linnaeus 1736a), contains the same origin story but presented from the standpoint of plants.

He further paraphrased his views on the creation of species and the number of initial specimens that inhabited the earth in his 'Oratio de telluris habitabilis incremento' ("On the increase of the habitable earth") (Linnaeus & Westmannum 1744, Linnaeus 1751a, 1781). According to his hypothesis, the globe was covered by sea and the earth was a small mountain, Paradise, where every singular sexual pair or individual of every hermaphroditic species of plants and animals lived. Based on Mosaic history, Adam gave names to every species of animals that God made appear in front of him. The initial pair of individuals/individual hermaphroditic species multiplied and increased their numbers with every generation. With the retreat of the sea, the size of the earth increased, and the individuals that initially multiplied in Paradise dispersed thereafter, thus increasing the overall area inhabited by species.

The 'nulla species nova' view can be traced in all early works by Linnaeus (e.g, 1735, 1736a, 1737a, 1740). To Linnaeus, Creation was the fundamental guarantee of order (Broberg 1980).

Linnaeus's species view did not include the idea of spontaneous generation (Larson 1968). Engel (1953) considered that constancy of the essential characters (i.e., particularity based on which she separated species) was a fact to the young Linnaeus and that he did not consider any progression or evolutionary change in these characters. This statement is only partially true since we can identify advanced views that stipulate progression in species in his early botanical publications proclaiming the fixed species concept. As such, he provides examples on the effects of the environment on species and the development of plant varieties already as early as 'Fundamenta Botanica' (Linnaeus 1736a: 30, aphorism 314), e.g., 'Locus aquosus folia inferiora, montosus autem superiora saepius sindit' ("A watery place often splits the lower leaves, but a mountainous one often splits the upper ones."). In 'Hortus Cliffortianus' (Linnaeus 1737b), Linnaeus discussed his belief that long-term exposure to different environmental conditions can lead to permanent changes in plants (see examples discussed in Ramsbottom 1938).

The fixed species concept applied to Amphibia in early works

Linnaeus clearly applied the fixed species concept throughout the complete first edition of 'Systema Naturae' (Linnaeus 1735), therefore to the 27 Amphibia itemized in the work as well. He recorded the divine creation of Amphibia in a

negative voice (Linnaeus 1735: x) 'Amphibiorum Classem ulteris continuare noluit benignitas Creatoris; Ea enim tot Generibus, quot reliquae Animalium Classes comprehendunt, vel si vera essent quae de Draconibus, Basiliscis, ac ejusmodi monstris oi τεταλόγοι fabulantur, certè humanum genus terram inhabitare vix posset.' ("The Creator in his benignity has not wanted to continue any further the Class of Amphibians; for, if it should enjoy itself in as many Genera as the other Classes of Animals, or if those things were true that the Tetralogists have fabricated about Dragons, Basilisks, and such monsters, the human genus would hardly be able to inhabit the earth.") (translation by Engel-Lederboer & Engel 1964). In the detailed expansion from Paradise discussion in 'Oratio de telluris habitabilis incremento' (Linnaeus & Westmannum 1744), he makes reference to a single representative of the Amphibia, *Vipera Caudisona* (*Crotalus Dryinas* (nomen corrigendum as per Article 32.5.2.5. of the Code (ICZN 1999) *Crotalus dryinas*) Linnaeus, 1758).

In early dissertations describing predominantly Amphibia (Linnaeus & Hast 1745, Linnaeus & Balk 1746, Linnaeus 1749b, 1749c) he did not discuss in depth the origin of species, but this could not be expected either, since these were contributions primarily focused on describing donations and collections (e.g. Krecsák & Wahlgren 2008, Krecsák et al. 2024).

Hybrids: a grain of sand in Linnaeus's fixed species concept (the 1740s)

In 1742, a student in Uppsala, Magnus Ziöberg, collected on an island in the Stockholm archipelago a common toad-flax (*Linaria vulgaris*) which would challenge the fixed species concept applied by the young Linnaeus and motivate him to dig deeper into the origins of the strange plant. The particular plant was almost identical to *Linaria*, but it had a differently built flower with five spurs instead of one spur characteristic of *Linaria*. Therefore, the difference in the sexual system mandated Linnaeus to place the plant in another class than the common toadflax. Linnaeus named the plant *Peloria*, Greek for monster (Linnaeus & Rudberg 1744, Linnaeus 1749a). While Linnaeus could not decipher the cause of the change in *Linaria* to *Peloria*, he highlighted key problems that the discovery poses: i) classes that differ in structure of fructification may therefore have the same origin and character, or one and the same class may possess different elements of fructification, and ii) more profoundly, that new and different species appear in the plant world. He concluded that such truths would mean the end of the use of fructification as the basis of all botany and demolish the natural classes of plants. He remarked that crossing of various kinds of species is not unknown in the animal kingdom, where the preternatural conjugation of two species creates an intermediate or mix of both, such as the Mule and a few other animals (Linnaeus & Rudberg 1744: 15). Similar to the majority of his student dissertations, Linnaeus revised this dissertation as well before its inclusion in 'Amœnitates Academicæ' (Linnaeus 1749a). In the latter, during the revision he added the example on the mating of a male Atlantic canary (*Fringilla canaria* in Linnaeus 1758) a female Eurasian siskin (*Fringilla spinus* in Linnaeus 1758), which produces fertile offsprings in the first generation, but upcoming generations become sterile (Linnaeus 1749a: 70). Recognizing and establishing the hybridization of *Peloria* would require a shift in the approach taken by natural historians. Similar conclusive thoughts are made on hybrid animals 'Hybrida vero haecce non propagantur, natura prohibente, ne plures, quam initio rerum fuere quadropedum species existant.' ("However, hybrids are not propagated in this way, nature forbids that there should be more species of quadrupeds than there were at the beginning of things.") (Linnaeus & Rudberg 1744: 15, Linnaeus 1749a: 70).

