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The taxonomic history of the Linnean genus *Lacerta* (Squamata: Sauria: Lacertidae) in the mirror of book-illustration

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Abstract. The taxonomic history of the Linnean genus *Lacerta* illustrates the general taxonomic history in herpetology and can be visualized by the history of book illustration. There is a cohesive pattern in lumping *Lacerta* (Linnaeus, 1758; comprising lizards, crocodiles and salamanders; expanding to almost 100 species in Shaw, 1802) and splitting (Laurenti, 1768; comprising among others his new genus *Seps*, a part of Linnaeus' *Lacerta*), since the creation of binominal nomenclature by Linnaeus, and proceeding above all to the controversy of Boulenger and Méhely after 1900. These wavelike advances through the centuries are also characterized by a slow consolidation of the higher systematic categories (class-order-family-subfamily, etc.) and by a gradual reduction of the term *Lacerta* to almost the species level. This development ended now in an enormous generic and specific splitting within the family Lacertidae (Arnold et al. 2007), mainly based upon mitochondrial DNA research. The remaining "true" *Lacerta* comprises at present only half a dozen species, all of them close relatives of the type species, *Lacerta agilis*.

There is an historical interdepency between verbal descriptions and illustrations in the taxonomic advances of the genus *Lacerta*. The first illustrations of lizards (in the 16th century) are in equal measure characterized by the lack of systematic insight and the lack of technical options. Copper engravings (handcoloured) were used a little later. Since the end of the 18th century, new techniques accompanied and immensely facilitated a better recognisability of taxa: wood engravings – lithographs – chromolithographs – photos – modern digital colour photographs. The better understanding of the diagnostic scale structures called for their schematic depiction, and a schema of the dorsal drawing pattern was established. Diagrams for identification keys and/or of the phylogenetic relationships have become an indispensable part of modern taxonomic work. On the contrary, the genetic revolution of the last 20 years caused a great loss in importance of morphological characters, whereas top-quality digitalized coloured photos have shifted their importance mainly to popular publications on ecology, ethology, field herpetology and terraristic studies.

Keywords. Genus *Lacerta*; history; interdepency text/illustrations.

1. INTRODUCTION: SOME COMMENTS ON THE ZOOLOGICAL TERM *GENUS*

The history of the Linnean genus *Lacerta* is likewise a history of the term "genus". As Mayr et al. stated in 1953, the genus is a collective taxonomic unit consisting of a number of similar or related species. It is distinguished from all other higher categories by being recognized in the scientific name. The nomenclature proposed in Linnaeus' Systema Naturae (1758; animals) is binominal, consisting of two names, each with its own function. The functions which Linnaeus visualized for the components of the scientific name are diametrally opposite. The specific name signifies singularity and distinctness; the generic name calls attention to the existence of a group of similar or related species – it relieves the memory (Mayr et al. 1953: 48).

Even before Linnaeus there was a recognition of the categories *genus* and *species*. So, Plato definitely recognized two categories, the genus ("genos") and the species ("eidos"), and so did his pupil Aristotle. The naturalists of the pre-Linnean era were not consistent in the Latin names they gave to plants and animals. These names ranged all the way from uninominals (a generic name only), and binominals (a generic and a simple trivial) to polynominals (a generic name with several trivial epithets). The reason for this confusion was that they tried to combine two different functions in the name: naming (in the restricted sense of the word) and describing (Mayr et al. 1953: 202; see the legends in the images of Gessner and Aldrovandi Figs 2 and 3 hoc loco).

An objective criterion for the generic rank does not exist equivalent to the biological species concept ("reproductive isolation") in species systematics (see Mayr 1984: 141, 219; Jahn 2004: 237, 397; Joger 1996) as a criterion. It is therefore impossible to give an objective definition of the genus. So Mayr et al. (1953: 48) came to the following conclusion: "A genus is a systematic category including one species or a group of species of presumably common origin, which is separated from other similar units by a decided gap". They suggest for practical reasons that the size of the gap be in inverse ratio to the size of the unit; the latter qualification should prevent the recognition of unjustified monotypical genera.

The general view on the definition of the category genus has not changed much since then, contrary to the different species concepts (e.g. Joger 1996). Even Mayr et al. (1953) had attenuated their clause appearing so strict ("An objective criterion does not exist …."; p. 48) when discussing the presence of an "ecological niche" (p. 50) between genera. Later on Dubois (1988) and recently Dubois & Bour (2010) have extensively discussed the demand of "hybridizability" as a criterion for the definition of genera and subgenera. Additionally, the genetic revolution in taxonomy since the 1990s has decidedly consolidated the phylogenetic trees. So Speybroeck et al. (2010), in the introduction to their recent species list of the European herpetofauna, come to the decision: "As a distinct genus, we tend to recognize monophyletic clades that are genetically as divergent as other widely accepted genera in the same group. This is usually the approach employed by authors of scientific papers….". As a conclusion one might assert, that it was molecular biology which gave rise to a still continuing revolution in herpetological taxonomy, and – above all – to an enormous generic splitting, be it of the old Linnean genera *Testudo*, *Rana, Coluber,* or *Lacerta,* the latter being discussed here.

2. A BRIEF HISTORY OF THE LINNEAN GENUS *LACERTA*

2.1 The "lumper" Linnaeus (1758 / 1766) and his followers

The history of the genus *Lacerta* reflects also a history of zoological terms and categories, which can be dealt here only with its basic intentions. The word "Lacerta" (or the male gender "Lacertus") is of Latin origin. One of its three meanings is the linguistically derived English term "lizard". In this sense it is traceable in the Historia Naturalis of Plinius or in some works of the classic Latin poets Ovidius and Virgilius (Scheller, 1796). Since the era of renaissance this term was renewed by natural scientists in both the male and female gender (see Figs 1, 2, 4). Thus the term *Lacerta / Lacertus* had a long history before Linnaeus began to use it in the different editons of his "Systema Naturae" since 1735.

Linnaeus (or "Linné" after nobilitation), in his famous 10th edition of 1758, divided the class "Amphibia" into three orders: I. Reptiles, II. Serpentes, III. Nantes. The "Reptiles" comprise the four genera *Testudo, Draco, Lacerta, Rana*; the Serpentes comprise the six genera *Crotalus, Boa, Coluber, Anguis, Amphibaena, Caecilia*. The Nantes comprise six genera, all of them being transferred later on into the class Pisces. The Linnean *Rana*, parts of *Lacerta* and *Caecilia* constitute the current class Amphibia whereas the other genera in Linné's orders Reptiles and Serpentes are comprised in the present-day – polyphyletic – Reptilia. Linnaeus' (1758/1766) large genus *Lacerta* is an aggregation of 43/49 species, e.g. comprising the current Lacertidae (type species of Linnaeus' *Lacerta* is *Lacerta agilis* by later designation in Fitzinger 1843: 20), many other Reptile orders (like the crocodylia) and families, and even amphibians (e.g., salamanders; see Fig. 1). His genus *Lacerta* is encompassed by the diagnosis "Corpus, tetrapodum, caudatum, nudum" (body with four legs, caudate, "naked"; the latter characterization being completely incomprehensible, since his genus *Rana* is also characterized to be "naked"!). It seems that Linnaeus did not misjudge completely the heterogenity of his genus *Lacerta*. He tried to resolve the problem by species groups, characterized by short diagnoses and different stars. So his *Lacerta agilis* is within a group characterized by "** Cauda verticillata" (Tail round) and the group with the fire salamander, "*Lacerta salamandra",* is characterized by "***** Palmis tetradactylis; Corpore alepidoto nudo" (fore legs with four toes; body without scutes, naked). Nevertheless the newt "*Lacerta vulgaris"* (number 25; now: *Lissotriton vulgaris*) is grouped together with geckos and skinks.

Gmelin (1789) was formally a follower of Linnaeus, but he undermined his concept in the so called 13th edition of Linné's "Systema Naturae" where he accumulated the number of *Lacerta* species up to 77. Gmelin introduced eleven species groups within *Lacerta,* characterized by short diagnoses and mostly (but not always!) naming them (nominative plural of a main species being included, like "Salamandrae" with five stars (*****), comprising the Linnean *Lacerta salamandra*, No. 47) – or his "Ameivae s. Sepes" ("s." = "sive"; English: "or") comprising the Linnean *Lacerta agilis* – or the "Lacerti" (with nine stars) covering current tailed amphibians and reptiles, except lacertids, like the newt "*Lacerta vulgaris*" (now: *Lissotriton vulgaris* which is therefore not a part of his "Salamandrae"!). It is clearly noticeable that Gmelin, following Linnaeus, avoided dividing the genus *Lacerta* formally, unlike Laurenti (1768) had executed. The non-scientific rea-

sons may have been similar as described below in the discussion on Shaw.

Donndorf (1798) followed Gmelin (1789). He used the German terms "Geschlecht und Gattung" instead of "Gattung und Art" (genus and species; "Vorrede" p. 5). In his genus *Lacerta* Gmelin's system with eleven species groups, characterized by eleven stars, is comprised; he added however 14 newer species ("neuere Gattungen") within these species groups and nine species of undetermined species groups.

Shaw's (1802) General Zoology (vol. III, part III, Amphibia) is the last of the great encyclopaedias around 1800 which formally retains the generic name *Lacerta* in the broad Linnean sense. Its number of species has increased up to 86. Like the preceding encyclopaedias Shaw divided *Lacerta* into nine "sections or sets" giving them English names. He admitted however: "The above divisions neither are, nor can be, perfectly precise..." His "4. Lizards proper " comprised also the current day Lacertidae, among them the "Green lizard" "*Lacerta agilis*" taking first place. Smith & David (1999: 12, 13), when discussing the taxonomic situation then, drew the conclusion: "The rudimentary level of understanding of herpetological classification in Shaw's time is admirably exemplified by his treatment of the Division Lacertae, containing only two genera – *Draco* and *Lacerta* – that are extremely disparate in diversity. Nevertheless, Shaw was much more aware of the diversity and affinities of members of his genus *Lacerta* than is apparent in the assignment to one genus, inasmuch as he recognized nine distinct groups. To us it seems strange that such diversity was not reflected taxonomically when the relatively minor specialization of *Draco* received such emphasis. However, although Shaw boldly named new species or changed names, he reflected the trepidation widely shared at that time among his colleagues in splitting Linnean genera. Change then, as

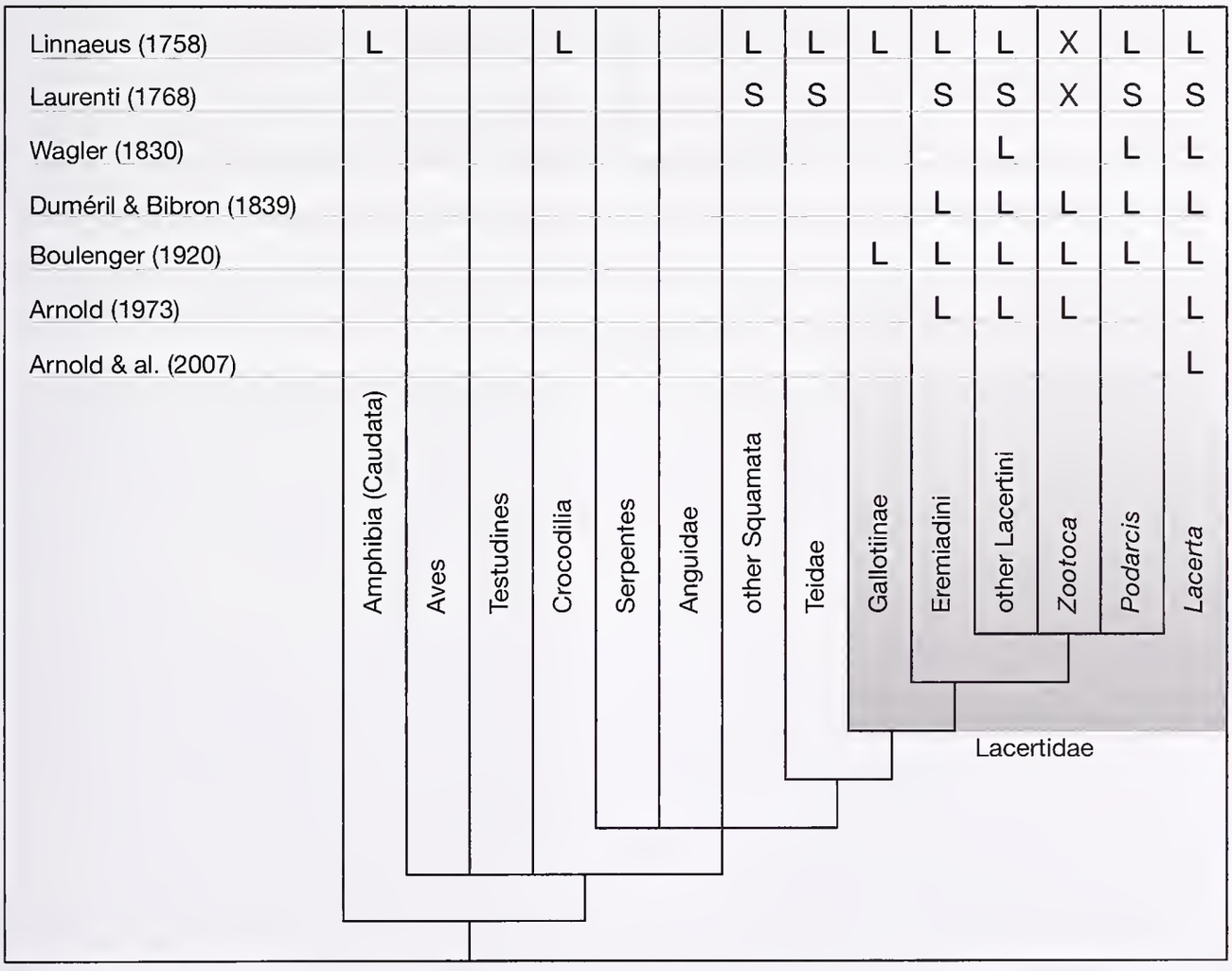

Fig. 1. Overview of the gradual reduction of the Linnean genus *Lacerta* (Laurenti's genus *Seps* respectively) from selected monographs: Linnaeus (1758) – Laurenti (1768) – Wagler (1830) – Duméril & Bibron (1839) – Boulenger (1920) – Arnold (1973) - Arnold et al. (2007: fig. 20); displayed upon a current phylogenetic tree (strongly simplified; from Dawkins, 2008, figs. p. 366, 422, 462; Arnold et al. 2007 figs.). The symbols ***L*** or ***S*** make clear a quotation of "*Lacerta*" (or "*Seps*" by Laurenti) within a given current systematical unit; ***X*** (no species from this group being described then).


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Der Koht von den Eydexen ſoll auch viel Krafft haben für etliche Kranckheiten der Augen. Lebendig in Oel gekocht/ ſoll ein zart Geſicht machen. Dahero Becherus:

Die Eydex lebendig in Oel man kochen thut/ Es macht ein weiß Geſicht/ iſt vor die Röhte gut.

Von der grünen Eydexe.

Lacertus viridis. Grüner Heydox/Egochs/Iltachs/ oder Eydex.

Fig. 2. "*Lacertus viridis*" from Gessner's (1671) last edition, the so called "Frankfurter Ausgabe". Wood cut.- The eye-catching bars across the tail indicate the whorls typical for a Lacertid tail. The text consists of medical and cosmetic advices, the latter in the form of a verse. The different insights of a painter and a mere engraver as well as the different qualities of a water colour compared with an engraving are shown by a comparison to an Aldrovandi image (Fig. 3).

now, came slowly. Shaw worked in a surprisingly substantial intellectual milieu of peers who would look critically at any change from established authority". A comparable thoughtfulness seems to have been widespread in scicnce – at least then (compare the situation of N.M. Oppel after his studies in Paris, being surrounded by "natural philosophers" in Munich since 1811; Schmidtler 2009: 509; Figs 16, 17 hoc loco).

The "Histoire Naturelle des Quadrupèdes Ovipares et des Serpens" by Lacepède (1788/89) is a milestone in the history of natural science. It highlights the beginning of the acceptance of Linnaeus's binominal system also in France, then leading in natural science. Up to that time the well known scientific controversies of Linnaeus (1708–1779) and Buffon (1708–1788) had prevented to a large extent the application of Latin binominal names in the French zoological and botanical literature, especially in the dozens of volumes of Buffon's "Histoire Naturelle" having appeared since 1750. The acceptance of Linnaeus' binominal system by Lacepède appears admittedly in a rather hesitant and concealed manner. It turns up only in the gigantic Latin "Synopsis methodica Quadrupedum oviparorum" beside the French "Table méthodique des Quadrupèdes ovipares" (see the elaborate description in David et al. 2002: Fig. 2). Here Lacepède accepted two classes. His first class ("Quadrupedes ovipari caudati") comprises two genera, *Testudo* and *Lacertus* ("Corpus absque testa"). The latter, with 56 species, is divided into eight divisions ("divisio") which are each described shortly, but not named. As Spix (1811: 342) pointed out there is however a contradiction between Lacepède's (1788) zoological findings in the text and the construction in the "Table méthodique" when stating that the salamanders are nearly related with the frogs. He accepted two current lacertid species in his third division (*Lacertus cinereus* and *Lacertus viridis*; both highly collective groupings, comprising among others the current genera *Lacerta / Timon* and *Podarcis / Zootoca* respectively; see also Schmidtler & Böhme, in prep.). The six species of salamanders are, contrary to Linnaeus and Gmelin, concentrated in one division ("VIII. Divisio"). It may be noted that the name with the male gender "*Lacertus*" Lacepède, 1788 is regarded to be an unjustified emendation

Fig. 3. *Podarcis siculus* ssp. From the collection of Aldrovandi's natural history images (16th century), see also Ceregato & Alessandrini (2007: fig. 462 upper part) and Delfino & Ceregato (2008). Water colour (Tempera). – The shapes and colours of lizards are excellently painted but the head shields are scarcely indicated. The naming of tail anomalies (especially *Lacerta* "biceps"!!!) reveals the lack of a species concept and the lack of a preset nomenclatural terminology. See chapter 3.2.

of *Lacerta* Linnaeus, 1758 (see David et al. 2002: 24). Lacepède's volume 1 and volume 2 (on the snakes) were rejected in general as a non-binominal work. This opinion remained heavily controversial (see David et al. 2002: 22; Dubois & Bour 2010). Anyway, one year later many species were adopted by Bonnaterre (1789) who has therefore become the correct author of many of Lacepède's names not being available. On Bonnaterre's *Lacerta* see more in chapter 2.2.