Hybrids and their origin preoccupied Linnaeus. During the 1750s and 1760s, he discussed the question of hybrids with several of his famous botanist collaborators, such as Bernard de Jussieu (1699-1777), Otto von Münchhausen (1716-1774), Johann Georg Gmelin (1709-1755), and Philip Miller (1691-1771). The available digitized original Linnaean correspondence can be accessed at Alvin, the Swedish national platform for digital collections and digitized cultural heritage. https://www.alvin-portal.org and The Linnaean Correspondence Collection at the Linnean Society of London. https://linnean-online.org/correspondence.html.

While working on the dissertation 'Plantae Hybridae' (Linnaeus & Haartman 1751) in a letter to his dearest friend, collaborator, and personal physician Abraham Bäck (1713-1795) dated 19 February [2 March according to Gregorian calendar] 1751 he wrote (Fries 1910: 140) "My battle nowadays, could I only be bothered, is to create new plants. I have found *Plantas hybridas* more generally than *Animalia hybrida* and quite a number of them. I believe myself about to open the door to a copious chamber of Nature, though she does not open without creaking. I don't enter anything myself, but I think that others will learn to have free access, since I opened the barrier." (translation from Swedish by Broberg 2023: 285).

In 'Plantae Hybridae' (Linnaeus & Haartman 1751, Linnaeus 1756), he listed a hundred plants believed to be hybrids, and additionally recorded partial hybrid animals and emphasized that hybrids are rare among animals. The Mule and the crossbreed of the Atlantic canary and the Eurasian siskin are the examples listed (Linnaeus & Haartman 1751: 3, Linnaeus 1756: 30–31).

By means of hybridization experiments between *Veronica maritima* x *Verbena officinalis* Linnaeus tried to show that all species within a natural genus originate from the same initial species (Linnaeus & Ramström 1759, Linnaeus 1763b). The hybrid-related thoughts were undoubtedly new, though the hybridization theory of Linnaeus was highly speculative (Müller-Wille & Orel 2007).

Linnaeus's thoughts on hybrids and the role of hybridization in the creation of new species were summarized in the essay 'Disquisitio de sexu plantarum' ("A dissertation on the sexes of plants") (Linnaeus 1760, 1790), where he stated that species appear though hybridization and highlighted the possibility that several plants within a genus that are recognized now as different species might have evolved from one initial species through hybrid generation. He was uncertain about the origin of species and left the question open in purpose 'At, num omnes hae species temporis filiae sint, an vero in ipso rerum primordio has vias definito quodam specierum numero Creator limitaverit, certo pronunciare non audeo.' ("But whether all these species be

the offspring of time; whether, in the beginning of all things, the Creator limited the number of future species, I dare not presume to determine.") (translation by Smith 1786).

Concept of hybrids and the Amphibia

While Linnaeus reported several hybrid examples from the animal kingdom, he never discussed the question in connection with the Amphibia. This does not come as a surprise, taking into account two key specificities. First, the captive keeping of amphibians and reptiles, which would have allowed hybridization experiments to be made, started at the end of the 18th century only (Heichler & Murphy 2004), although experiments are known from the early 18th century (Terrall 2014). Second, Linnaeus did not like Amphibia (Wahlgren 2012); his findings connected to the group were almost exclusively based on preserved material and descriptions provided by his students and collaborators. His field studies and teaching trips around Uppsala were almost exclusively focused on botany. Linnaeus issued a number of field notes on Amphibia (e.g., Linnaeus 1746, 1761). Still, these were limited to natural history observations only (Krecsák & Wahlgren 2008, Wahlgren 2012, Krecsák & Bauer 2025).

Progressive views: the complex species concept of old Linnaeus (particularly from the 1750s)

Whereas the shift from the firmly proclaimed fixed species concept to a variable species concept is clearly recognizable, the progressive views of old Linnaeus are less salient.

His publications contain multiple examples on his opinion that species progress and change, although not as detailed and explained in length as his general systematic views.

His first thought about extrinsic factors influencing the morphology of species can be found in 'Critica Botanica' (Linnaeus 1737a: 188-189) 'Omnes species originem familiæ suæ primam ab ipsissima Omnipotentis Creatoris manu numerant; creatis enim speciebus æternam legem generationis & multiplicationis intra speciem propriam imposnit Naturæ Author rebus. Concessit quidem externum sæpe lusum, at metamorphosin ex una in alteram speciem nunquam. Hinc duplices hodie inter plantas differentiæ; alia vera, Sapientissimâ manu omnipotentis producta diversitas; alia vero, ludentis naturæ, in externa crusta varietas. Seratur Hortus mille diversis feminibus, accedat Hortulanorum diligens cura in producendis monstris, & poft annos aliquot continebit sex millia varietatum, quas Botanicorum vulgus species dicit. Ego itaque distinguo species Omnipotentis Creatoris seu veras, a varietatibus Hortulanorum monstrosis; istas ob Authorem maximi facio, has ob authores respuo. Istæ persistunt, & perstitere cum mundo; hæ, ut monstra, brevi gaudent vita.' ("All species reckon the origin of their stock in the first instance from the veritable hand of the Almighty Creator: for the Author of Nature, when He created species, imposed on his Creations an eternal law of reproduction and multiplication within the limits of their proper kinds. He did indeed in many instances allow them the power of sporting in their outward appearance, but never that of passing from one species to another. Hence to-day there are two kinds of difference between plants: one a true difference, the diversity produced by the all-wise hand of the Almighty, but the other, variation in the outside shell, the work of Nature in a sportive mood. Let a garden be sown with a thousand different seeds, let to these be given the incessant care of the Gardener in producing abnormal forms, and in a few years it will contain six thousand varieties, which the common herd of Botanists calls species. And so I distinguish the species of the Almighty Creator which are true from the abnormal varieties of the Gardener: the former I reckon of the highest importance because of their author, the latter I reject because of their authors. The former persist and have persisted from the beginning of the world, the latter, being monstrosities, can boast of but a brief life.") (translation by Ramsbottom 1938).