As obvious from the title, Bechstein's encyclopedia (1800–1802), "Herrn De la Cepede's Naturgeschichte der Amphibien" is first of all a translation from Lacepède's (1788 / 89) Histoire Naturelle, but comprising many additions. Bechstein used German terms. In his "Methodische Übersicht der eyerlegenden vierfüßigen Thiere" he translated Lacepède's system with the terms Classe, Gattung (genus) and Art (species), inserting the term "Familie", apparently in the sense of a species group below his "Gattung" in some genera, like the "Eidechsen" (lizards). He neglected Linnaeus' Latin binominal teminology to a large extent. His terminological system concerning the category "Art" (species) is inconsistent and confusing. In his "Zweyte Gattung, dritte Familie" (vol. II, like in Lacepède 1788) some current Lacertidae ("*L. cinereus*, die graue Eidechse" and "*L. viridis*, die grüne Eidechse") are comprised. He gave an excellent picture of the "Graue Eidechse / *L. cinereus*" (vol. II, Taf. 1; depicting the male and the female of a present-day *Lacerta agilis*), and demonstrating thereby that this important taxon was then differently understood in different European countries (see

Fig. 4. *Lacerta agilis* (male). Left figure: Draft of the right figure; drawer Rösel von Rosenhof (Cod. Icon. 48, Bayerische Staatsbibliothek München; before 1758). Water colour. – Right figure: Frontispiece in Rösel v. Rosenhof (1758). Hand coloured engraving.- The changes in scientific insight by the famous drawer and natural scientist Rösel mirror as well his personal "metamorphosis" as the changes in general views in differentiating a "salamander" (left: with its nude skin!) from a lizard (right: with its lifelike scaly skin and pileus scutes; but: occipital and interparietal scutes are still lacking!). Both, salamanders and lizards, became in the same year parts of the Linnean genus *Lacerta*.

also Schmidtler 2004; Schmidtler & Böhme in prep.). In his "Anhang" (additions; vol. II, 297–325) however, Bechstein on the one hand accepted the modern binominal terminology of Laurenti (1768) and Schneider (1799; e.g. *Stellio phylluros*, p. 307) or used Gmelin's (1789: 1060) Latin species group terms, (p. 311; like *Stelliones* = "Spiegeleidechsen").

2.2. Early generic splitting after Linnaeus

Laurenti (1768) was the first to subdivide the Linnean genera of amphibians and reptiles (Testudines excluded) in a comprehensive work, especially Linnaeus' large genera *Lacerta* and *Coluber*. Laurenti totally suppressed the name *Lacerta*, but established instead of 11 new genera within his order II "Gradientia" (see Kuzmin 2005: 246), among them "*Seps*" comprising also the current species of Central European *Lacerta* and *Podarcis* and some of their synonyms (see chapter 2.4; see Fig. 1). After Stejneger's (1936) type species designation (*Seps caerulescens* = *Lacerta agilis*; see also Dubois 2010; and Fig. 6 hoc loco) Laurenti's *Seps* became a junior synonym of *Lacerta*. *Seps* Laurenti comprised after all only four current families, all within the Squamata (Lacertidae, Scincidae, Teiidae, Gymnophthalmidae) and appears therefore much more restricted than the Linnean *Lacerta*.

Laurenti's splitting had still an earlier forerunner in Garsault's (1764) long forgotten and just rediscovered work "Les Figures des Plantes et Animaux" here concerning in particular the French herpetofauna around Paris in ten plates (see Welter-Schultes et al. 2008, 2009; Dubois & Bour 2010; Fig. 5 hoc loco). Garsault (1764) used the species names *Lacertus terrestris* (now: *Podarcis muralis* (Laurenti); nomen conservandum), *Lacertus viridis* (now: *Lacerta bilineata* Daudin; nomen conservandum), the genus names *Scincus, Salamandra* (with the French name "salamandre" behind; depicting *Salamandra salamandra terrestris* Bonnaterre). A certain systematic unstableness is however unmistakable when depicting the crested newt (today *Triturus cristatus* (Laurenti), nomen conservandum) under the Latin nomen *Lacertus aquatilis*, but simultaneously under its French name "Salamandre d'eau".

Valmont de Bomare in the second issue of his "Dictionnaire d'Histoire Naturelle" (1767/68) added for the first time Latin names to the French names. There appear likewise considerable systematic inconsequences: On the one hand, under the key word and generic name "Lézard / *Lac-*

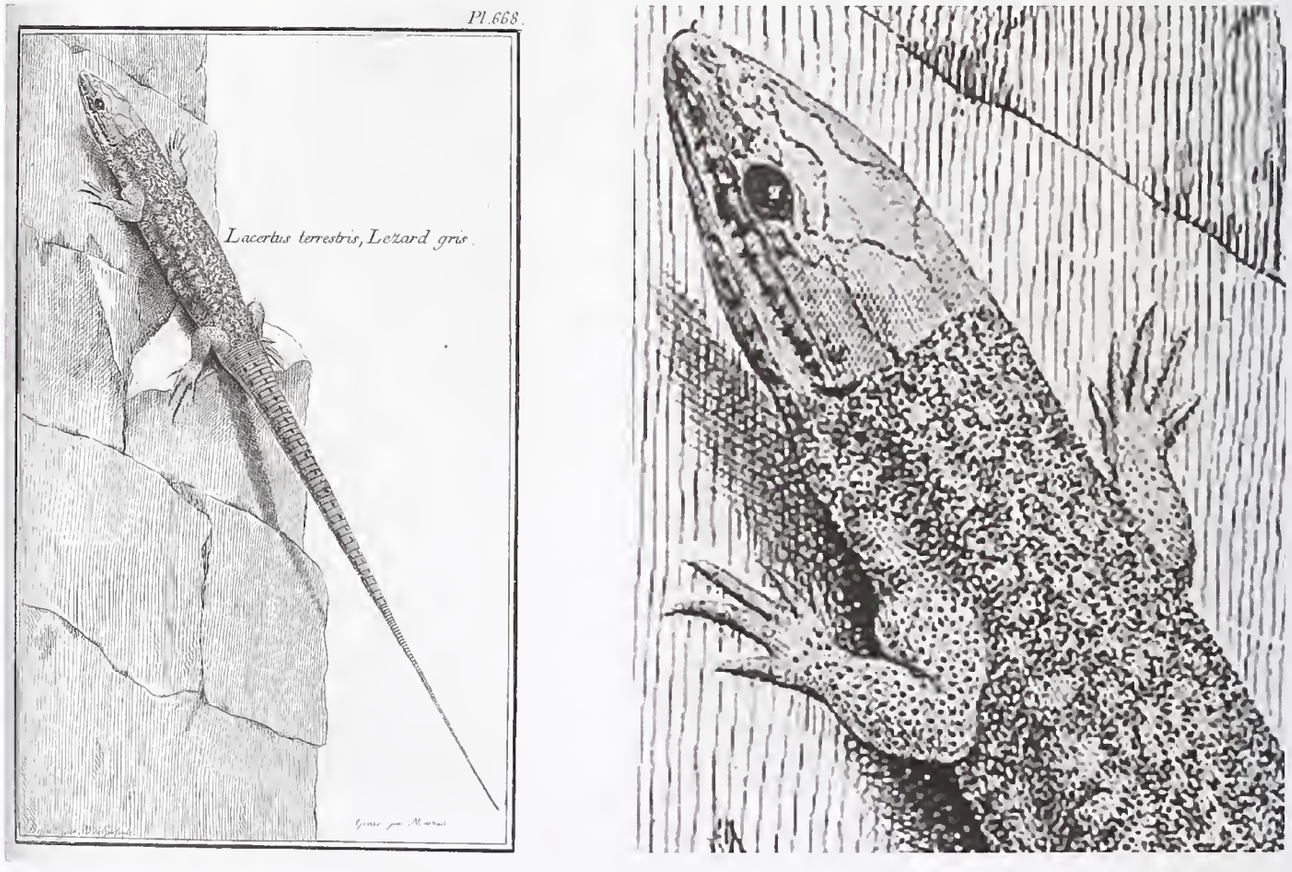


Fig. 5. "*Lacertus terrestris*" (= *Podarcis muralis*; western subspecies) from Garsault (1764), a forerunner of Laurenti (1768), having been rediscovered in the last years (see Dubois & Bour 2010). Copper engraving. – The pattern of the upper head scutellation (right figure) is not yet perfect; the frontal and postfrontals are not executed within the central part of the pileus.

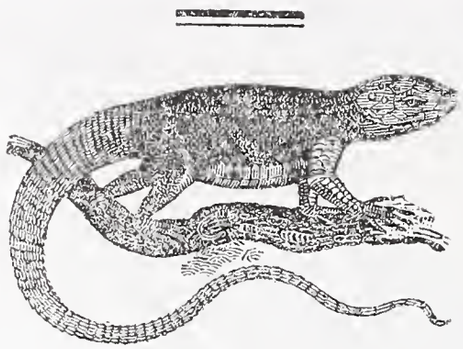
Fig. 6. *Seps caerulescens* (= *Lacerta agilis*; Fig. III), *Seps muralis* (= *Podarcis muralis*; Fig. IV), *Seps argus* = a juvenile *Lacerta agilis*; Fig. V). From Laurenti (1768: Tab. I, upper part). Copper engraving. – Laurenti's (1768: Tab.I, fig.III) *Seps caerulescens* has accomplished perfection for the first time in the history of a lacertid engraving: The arrangement and shape of all of the pileus scutes are accurate. In equal measure the dorsal pattern is very representative for the species. This figure is all the more outstanding, as Laurenti himself was obviously not yet aware of the enormous impact of head scutellation in species recognition. So it was the exactness of the drawer and the engraver who were solely responsible for the quality of the figure. Developments like these demonstrate the prospective relevance of naturalistic figures in book illustration for the scientific progress in reptile systematics about 1800. Otherwise, the quality of the smaller figures IV and V is considerably lower and does scarcely contribute to species recognition.

ertus" (Vol. III, p. 548, 1768), all the "amphibian species" in Linnaeus' (1758) sense are understood. On the other hand, under the keyword Salamandre / *Salamandra,* Valmont de Bomare (vol. V, p. 441, 1767) described only "real" salamanders, and explicitely the two species *Salamandra terrestris* (currently: *Salamandra salamandra terrestris* Bonnaterre) and *Salamandra aquatica* (apparently a collective species comprising some current species of water newts, especially *Triturus cristatus*). This dictionary was however suppressed by the ICZN (Anonymus 1925; Dubois & Bour 2010), its nomenclature not being always binominal for species.

Although Bonnaterre (1789; see also 2.1), often misunderstood as a mere copyist of Lacepède, took over many details from Lacepède (1788) in his "Tableau Encyclopédique", he did not follow him (nor indirectly Linnaeus) in his generic lumping. On the contrary, he widely accepted the generic splitting by Laurenti. His first class ("Reptilia ecaudata") comprised the three genera of Laurenti: *Rana, Hyla, Bufo,* whereas his second class (Reptilia caudata) with seven genera approached Laurenti's second order (less genera indeed), excluding the snakes as well, but comprising the turtles (*Testudo*). Bonnaterre's *Lacerta* comprised 52 species, among them still some of Laurenti's new "lizard" genera, like *Basiliscus, Iguana, Ameiva, Stellio.* Bonnaterre suppressed Laurenti's generic name *Seps* and the current Lacertidae are comprised in his genus *Lacerta*. He also doubted the validity of some of Laurenti's new species (e.g. *Seps caerulescens,* now *Lacerta agilis*).

Latreille in Sonnini & Latreille (1801) in gross terms accepted the generic systematics of Laurenti (1768). Some of Laurenti's species of the new genus *Seps* were included in the "IIIe genre Lézard, *Lacerta*". Latreille anticipated many of Daudin's (1801–1803; see chapter 3.3) descriptions and took the opportunity to thank him for his communications (1801, vol. 1, p. 215; "M. Daudin...a eu l'amitié de me communiquer, par extrait, les descriptions qu'il a faites de plusieurs reptiles de la famille des lézards... Il me sera doux, en le citant, de lui payer à la fois le tribute de mon estime et celui de l'amitié"). Harper (1940) named this procedure a certain sort of piracy.

In early regional faunas, which do not cover the whole family of lacertids, the acceptance of Linnaeus' lumping or Laurenti's splitting was heterogenous. Being one of the first authors, Schrank (1784 and 1798) completely adopted Laurenti's genera (e.g. "*Salamandra atra*" Laurenti, "*Seps viridis*" Laurenti), whereas Razoumowsky (1789) or Wolf in Sturm (1799, 1802, 1805) were using Linnaeus' terminology system (e.g. "*Lacerta agilis*" Linnaeus or *Lacerta paradoxa s. helvetica*" (n.sp.; now the newt *Lis-*



THE GREEN LIZARD.

The colours of this species are subject to variety, becoming pale at certain seasons of the year, and more particularly after the death of the animal. The upper parts of the body are of a beautiful green, more or less variegated with yellow, grey, brown, and even sometimes with red. In warm regions it grows to a larger size than in more temperate countries, being sometimes found thirty inches in length. The inhabitants of Africa eat the flesh of this animal.

Fig. 7. "Green lizard" (= *Lacerta viridis*); probably the first lizard in the renewed wood cut technique by Bewick (1809 – 1816; "wood engraving"; cf. Dance, 1989, Schmidtler, 2007). As usual then, engravings of the "abhorrent" reptiles (so Linnaeus 1758:194) were significantly of a lower quality than the birds or mammals (cf. the images in Bewick 1791). Nevertheless this green lizard is recognizable here. It was a great advantage of this printing technique that the images could be printed together with the text upon the same page (unlike copper engravings or lithographs - these upon separate plates). So, later on, wood engravings proved to be adequate for the popular small English "chap books", or the German "Naturgeschichten". This kind of letter press was also often used for schematic figures in a text page.

sotritou helveticus) in the former; "*Lacerta atra*" (Laurenti), and "*Lacerta agilis*" Linnaeus in the latter. In contrast Koch in Sturm (1828) made use of Laurenti's generic names ("*Seps stellatus*" Schrank, "*Triton alpestris*" Laurenti) in the same "Deutschlands Fauna".

2.3. An enormous increase of knowledge since 1800

Since about 1800 the knowledge in natural science increased immensely and many new species were described. Laurenti's (1768) system of splitting the Linnean genera began to win recognition. Nonetheless, Laurenti's total replacement of the generic name *Lacerta,* e.g. by *Seps*, was usually not accepted.

Some months after the issue of Sonnini & Latreille's (1801) encyclopaedia Daudin started his "Histoire Naturelle des Reptiles" ("An X" = 1801; see Harper 1940 for the exact data). His "Second ordre. Les Reptiles Sauriens" approximately conforms with the genus *Lacerta* lumped by Linnaeus and Lacepède (1789), but the salamanders were transferred to his fourth order "Les Reptiles Batraciens" comprising also the frogs. His genus *Lacerta* is one of 16 genera within these "sauriens", most of them being current lacertids except the Ameivas. His generic systematics resembles Laurenti's (1768) splitting system in general. One of the decisive differences was its essential feature in the formal persistence of a large genus *Lacerta*, whereas Laurenti's generic name *Seps* was made use of for only some two- or four-legged saurians. Daudin's greatest progress may be the redivision of his newly split genus *Lacerta*: It comprised 32 species subdivided into seven unnamed "sections". These sections presage the present lacertid genera in some very ambiguous outlines. For example, his second section "Lézards verds" contains *Lacerta ocellata* (now *Timon lepidus*) and *Lacerta viridis* (now: within *Lacerta* s. str.) as well, whereas his fourth section "Lézards tachetés" contains "*Lacerta lepida"* (a young *Timon lepidus*) and his new *Lacerta maculata* (a very cryptic name in some respects). Especially with Daudin the level of knowledge began to increase immensely. This growth did not only include further generic taxa but also an inflation of species names by naming "real" new species, also individual or local variations, both sexes or juveniles. Replacement names took the upperhand more and more. The names for the one current species *Lacerta agilis* (three *Seps* species names in Laurenti (1768); see Schmidtler 2004 and Kuzmin 2005) were augmented by Daudin to three more names (male, female, young) in his fifth section "Lézards gris". This fifth section comprised also his "lézard gris" with the Latin name "*Lacerta agilis*" (currently *Podarcis muralis*).

Until very recently Oppel (1811, see Fig. 16) was held as the author of the family Lacertidae ("Lacertini") (now: Lacertidae Batsch, 1788; cf. e.g. Speybroeck & al. 2010). Based upon Duméril (1806) he moved ahead the systematics in the higher categories and made them clear by trees as a forerunner of evolutionary ideas (Schmidtler 2009).

Merrem (1820) was the first to publish a schematic image and a terminology of the lacertid head scutellation (chapter 3, Fig.12). His genus *Lacerta* comprised 27 species, some of them being new. His systematics is based in general upon Daudin (1801–1803), Oppel (1811) and Cuvier (1819). He introduced some new terms and taxa in the higher categories. So his genus *Lacerta* is part of the "stirpes" A. Ascalabotae, the "tribus" 1. Gradientia, the III. order Squamata and the class 1. Pholidota (the 2. class is named Batrachia).