Manuscripts prove the duality in Linnaeus's deep religious faith and his continuous struggle with his novel ideas when building his classification. In the first edition of 'Systema Naturae' (Linnaeus 1735), he placed man in the animal kingdom, class Quadrupedia, order *Antropomorpha* (later Mammals, Primates). He felt obliged to publish his thoughts although being aware that due to their nature these might draw the disapproval of the Lutheran church, and thus may result even in a cessation of his professorship. The most illustrative example is probably the paragraph in a letter dated 14 February [25 February according to Gregorian calendar] 1747 to his friend, fellow botanist, professor in Saint Petersburg, Johann Georg Gmelin (1709-1755): 'Non placet quod Hominem inter ant(h)ropomorpha collocaverim; sed homo noscit se ipsum. removeamus vocabula, mihi perinde erit, quo nomine utamur; sed quaero a Te et Toto orbe differentiam genericam inter hominem et Simiam, quae ex principiis Historiae naturalis. ego certissime nullam novi; utinam aliquis mihi unicam diceret. Si vocassem hominem simiam vel vice versa omnes in me conjecissem theologos. debuissem forte ex lege artis.' ("You disapprove my having located Man among the Anthropomorphi But man knows himself. Now we may, perhaps, give up those words. It matters little to me what name we use; but I demand of you, and the whole world, that you show me a generic character-one that is according to generally accepted principles of classification-by which to distinguish between Man and Ape. I myself most assuredly know of none. I wish somebody would indicate one to me. But, if I had called man ape, or vice versa, I should have fallen under the ban of all the ecclesiastics. It may be that as a naturalist I ought to have done so.") (published in Plieninger (1861: 54-56), translated by Greene (1909)) (Fig. 1).

While the illustrative example of primate systematics was indeed highly visible and controversial, Linnaeus was typically less vocal when presenting his possibly contestable ideas. Therefore, we do not find evolutionary ideas in 'Philosophia botanica' (Linnaeus 1751b) which was a textbook written to his students in a reader friendly way, thus a book that could be read even by the Lutheran ecclesiastics who controlled the University in Uppsala. On the other hand, in the footnotes or hidden in obscure places in the text of the highly scientific 'Species Plantarum' (Linnaeus 1753, 1762, 1763a), a work specifically interesting for botanist only, he could securely express his more profound convictions, feel safe and be safe (Greene 1909). This presumption of Greene seems correct, the Roman Catholic Church had banned Linnaeus and Pope Clement XIII (1693-1769) ordered in 1758 to have all works by him placed in the 'Index Librorum Prohibitorum' and condemned to be burnt, not due to his

ideas on species but due to his teaching on the sexual system of plants (White 1897, Ramsbottom 1938). The ban persisted until 1773, when Cardinal Zelanda gained permission from Pope Clement XIV (1705-1774) to have the sexual system of Linnaeus presented at the University of Rome by the Dominican monk and naturalist Antonio Minasi (1736-1806) (Ramsbottom 1938). I share Greene's (1909) view that Linnaeus deliberately took a safe approach to publish his novel ideas, either because of his faith or because he wanted to maintain his professorial chair, or both.

Greene (1909) and Ramsbottom (1938) traced multiple instances of Linnaeus tacitly accepting that a species was derived from other species through the altered environment. The difference between *Thalictrum lucidum* and *Thalictrum flavum* for example 'Planta, an satis distincta, a *T. flavo*? videtur temporis filia.' ("The plant is possibly not so very different from *T. flavum*. It seems to me to be a product of the environment.") (Linnaeus 1753: 547 translated by Greene 1909); Linnaeus recognized *Clematis maritima* as species (Linnaeus 1762: 767) although he states 'Varietatem *C. Flammulæ* statuunt Magnol & Rajus; meam potius *C. rectæ* judicarem ex solo mutatam?' ("Magnol, and also Ray have adjudged this to be a variety of *C. Flammula*. I should rather think it is derived from *C. recta* under altered conditions.") (translated by Greene 1909). In connection with the alpine or Siberian yarrow (*Achillea alpina*) he added the question whether the species was not moulded by the Siberian mountain soil and climate from the sneezewort (*Achillea ptarmica*) (Linnaeus 1763a: 1266). Similar examples are the sea beet (*Beta vulgaris*) (Linnaeus 1762: 322) *Kosteletzkya pentacarpos* (*Hibiscus pentacarpos*) (Linnaeus 1763a: 981) where he noted that they sprang from another species.

These succinct speciation ideas were never discussed in details and it is not clear whether Linnaeus considered these events as byproducts connected to the divine creation, or the result of environmental effects completely separate from the divine intervention, which result in such changes to the essential characters which he has previously attributed to God's creative work solely.

The above examples are more striking if we analyse them by having the Linnaean definition of variety in mind; (i.e., variety = transient forms, developed mostly under cultivation Linnaeus 1737a: 254). Linnaeus treated taxa that sprang from another species as a result of environmental condition as species and not varieties. This clearly shows an evolutionary species approach (Greene 1909).

Variety as a permanent form attached to its species can be traced in the early publications (e.g., Linnaeus 1737b) and not all varieties he listed were claimed to be produced by cultivation but some he reported as being produced by nature. His variety was often what is now known today as variation (e.g., size, colour, taste variations). Ramsbottom (1938) provides multiple examples of varieties produced by nature in his review of the Linnaean work 'Hortus Cliffortianus' (Linnaeus 1737b).

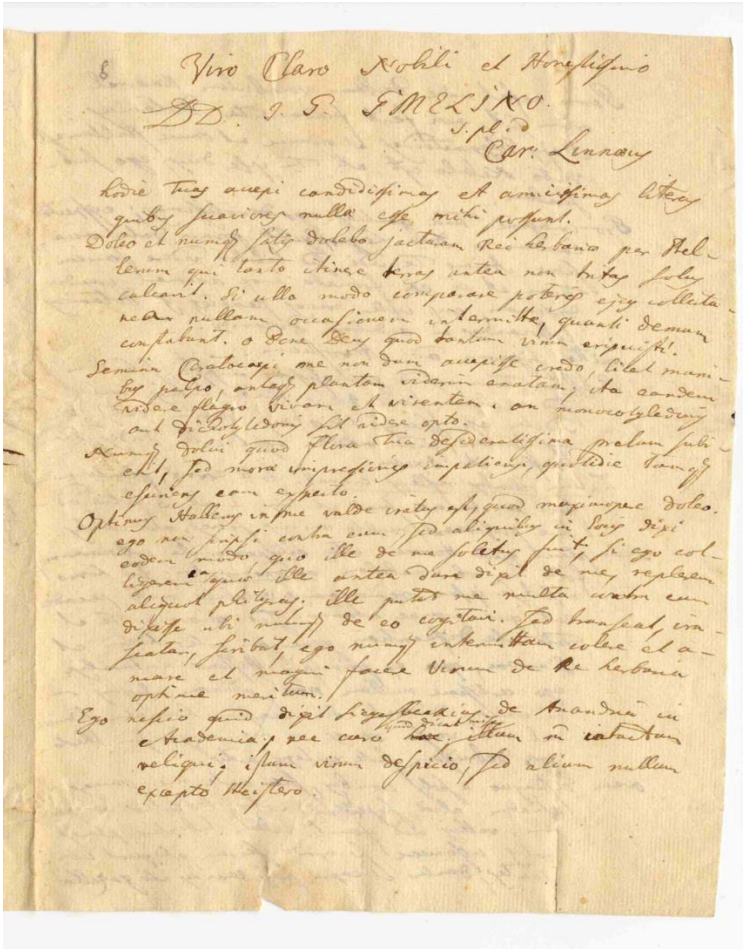


Figure 1. Letter from Linnaeus to Johann Georg Gmelin, St Petersburg. Source: alvin-record:223725.

'Fundamenta Botanica' (Linnaeus 1736a: 30–31) aphorisms 306-317 cover the variety. While most are applicable to plants only, Linnaeus would apply some to the animal kingdom as well, without detailing them, as reported above. Aphorisms include: ' 308. Sexus variationes naturales constituit, reliqæ omnes monstrosæ sunt.' ("308. Sex constitutes natural variations, all the rest are monstrous."); ' 317. Variationes diversas sub earum specie colligere, non minoris est æstimationis, quam qui sui species sub suo genere, collocare queat.' ("317. To collect different variations under their species is of no less value than to classify species under genera".).

Aphorism 317 is particularly interesting, since in connection of Amphibia he used variety for specimens he deemed particularly interesting as I shall show below.

Linnaeus never provided a clear definition of variety in his zoological works. Although he used variety consistently for animals as well, we can only deduct that he applied the same definition he has detailed in connection with plants (obviously as applicable to the animal kingdom). For example, aphorism 313 in 'Fundamenta Botanica' (Linnaeus 1736a: 30 aphorism 313) states 'Color corollæ, in cœruleis purpureisque petalis, facillime variat.' ("The colour of the corollas, in blue and purple petals, varies very easily.") In 'Fauna Svecica' Ed. 1 (Linnaeus 1746: ratio operis) he did not provide a definition of variety, only reported it to be a difference visible, such as white colour. He never commented on variation caused by sex in connection with animals.

In 1736 Linnaeus published a broadside 'Methodus' (Linnaeus 1736b), containing an explanation of his method for the descriptions of natural objects. Having the same size as the first edition of 'Systema Naturae' (Linnaeus 1735), the two publications were distributed together (Schmidt 1952, Wahlgren 2012). 'Methodus' with small alteration was republished in all 'Systema Naturae' up to Ed. 9 (Schmidt 1952, Cain 1992). Variety is mentioned and Linnaeus advises scientists to list all varieties published in the scientific literature but 'hæ sub specie certa, cum ratione facti, redactæ.' ("reduce these Variations under the natural species, with reasons made out.") (translation by Cain 1992). We can find direct proofs of the shift in his perception of species. Linnaeus crossed out the fixed and non-evolutionary species statement 'Natura non facit saltus' ("Nature does not jump") from his copy of the 'Philosophia Botanica' (Linnaeus 1751b: 27) (Fig. 2). It must be noted that the statement appeared one additional time in the publication (Linnaeus 1751b: 36) worded slightly differently (i.e, 'Natura enim not facit saltus.'/"For nature does not jump."), and that entry has was not removed. Therefore, an alternative explanation could be that Linnaeus only tried to avoid repetition (Mülle-Wille pers. comm.).

Müller-Wille & Orel (2007) highlight a key element in Linnaeus's distinction of species and variety, namely the fact that he has furnished naturalists with an operational criterion to distinguish the two. In the Linnaean view if plants belonging to one and the same species and brought under a regime of perfectly homogenous external conditions, they should be perfectly identical in all respects. Should differences be observed these would count as specific differences.

In the sixth edition of 'Genera Plantarum' (Linnaeus 1764), he provided a more sophisticated opinion on the origins of species: God created the orders, mingled them, and created the genera; nature mingled genera and created the species. Random mixing of these species occurred, and this resulted in the emergence of varieties. A similar overview of the creation of animals was never published by Linnaeus, who only discussed them in his lectures (Broberg 2023: 343). His view was like that detailed for plants: species mingled with each other in nature, and this resulted in new species.