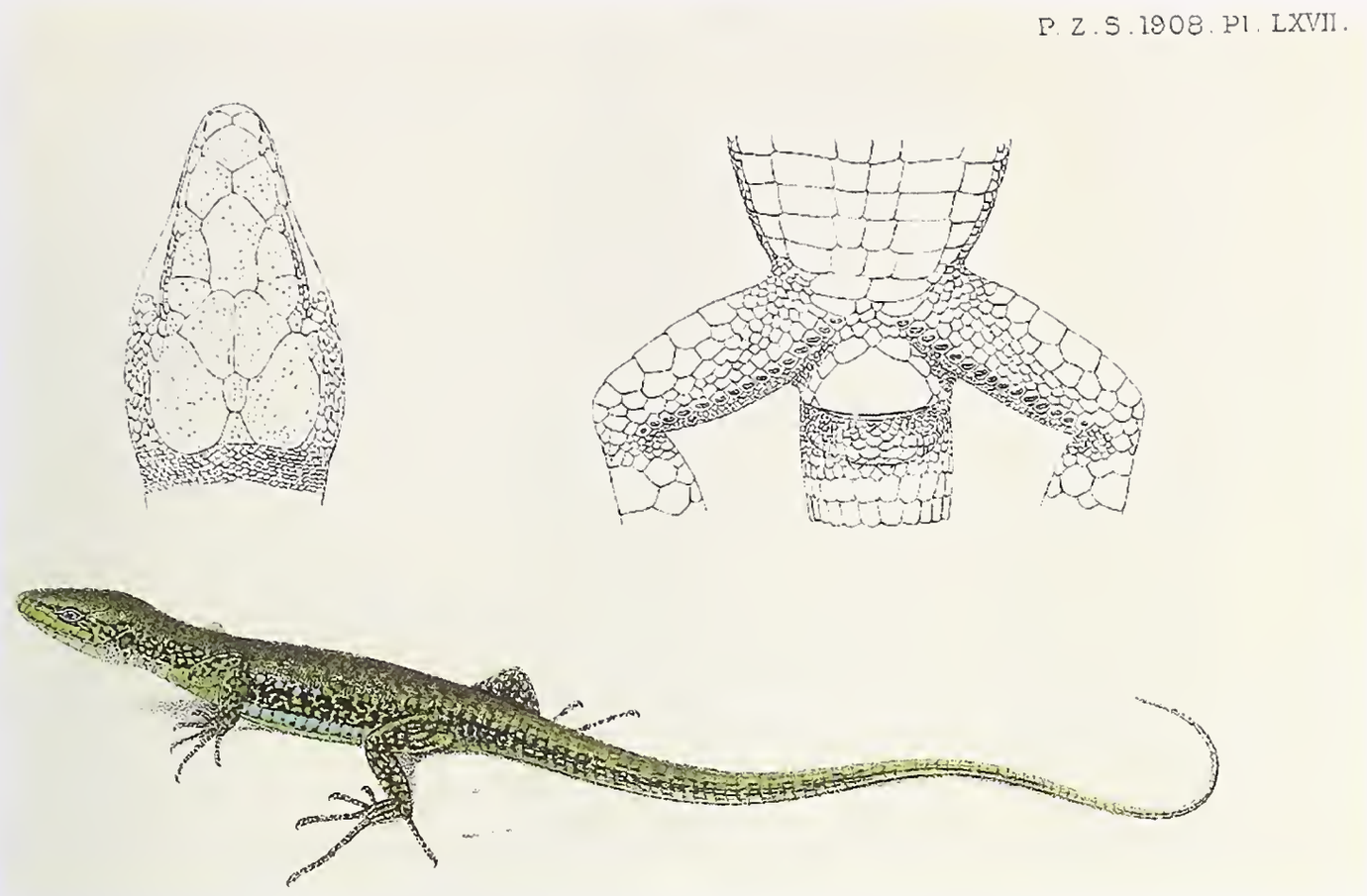


Fig. 8. *Lacerta chlorogaster (= Darevskia chlorogaster)* from Boulenger (1909: Pl. LVII). Below one chromolithograph (i.e. an image printed successively with differently coloured lithograph plates), and above two (pen-) lithographs (scutellation of pileus and surroundings of the anal region). The highly informative combination of naturalistic and schematic figures upon one lithographic plate turned up at first in the middle of the 19th century.

The "Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften" was Fitzinger's (1826) first important work (see Mertens, 1973). His "XI. Familia. Lacertoidea. Lacertoiden" comprises three genera, among them *Lacerta* with 17 species. It was apparently the first time in a systematic listing that neither this family nor the genus *Lacerta* comprehended any taxa now being ranked outside the present-day Lacertidae.

It was the age of the great systematic monographs and shortly afterwards Wagler (1830) published his "Natürliches System der Amphibien mit vorausgehender Classification der Säugethiere und Vögel". Wagler's monograph is especially distinguished by comprehensive and progressive morphological and anatomical descriptions and considerations (pp. 211–344). His genus *Lacerta* only comprised lizards belonging to the current genera *Lacerta* (s.str.) and *Timon*. His "Familia III. L. autarchoglossae" comprehended the Linnean taxa *Lacerta* and *Tachydromus*, as well as the new lacertid genera *Zootoca, Podarcis, Aspistis, Psammuros* (the latter two are still synonyms of *Psammodromus* Fitzinger), apart from some genera belonging to other current families. *Zootoca* and *Podarcis* were regarded mostly as synonyms subsequently, but were revalidated more than 150 years later. All in all Wagler's systematics of the genus *Lacerta* appears rather modern (Fig. 1).

The "Histoire Naturelle des Reptiles" in eight large volumes by Duméril & Bibron (1834–1854) represents a new kind of herpetological monograph, compared with Daudin's (1801–1803) work. Especially because of the immense growth of knowledge the different species chapters increased, comprising different sub-chapters (e.g. in *Lacerta vivipara*: "caractères, synonymie, déscription" with "patrie et moeurs" in seven pages). His species chapters on *Lacerta* were based on many detailed new works, including also relatively new disciplines (e.g. reproduction biology) by Milne Edwards (1829), Dugès (1835), Cocteau (1835) and Tschudi (1837). Duméril & Bibron (1839) were lumpers, compared with Wagler (1830). Their genus *Lacerta* comprised 16 species (some of them new), subdivided into three species groups. Their genus *Lacerta* is currently ranked in 14 genera, some of them having