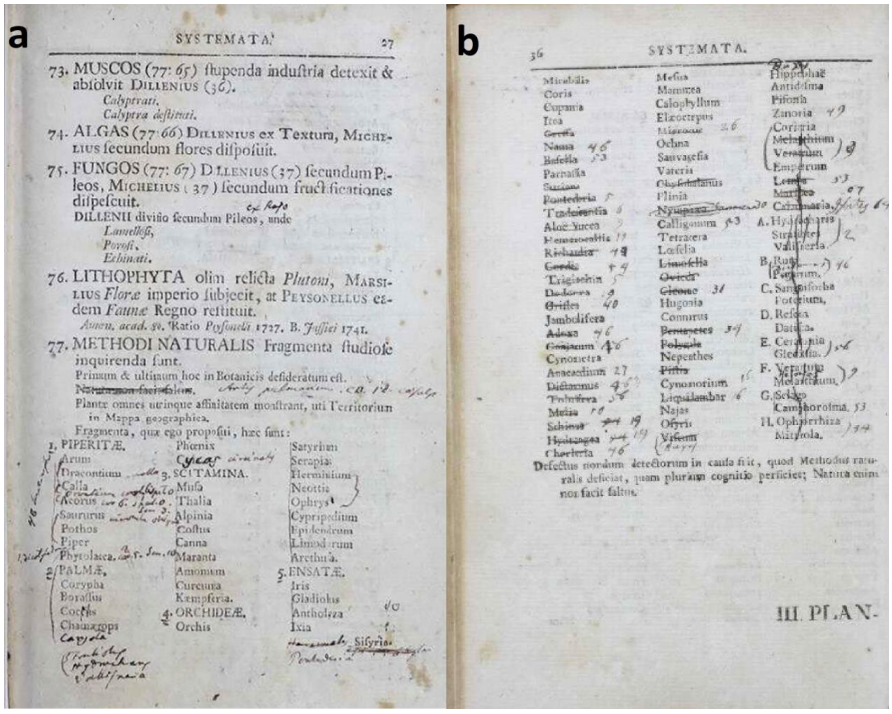


Figure 2. Page 27 (a) and 36 (b) of Linnaeus's own copy of 'Philosophia Botanica' (Linnaeus 1751b).

Although it might be perceived today as rudimental and naive, the concept applied by the old Linnaeas was a biological one. Müller-Wille (2007) phrases it appropriately as follows 'Linnaeus thought of species as composed of individuals connected by reproductive, or more precisely, genealogical relations that were governed by 'laws of generation' which could be studied empirically'.

The advanced evolving species by Linnaeus can still be denoted as rudimentary and fixist, still as Ramsbottom (1938) argued, the fixity idea applied by Linnaeus was one that a modern systematics would have to apply as well, since without some degree of fixity, systematic work would cease to exist.

Progressive species as seen with Amphibia

The class as a proper example of the advanced species view of the mature Linnaeus resurfaces during the 1750s, in the book containing the description of selected animals from the collection of King Adolf Fredrik (1710–1771) entitled 'Museum S:æ R:æ M:tis Adolphi Friderici Regis' (Linnaeus 1754). In the introduction of the publication Linnaeus mainly reproduced the expansion from Paradise discussion in 'Oratio de telluris habitabilis incremento' (Linnaeus & Westmannum 1744). This publication is particularly interesting, since, although he emphasized the fixed species concept in the introduction of the work, in the main part of the book he recognized that there is variability within the essential characters (primarily in the number of ventral and subcaudal scales for snakes) based on which he separated species. As such he used variety, to denote difference in snake specimens.

This was the first zoological work where Linnaeus consistently used binominal nomenclature. It is one of the most important pre-1758 Linnaean publications on the Amphibia. The book was published in folio format, with text in parallel columns in Latin and Swedish and included 33 copper-plate engravings (Krecsák 2006). Species descriptions were printed on 96 pages. On 32 pages he described 90 Amphibia species (2 *Caecilia*, 2 *Amphisbaena*, 3 *Anguis*, 47 *Coluber*, 2 *Boas*, 1 *Crotalius*, 1 *Draco*, 21 *Lacerta*, 9 *Rana*, and 2 *Testudo*) and in addition 22 of the 33 copper-plates depict solely Amphibia and one species was additionally added on Plate 28, depicting fishes.

Within Amphibia Linnaeus used variety for the following genera: *Testudo* (Linnaeus 1758, Linné 1766), *Lacerta*: (Linnaeus 1758, 1761, Linné 1766), *Rana* (Linnaeus 1758, Linné 1766), *Anguis* (Linnaeus & Hast 1745), *Coluber* (Linnaeus 1749b; 1754), and *Crotalus* (Linnaeus 1754). The use of variety was not linked to a specific period, nor to a specific genus, but rather connected to the level of knowledge accumulated about the different genera during various timepoints. Variety was a lowest systematic category in the Linnaean classification and natural varieties represented phenotypic variants he deemed systematically relevant to record.

Linnaean species within the genus

When discussing the question of the Linnaean species we must touch base on his view of the genus as well. Focus from the species of the young Linnaeus shifted, at least in connection with plants, towards the genus.

Müller-Wille & Charmantier (2012) showed that the genus in the early Linnaean publications was an expedient paper technology aimed to capture the continuously growing number of species that were described by the European naturalists. Similar to the progress and enhancement of the natural history knowledge, these simple placeholders evolved and developed into different concrete research objects and formed his 'natural system'.

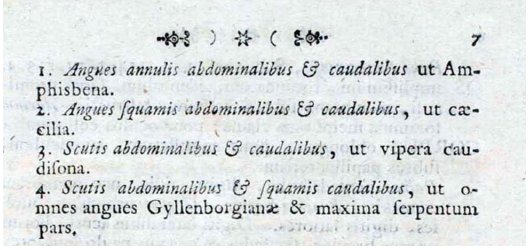
As Linnaeus's focus shifted towards the genus, he introduced the term 'essential character', which is not an essentialist approach (although, as shown below, it was erroneously considered as one), but a denotation used in a 'taxonomically useful' sense, therefore in similar sense as medieval philosophers (Winsor 2006a). The essential character was the particularity of that genus and not that of the species, a characteristic which distinguished one genus from the other. Linnaeus provided the following definition in 'Methodus' (Linnaeus 1736b): 'Character Essentialis notam generi maxime propriam tradens.' ("The Essential Character, setting out the note most exclusive to the genus.") (translation by Cain 1992).

Characteristics of the species within a genus could be classified into three groups: 1) characters that every member of a genus possesses but might be possessed by species of other genera as well; 2) characters that every member of a genus possesses and are unique to the genus; and 3) characters which are specific for a single member of the genus only (Stearn 1959).

The natural classification developed by Linnaeus would have implied that he should have taken decisions in the following order: 1) with the increase in the number of species he described and especially the ones which greatly matched to a certain extent those he placed in a particular genus, but which diverged from the species within the genus in the essential diagnostic characters plus other particulars (e.g., ecology, activity patters etc., elements he knew about, but rarely detailed in his publications) which therefore deserved and were placed, in another genus; followed by 2) reediting the essential characters of the genus to match the species included. Although he most probably intended to re-edit them, due to his extreme workload, and continuous new topics that he started writing about, this rarely happened (Stearn 1959).

Species and essential characters in Amphibia

In 1745 (Linnaeus & Hast 1745) he introduced the number of ventral and subcaudal scales as essential characters for the genus *Anguis* (at that timepoint the name for snakes) and a year later (Linnaeus & Balk 1746) scales and scutes as essential characters defining the *Amphisbaena*, *Caecilia* and *Anguis* (Fig. 3).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1. *Angues annulis abdominalibus & caudalibus* ut Amphisbena.
2. *Angues ſquamis abdominalibus & caudalibus*, ut cæcilia.
3. *Scutis abdominalibus & caudalibus*, ut vipera caudiſona.
4. *Scutis abdominalibus & ſquamis caudalibus*, ut omnes angues Gyllenborgianæ & maxima ſerpentum pars.

Figure 3. Page 7 of the dissertation 'Museum Adolpho-Fridericianum' (Linnaeus & Balk 1746) containing the first description of essential characters for Amphibia.

He would later emphasise these key characters to differentiate species within Amphibia in 'Systema Naturae' Ed. 6 (Linnaeus 1748: Lectori (To the reader) Ed. 10 (Linnaeus 1758: 196) and Ed. 12 (Linné 1766: 349) (Fig. 4). Interestingly, he considered coloration as a hugely variable character, not suitable to differentiate Amphibia (Linnaeus & Hast 1745: 4, Linnaeus & Balk 1746: 6, Linnaeus 1749b: 112, 1749c: 283). In particular, snakes were, in his opinion, extremely hard to distinguish, and various authors made errors in describing them 'quippe qui artubus destituuntur & prorsus univormes sunt' ('since they are deprived of limbs and are completely uniform') (Linnaeus & Hast 1745: 4, Linnaeus 1749b: 112).

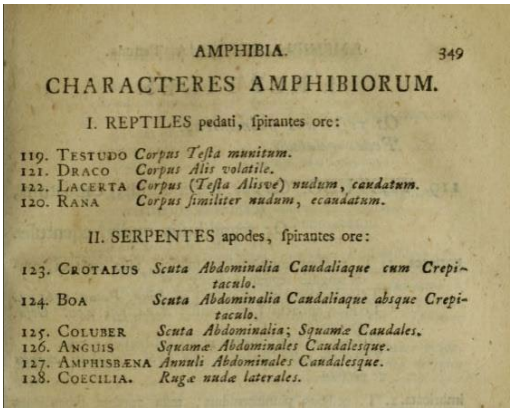
The first visual of the essential characters and their recording was provided on Tab. III of 'Systema Naturae' Ed. 6 (Linnaeus 1748) (Fig. 5).

Linnaeus would later use scale counts for all genera and species within the order *Serpentes*, but never for those he classified in *Reptiles*. He would use the same essential characters, but expanded, as the number of genera was higher, in 'Systema Naturae' Ed. 10 (Linnaeus 1758) and 'Systema Naturae' Ed. 12 (Linné 1766).

In the first and second editions of 'Systema Naturae' (Linnaeus 1735, 1740) Linnaeus included a single order *Serpentes* within class Amphibia (Krecsák 2025). In these publications he did not aim to provide a complete list of the known taxa, but only examples to highlight the classification proposed, therefore the number of species included is rather low (Krecsák 2025) (Fig. 6).

With the increase of his knowledge about various taxa, the number of orders, genera and species increased significantly. It is interesting to note that Linnaeus's high level classification (order and genera) for Amphibia was, with one exception, complete by 'Systema Naturae' Ed. 6 (Linnaeus 1748). The exception was the order *Meantes* that contained one species, *Siren Lacertina* (nomen corrigendum as per Article 32.5.2.5. of the Code (ICZN 1999) *Siren lacertina*), included in volume 2 of 'Systema Naturae' Ed. 12 (Linné 1767).

As such, in 'Systema Naturae' Ed. 6 (Linnaeus 1748) we already find two orders *Reptiles* (Footed, air breathing) and *Serpentes* (Legless, air breathing), *Reptiles* including 4 genera and *Serpentes* 6 genera. In later editions of the work (Linnaeus 1758; Linné 1766) he would only rename two genera and add further species, but otherwise maintained the classification intact (Fig. 7).



AMPHIBIA. 349

CHARACTERES AMPHIBIORUM.

I. REPTILES pedati, ſpirantes ore:

119. TESTUDO *Corpus Teſta munitum.*
121. DRACO *Corpus Alis volatile.*
122. LACERTA *Corpus (Teſta Aliſve) nudum, caudatum.*
120. RANA *Corpus ſimiliter nudum, ecaudatum.*

II. SERPENTES apodes, ſpirantes ore:

123. CROTALUS *Scuta Abdominalia Caudaliaque cum Crepitaculo.*
124. BOA *Scuta Abdominalia Caudaliaque abſque Crepitaculo.*
125. COLUBER *Scuta Abdominalia; Squamæ Caudales.*
126. ANGUIS *Squamæ Abdominales Caudalesque.*
127. AMPHISBÆNA *Annuli Abdominales Caudalesque.*
128. COECILIA. *Rugæ nudæ laterales.*

Figure 4. Section of page 349 of 'Systema Naturae' Ed. 12 (Linné 1766: 349) with the description of essential characters for the Amphibia (present amphibians and reptiles).