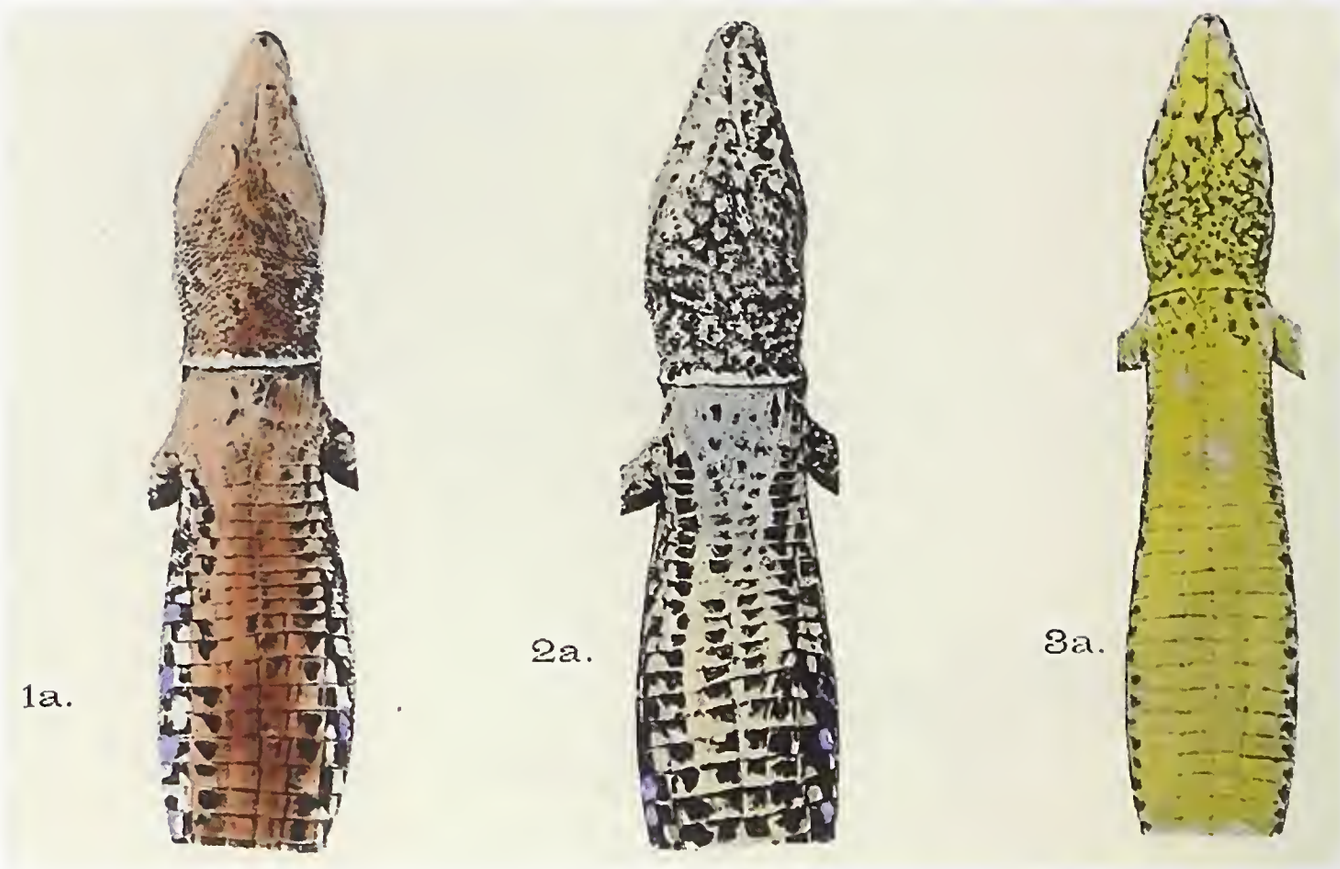


Fig. 9. Ventral sides of "*Lacerta muralis* vars. *lilfordi / serpa / brueggemanni*" (i.e. now three different species of *Podarcis*), from Boulenger (1905: pl. XXII). – Hand coloured photos (The combination of hand colouring and photographs was very unusual then in natural science). The spotting and the colouration are of systematic importance in these "varieties". The diagnostic features, especially the sutures of the shields, are not presentable simultaneously in the same figure (See Fig. 8!). – In 1853 the new technique of photography had been received with enthusiasm after a publication on reptiles (varans and a crocodile) and other animals ("Even the best painter would not have the patience and ability to make visible all the details and structures…"; see Niekisch 2010).

been described before Duméril & Bibron. The present-day Lacertidae corresponds to Duméril & Bibron's subfamily "Coelodontes" comprising nine genera. Duméril & Bibron (1839: 1–19; 181–189) published a substantial historical outline of their family "Lacertiens ou Autosaures" and their genus *Lacerta,* respectively.

It is worth mentioning the chapters on "Erpétologie" or "Lézards" in different French natural science dictionaries, which are now more or less forgotten. They mirror imposingly the general advances in herpetology between 1800 and 1850 and in *Lacerta* in particular: See Bosc d'Antic (1817: 521–528), Cloquet (1819/1823), Bory de Saint-Vincent (1826/1828), Cocteau (1835) and Meunier in Guérin (1836).

Contrary to Duméril & Bibron (1839), Fitzinger (1843) proved to be a splitter. Within his class Reptilia he included the categories "Series", "Ordo", "Tribus" and "Familia". The present-day Lacertidae were divided into three families: Lacertae, Tachyscelides and Eremiae. His first family Lacertae comprised four genera (*Scelarcis, Podarcis, Chrysolamprus, Lacerta*), most of them being subdivided into subgenera. As Mertens (1973: V) stated, Fitzinger's (1843) work is of tremendous significance for the study of amphibians and reptiles, not so much of the nearly one hundred new generic and subgeneric names proposed, but because he always cited generic type species. In the case of *Lacerta* this tremendous significance is manifested in Fitzinger's (1843: 20) determination of "*Lacerta agilis*. Linné" as the type species of *Lacerta.* The excellent coloured engraving by Wolf (1799) may have been here the decisive motive. Like Kaup (1836; see also Fig. 17), Fitzinger (1843: 12) was also a follower of the so called, unusual "Naturphilosophie" (natural philosophy), then distributed above all among German speaking natural scientists.


Die Grünen
vom Kaiserstuhl

Text und Fotos von Walther Rohdich

Der Kaiserstuhl ist Deutschlands wärmstes Weinbaugebiet und vulkanischen Ursprungs. Die dortigen Lößberge südlicher Lagen erwärmen sich im Hochsommer bis auf 40 °C und darüber. Aber das macht ein vorzügliches Weinbaugebiet noch nicht aus – erst die Durchschnittstemperaturen sind es, die Spitzenweine, aber auch seltene Tiere und Pflanzen gedeihen lassen.

Unsere Smaragdeidechsen

Klimatisch bevorzugte Inmitten kühlerer Gegenden – der Kaiserstuhl liegt zwischen den ruppigen Gebirgen Schwarzwald und Vogesen – sind meistens Oasen für ungewöhnliche Tiere und Pflanzen. So auch hier: Hauptlebensräume, die weiter südlich liegen, haben Ausläufer nach Norden geschoben: für Orchideen, Insekten und Reptilien. Damit kommen im Kaiserstuhl Arten vor, die wir erst wieder, und da sehr zahlreich, im Mittelmeerraum antreffen. Dem uns hier am meisten interessierenden Tier wollen wir uns jetzt zuwenden. Es ist ein Kleinod besonderen Formats: unsere größte und prächtigste Eidechse, die Smaragdeidechse (*Lacerta bilineata*). Sie ist zwar selten in Deutschland, aber sie oder ihre östliche Schwesterart *Lacerta viridis* kommen an einigen Stellen inselartig vor. Die Smaragdeidechse ist die Wärmebedürftigste unserer Eidechsen. Außer am Kaiserstuhl lebt sie noch in der Mark Brandenburg und im Donaugebiet bei Passau (*L. viridis*) sowie an Mosel und Rhein (*L. bilineata*). Das Vorkommen von *L. bilineata* am Kaiserstuhl ist zweifellos am bekanntesten. Hier haben ihr die landwirtschaftlichen Umwälzungen der letzten Jahrzehnte, wie der Terrassenausbau der Weinberge, wenig anhaben können. Der Bestand scheint gesichert.

Kurz einige Sätze zu ihrer Biologie: Die Smaragdeidechse ist die größte Eidechse Mitteleuropas, mit einer Länge von 40 cm. Sie ist durchgehend leuchtend grün gefärbt, mit verschiedenen Anordnungen dunkler Zeichnungselemente, wie Punkte und Flecken. Die Männchen sind in

Ein Maikäfer ist ein fetter Happen für dieses prachtvolle Männchen im Hochzeitskleid.

Fig. 10. Male of *Lacerta bilineata* from the journal "Reptilia" (Nr. 20, 2004: 68): A perfect layout and a perfect digital colour photo have been combined here. The beautiful and viewable photos serve firstly for keepers (demonstrating feeding habits, etc.) and field herpetologists (identification in the field / shop) in popular articles. In the light of modern genetic methods the images have lost their traditional predominance in underlining systematic descriptions.

2.4 The era of George Albert Boulenger (ca. 1880–1920)

The end of the 19th century was initially characterised by new questions and topics as is displayed by Eimer's (1881) indication of «darwinism» in the caption of his article. There infrageneric and infraspecific, geographical researches came to the fore. I should like to emphasize the basic advances, such as his formation of terminologies in the dorsal pattern (Fig. 14). We may remember here his long-standing controversy with Bedriaga concerning the origin of colouration in insular lizards (see Müller 1994).

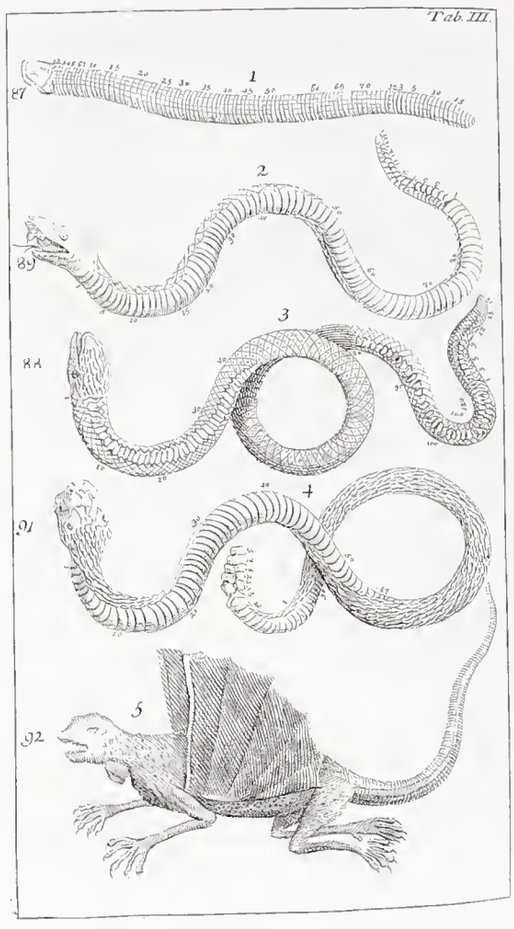
In this Darwinian sense Bedriaga (1886) tried to explain the phylogenetic relations and origins of lacertid taxa (the genus *Lacerta* with the five subgenera *Lacerta, Algyroides, Tropidosaura, Zerzumia, Bettaia*) by detailed discussions. His subgenus *Lacerta*, however, contained still species of all current subfamilies and tribes. With respect to book illustration (see chapter 3) it may be regretted that his descriptions were corroborated by a single lithographic plate only. The reasons here – as ever – may have been economical ones.