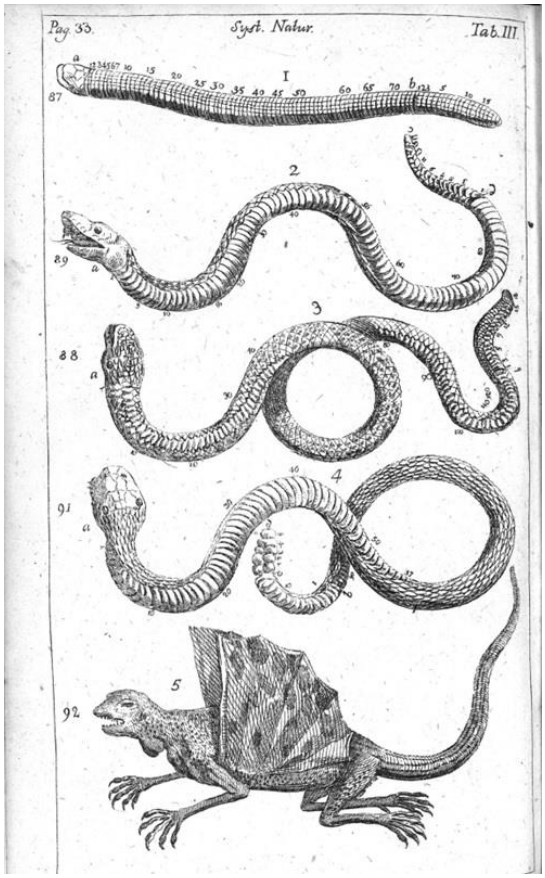


Figure 5. Tab. III of 'Systema Naturae' Ed. 6 (Linnaeus 1748), the first visual of essential characters for Amphibia.

Criticism of the Linnean species concept

During Linnaeus's lifetime the strongest criticism of his plant sexual system and thus his species concept as well was issued by the French naturalist, mathematician and cosmologist Buffon (complete name Georges-Louis Leclerc Comte de Buffon (1707-1788) in the first volume of his encyclopedic work 'Histoire naturelle, générale et particuliére' (Buffon 1749). Their feud was discussed in detail by multiple authors such as Sloan (1976), Barsanti (1984), Broberg (2023), therefore, it will not be reviewed here.

During the 1950s Ernst Mayr (e.g., Mayr 1957) started classifying Linnaeus's approach as a typological one, an incorrect classification schema based on Plato's concept of the eidos, a monotypical morphological species approach which does not take into account intraspecific variation and population structure (Mayr 1963, 1969). In his opinion the Linnaean species was one without dimensions, where the species is always separated by a complete gap from other sympatric species, lacking the dimensions of space and time and not evolving (Mayr et al. 1953). The Linnaean species concept without taking into account the obvious development as shown above was erroneously classified as strictly essentialist (Cain 1958, Mayr 1982, Ereshefsky 2000).

Multiple further works have proven that Linnaeus was not an essentialist (e.g., Müller-Wille 2007, 2011, 2013, Winsor 2001, 2003, 2006a, 2006b, Lidén 2020, Witteveen 2020).

On the contrary, Linnaeus's taxonomic methods aimed to describe the 'natural system' and were inductive and empirical, although disciplined, almost straight-jacketed, by a

complex apparatus of methodological, terminological, and nomenclatorial conventions (Müller-Wille 2007). Most importantly it was inductive in nature, since it was tied to concrete exemplars-individual specimens. As shown above, Linnaeus's views of genera and species changed with the increase in the number of observations he was able to make. The question whether Linnaeus approached the classification with or without any 'type concept' in mind is and was a topic of debate (e.g., Lidén 2020, Witteveen 2016, 2018, 2020).

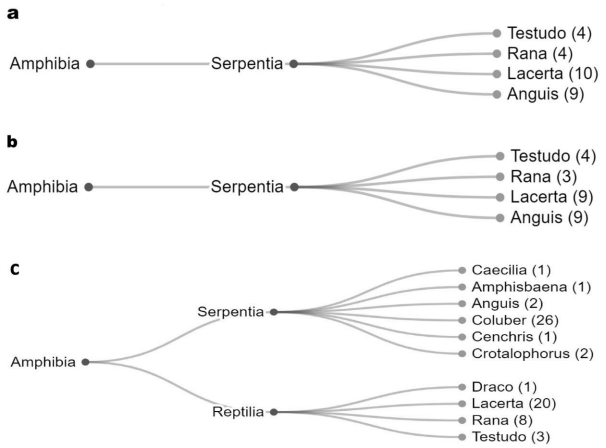


Figure 6. Classification of Amphibia in 'Systema Naturae' a) Ed. 1 (Linnaeus 1735), b) Ed. 2 (Linnaeus 1740) and c) Ed. 6 (Linnaeus 1748).

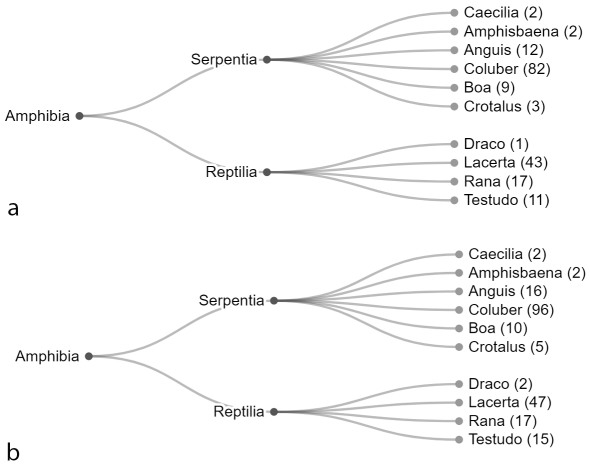


Figure 7. Classification of Amphibia in 'Systema Naturae' a) Ed. 10 (Linnaeus 1758) and b) Ed. 12 (Linné 1766).