Simultaneously the time of Boulenger's great comprehensive catalogues in herpetology commenced. In the introduction of his Catalogue of the Lizards (three volumes) Boulenger (1887) displayed the immense increase in the numbers of lacertid species known and characterized: Duméril & Bibron (1839), 43 species – Gray (1845), 57 species – Boulenger (1887), 97 species. Boulenger's Lacertidae comprised 17 genera and his genus Lacerta comprised 21 species, among them species of the whole Eurasian and African range, i.e. species within the current subfamilies Gallotiinae and Lacertinae (some species of the current tribe Eremiadini not excluded; see Figs 1 and 19). The chapter «11 *Lacerta muralis*» (1887: 28) with many «varieties» underlines his very typical species concept. Boulenger's vol. III contains a set of excellent lithographs, among them the new species *L. parva* (now *Parvilacerta*) and *L. yayakari* (now *Omanosaura*).

Méhely (1909) carried out intensive studies on morphology and osteology of European and Caucasian lacertids. Aside from the further development of the terminology of scutellation, osteology (Fig. 13), and pattern of muralis-like lacertids, he described the genus *Apatlya* and the «I. Gruppe: Archaeolacertae» of his genus *Lacerta*, comprising species of the current genera *Anatololacerta, Phoenicolacerta, Hellenolacerta, Dinarolacerta, Iberolacerta* and *Darevskia*. His victorious species concept («species» instead of Boulenger's *L. muralis*-varieties) displays his famous controversy with Boulenger.

Schreiber (1912) adopted the view of Méhely and his species concept within the European-Caucasian lacertids. Within the current genus *Podarcis* he accepted as the first in a large monograph not less than eight species, most of them, especially *Lacerta muralis* and *Lacerta serpa (= Podarcis siculus)*, comprising many varieties and subvarieties.

Boulenger (1920 / 1921), covered the lacertids in their whole Eurasian and African range. Irrespective of the acceptance of six «sections» within *Lacerta* he insisted upon his system of the one *muralis*-like species, following his catalogue (Boulenger, 1887) and later papers (1905 and 1913 especially; see Fig. 19). His *Lacerta muralis* (belonging to his subgenus *Podarcis* Wagler) covers not less than 31 (!) «varieties». Most of them are presently species or subspecies or invalid forms within the genus *Podarcis*, but there are also taxa of the current genera *Archaeolacerta, Iberolacerta* and *Darevskia* to be found. It seems now that



TABULA III.

AMPHIBIA *nonnulla ſiſtens.*

1. AMPHISBÆNA 87. annulis circularibus trunci 1—70; caudamque 1—15 cingentibus.
   a. *Caput.* b. *Anus.*

2. COLUBER 89 ſcuta abdomen tegentia 1—80; ſquamæ caudam ſubtus tegentes 1—17.
   a. *Caput.* b. *Anus.* c. *Apex caudæ.*

3. ANGUIS 88. ſquamæ abdomen tegentes 1-120; ſquamæ caudam tegentes 1—17.
   a. *Caput.* b. *Anus.*

4. CROTALOPHORUS 91. ſcuta abdominis 1—90; ſcuta caudæ 1—13; crepitaculi articuli 1—5.
   a. *Caput.* b. *Anus.* c. *Crepitaculum.*

5. DRACO 92. pedes quatuor; cauda; Alæ duæ cum radiis cartilagineis alarum.

Q 5 TA.

Fig. 11. Some reptiles and their scale countings depicted by Linnaeus (1756: Tab. III; 9th edition. Copper engraving). The scale countings refer mostly to the ventrals and subcaudals in snakes and were given especially in the text on the genus *Coluber*. In the diagnoses of the genus *Lacerta* no scutellation features were used then. This is apparently the first attempt of a schematic delineation and description of body shields in herpetology. The same features were used also, without depictions, in the text of the 10th and 12th editions (1758 / 1766).

his system was a relatively superficial morphological one, because he accepted also some (morphologically) conspicuously different species besides his «*L. muralis*», like *Lacerta taurica* (now within *Podarcis*), or *Lacerta chlorogaster* (now within *Darevskia*). This was one of Boulenger's rare mistakes in which, soon later, the herpetologists of this time did not follow his exceptional authority.

Mertens & Müller (1928) adopted Boulenger's (1920) European subgenera (*Archaeolacerta, Podarcis, Zootoca, Lacerta*), but they did not diverge in substance from the species concept of Méhely (1909) and Schreiber (1912). They were the first to accept geographical subspecies (see Wermuth in Böhme 1981), i.e. a trinominal nomenclature in European herpetology (e.g. «*Lacerta agilis exigua* Eichwald»). In addition they carried out some changes being nomenclaturally necessary (e.g. *Lacerta lepida* Daudin, 1802 - instead of the preoccupied *Lacerta ocellata* Daudin, 1802).

In Mertens & Wermuth (1960) there are considered many new discoveries of the European herpetofauna (especially new descriptions of many lizard subspecies of *«Lacerta» sicula, L. erhardii, L. melisellensis, L. lilfordi*, etc., from Mediterranean islands, by Cyrén, Müller, Wettstein, Radovanovic, Eisentraut, Buchholz, in various papers each, since the second list of Mertens & Müller (1940). Nevertheless this «Dritte Liste» characterizes the relatively stable generic and specific systematics and nomenclature in lizards between 1940 and 1990.

2.5 Towards a final breaking up of the genus Lacerta by new methods and techniques

The basic works of Arnold (1973, 1989) and Böhme (1971) broke new ground in the systematics of the Lacertidae. New techniques (genital-morphological, karyological, electrophoretical, albumin-immunological, genetic features) and modern univariate and multivariate statistics were executed.

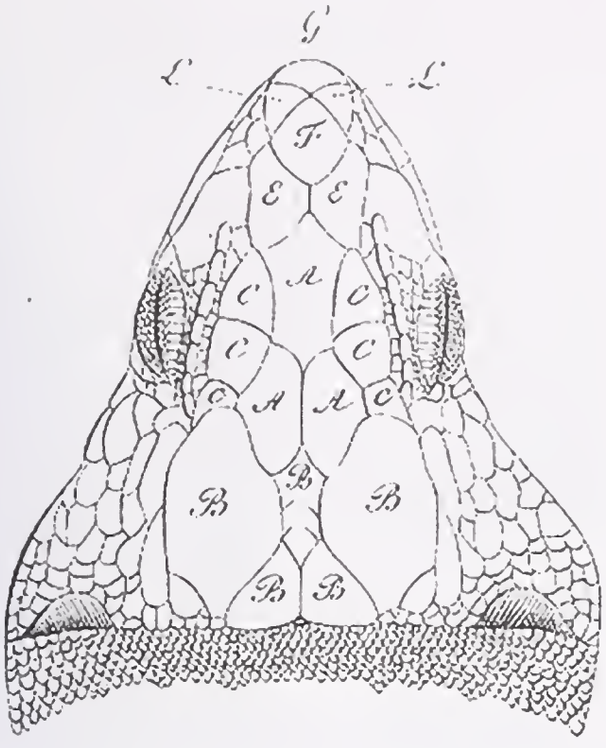


Fig. 12. Schema of the pileus scutellation in Merrem (1820: p. XII–XIII and fig. p. 191 upper part). (Pen-) lithography. – The decisive step ahead in the schematic depiction of lizards was made by Merrem (1820). Based upon his similar system in snakes (Merrem 1790 and 1820), he gave names to the pileus shields of an adult *Lacerta ocellata* (now: *Timon lepidus*; see his pages XII and XIII) and depicted their abbreviations in this figure. The description covered seven types of scutes with the letters A (Wirbelschilder – Scuta vertebralia), B (Hinterhauptschilder – Scuta occipitalia), C (Augenbrauenschilder – Scuta superciliaria), E (Stirnschilder – Scuta frontalia posterioria), F (Schnautzenschilder – Scuta frontalia anterioria), G (Rüsselschild – Scutum rostrale, L (Nasenlöcherschilder – Scuta nasalia). This system was later on differentiated and improved by Milne Edwards (1829: pls. 5–8) who depicted and described also the shields of the lower sides of head, body and limbs. The concept of Merrem (1820) and Milne Edwards (1829) remain valid today.

The first results of Arnold's (1973, 1989; see Fig.1) elaborate researches, based mainly on morphology were the revalidation of the old Waglerian genus *Podarcis* and of *Gallotia* Boulenger, 1916 (then a subgenus) besides two very preliminary groups, named "*Lacerta* groups I and II".

The taxonomic tentativeness at that time found its way into the comprehensive "Handbuch der Reptilien und Amphibien Europas" (Böhme in Böhme 1981, Böhme, 1981).

Mayer & Bischoff (1996) (re-) established further separations from the so far comprehensive genus *Lacerta* (*Zootoca, Omanosaura, Timon, Teira*). They visualized a phylogenetic tree of the Lacertidae from the relationships of their serum albumins.

The numerous and very detailed morphological works of Arribas (1997/1999) resulted in the splitting off of the mainly SW-European genus *Iberolacerta* Arribas 1997, and above all of the mainly Caucasian genus *Darevskia* Arribas, 1997 from *Lacerta*. Thereby also a very old controversy (especially of Méhely and Boulenger; see chapter 2.4) on the *muralis*-like "Archaeolacertae" could be finished. The name *Darevskia* was given in honour of the great Russian herpetologist I.S. Darevsky (1925–2009) who had detected parthenogenesis in these lizards, and therewith in reptiles (see Darevsky 1967; Schmidtler 2010).