Larson (1968) pinpointed the key empirical elements in Linnaeus's species concept, the individual nature of the species (the plants found in nature are admittedly individuals, but some individuals resemble one another more than they resemble the individuals who surround them) and the constant nature of species (the characters of species members are relatively constant, and species members tend to breed true). While most seeds will produce plants that are very similar to the parent plant, the individuals present some variation, thus they vary in colour, figures, size. Linnaeus's species concept therefore relies on two distinct marks, the intrinsic ones that are fixed and define the species, and the extrinsic ones, which are immaterial, variable, and somewhat unreal (Larson 1968).

Mayr (1999: 108) viewed the Linnaean system as linked to a static and strictly morphological species concept. His argument was that, according to Linnaeus, every species was a separate act of creation and therefore clearly separated from all other species. Taxonomists who follow this concept set up several standards (types) which they name, and as they receive additional specimens from new localities, they compare them with the standard and if they differ, they describe them as separate species.

As shown above, this critique was ill-grounded since Linnaeus's species was not static. The Amphibia species was indeed one primarily based on morphology, but not in totality. Linnaeus accepted the work of a limited number of scientists only (Bauer 2012, Krecsák et al. 2004, Krecsák & Bauer 2025), therefore he primarily based his descriptions on specimens he has examined in his own collection, or that of the King or the Royal Swedish Academy of Sciences and complemented the description with observations from his pupils (Adler 2012), close collaborators and the books authored by the limited number of trusted scientists. As such, the ecology and natural history elements in the descriptions are limited, but definitely not non-existent. For example, two of the Swedish adder species, *Coluber berus* Linnaeus, 1758 and *Coluber chersea* Linnaeus, 1758, are based on scale numbers, colour pattern, and venom potency (Krecsák & Wahlgren 2008).

Discussion

Linnaeus' species concept shifted from the fixist 'nulla species nova' concept in the first edition of 'Systema Naturae' (Linnaeus 1735), to a progressing almost 'evolving' species by 'Systema Naturae' Ed. 12 (Linné 1766). One may argue that he randomly threw his views in the books, since the same encyclopedic works may contain two different views, as demonstrated above. The reason for the inconsistency is time. Several years elapsed from the first draft of an opus magnum until its printing, therefore, the sections written during different periods may contain different views. 'Species Plantarum' (Linnaeus 1753), for example, took him about nine years to finish (Ramsbottom 1938). Similarly, he presumably worked on 'Systema Naturae' ed. 10 (Linnaeus 1758) for close to ten years.

In the works of the young Linnaeus, we can trace a parallelism in the use of the same ideas in his botanical and zoological works. Views on progression in species and the effect of environment in creation of varieties was a subject discussed solely for plants., which could be expected, since at that stage of his scientific carrier he focused his research almost exclusively on plants. Amphibia are listed as typical examples of divine creation, although as a negative one.

Further to the above empirical and theoretical approach to species, Linnaeus's strong religious belief almost mandated the fixed species concept, at least during his youth. The fixed species concept implied that the essential characters of a species do not change over time. Whether the strong argument regarding creation in early works was indeed a firm

statement of conviction or a combination of conviction and academic politics remains to be determined. The topic would require review in light of multiple factors: i) Linnaeus's strong religious upbringing, ii) his strong motivation to teach and make a career in an educational system dominated by the church and iii) his duty towards his financiers, many of whom were strongly religious, who not only had to be acknowledged in long appreciation and dedication sections at the beginning of the publications, but who were allowed to see and review the manuscripts before publication.

Although Linnaeus conducted hybridization experiments on plants only, he expanded and discussed his views in connection with animals (mammals and birds) as well. Contrary to the fixed species period, during the 1740ies, his discussion on hybridization and hybrids did not include examples from the Amphibia. As recorded above, this could be expected since this was prior to the era of the captive keeping of amphibians and reptiles.

Similar to the publications on hybrids, the forerunners in propagating his rudimentary progressive species concept were his publications in botany. While with plants, he accepted cases in which a species was derived from other species through the altered environment, and he published only a small number of zoological examples when varieties might be the result of extrinsic factors. The examples from Amphibia are less salient, though present.

With the increase in his knowledge about a genus or class, the way Linnaeus approached the 'natural system' meant that a species named in a certain way would be renamed later, and the same specimen or drawing would become the modern day 'type' of another species (Kirby 1892). His opinion about the species within a genus changed with the increase in the number of individuals he studied. In 'Museum Adolphi Friderici' (Linnaeus 1754) for example he recorded three varieties (alpha, beta and gamma) of *Crotalus* (in the publication *Crotalius*) *horridus* and noted that the number of scales of the specimens is substantially different, furthermore their colour and characteristics let him judge that there are multiple species within the genus. In 'Systema Naturae' ed. 10 (Linnaeus 1758), the three specimens are described as three different species, namely *C. horridus*, *C. dryinas*, and *C. durissus*.

Conclusions

The Linnaean fixed and stable animal species created by God, as seen by the young scientist in the mid 1730s, underwent substantial change through the course of Linnaeus's career. Hybrid plants discovered in the early 1740s slowly shifted his opinion and drove his views to the possibility of species development through hybrid generation. While this view was supported for plants, he ruled out the long-lasting speciation effect of hybridization in animals.

From the 1750s, his views of species shifted to a rudimentary evolutionary one, and he recognized that species progress and that environmental effects may cause species to develop into varieties and later into separate species.

The development and change in his views can be appropriately documented (except for the views on hybrids) in relation to his Amphibia as well, which shows that although he disliked the group, he deemed it appropriate to be studied and documented.

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