Beginning with the comprehensive work of Harris et al. (1998) new genetic methods have also been adopted in the systematics of the lacertids and they have caused here, like everywhere in systematics, a revolutionary situation. DNA sequences from parts of the 12S, 16S and cytocrome b mitochondrial genes, together with morphological information, were used to estimate the relationships within the family. This work was continued by Arnold et al. (2007; Fig. 20 hoc loco). DNA sequences indicated that the Lac-

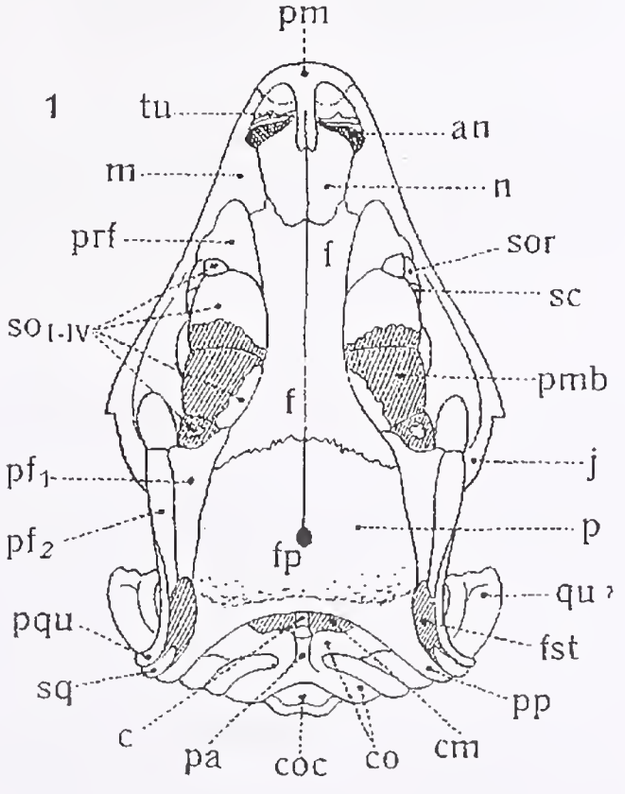


Fig. 13. Schema of skull bones (*"Lacerta horvathi"= Iberolacerta horvathi*) in Méhely (1909: Taf. X, upper part) on the basis of Siebenrock (1894). – In the middle of the 19th century important osteological investigations also were executed in lacertids. They allowed taxonomic research in the higher categories but also within lacertid genera and species, after a reasonable schematization in osteology, above all in skull terminology, had been found.

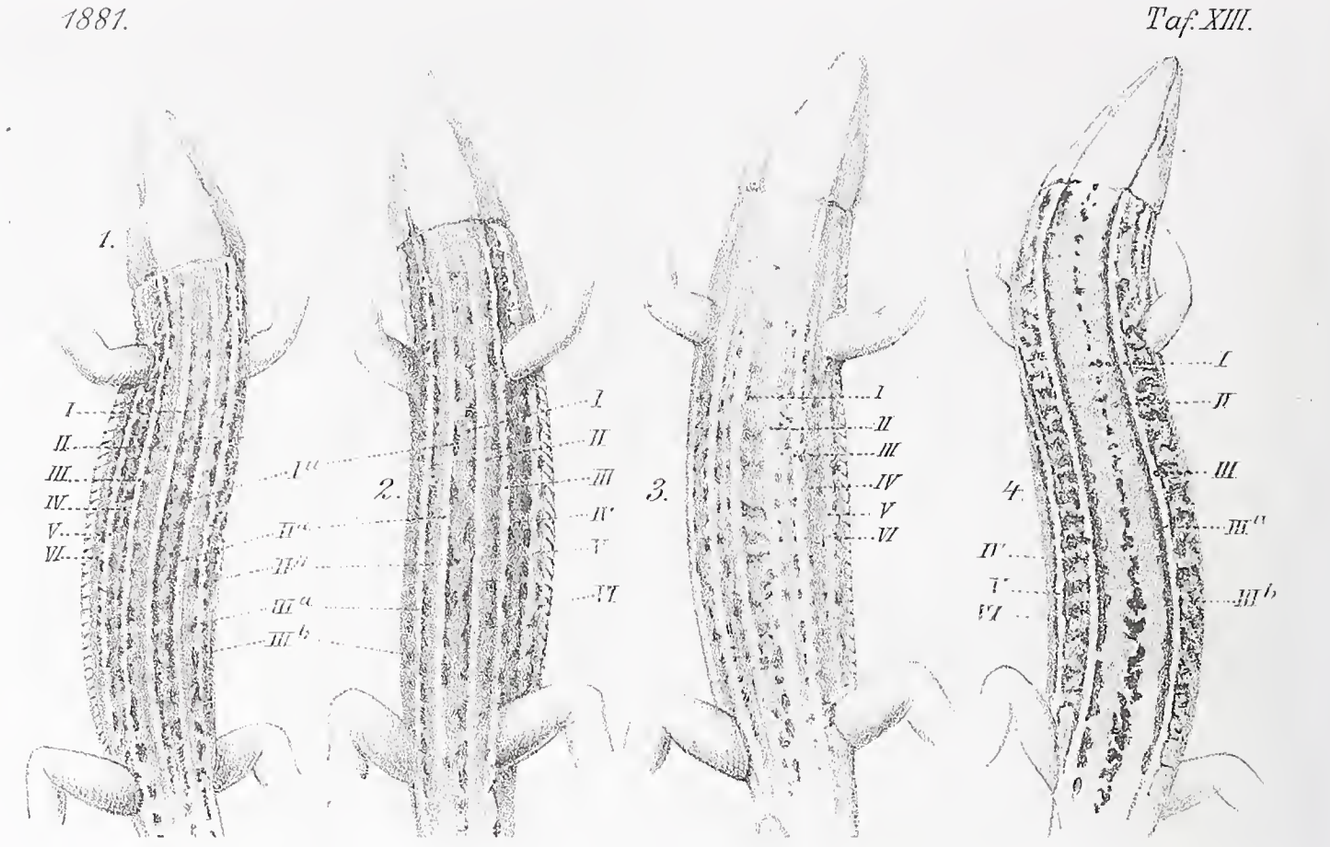


Fig. 14. Schema of the dorsal pattern in some *Podarcis* by Eimer (1881: Taf. XIII). Lithograph. It was the research since the middle of the 18th century which revealed the crucial importance of the dorsal pattern especially in the specific and infraspecific taxonomy of the current genus *Podarcis*. Eimer (1881: Taf. XIII) named the different longitudinal zones ("I bis VI erste bis sechste Zone") which usually exhibit a system of narrow light longitudinal streaks (nrs. I and III, "Grenzlinien") and dark bands (nrs. II," inneres / äußeres Band"). Méhely (1909: Fig. 1) eased his terminology and gave it the presently valid content; the seven light streaks and dark bands were named after their initial points at the pileus shields (like "Supraciliarstreifen" and "Occipitalband"), see also Schreiber (1912: Fig. 68; p. 333–335) and Mertens (1915: Fig. 3).

ertidae contain two subfamilies, Gallotiinae and Lacertinae, the latter comprising two monophyletic tribes, the Eremiadini of Africa and arid southwestern and central Asia, and the Lacertini of Europe, northwestern Africa and southwestern and eastern Asia. Relationships within the 108 species of Lacertini were explored using mtDNA for 59 nominal species. The morphology of the tribe was reviewed and also used to assess relationships. The Lacertini were assigned to 19 monophyletic units of 1 to 27 species. There were described five new Lacertini-genera out of the old collective genus *Lacerta*: *Dalmatolacerta, Dinarolacerta, Hellenolacerta, Iranolacerta, Phoenicolacerta* (see Fig. 20 for a complete listing of current genera). The new generic concept does not include subgenera except in *Iberolacerta* (*Pyrenesaura* Arribas, 1997). The genus *Lacerta* is presently restricted to eight species, the majority of them being polytypic: *Lacerta agilis* Linnaeus, 1758 (type species), *L. bilineata* Daudin, 1802, *L. media* Lantz & Cyrén, 1920, *L. pamphylica* Schmidtler, 1975, *L. schreiberi* Bedriaga, 1878, *L. strigata* Eichwald, 1831, *L. trilineata* Bedriaga, 1886, *L. viridis* Laurenti, 1768.

Thus the genus *Lacerta* appears to have finished its reduction through the centuries (Fig. 1) and to have stabilized at a level a little above the species level (according to the biological species concept). It seems however, that the species systematics of the eight species of *Lacerta* has not yet drawn to a close.

3. THE INTERACTION OF VERBAL DESCRIPTIONS AND ILLUSTRATIONS IN LACERTID TAXONOMY

3.1 General notes

Zoological publishing in a modern sense, and together with it, zoological book illustration, started at the end of the middle ages, at the beginning of the renaissance era in the 16th century (Nissen 1978: 113). They included above all Belon, Gessner, Rondelet and Aldrovandi – all of them physicians – who did no more than see their crucial challenge in lining up reports and opinions of ancient

De Animalibus in genere. 53

Animalium Tabula generalis.

Animalia ſunt vel
- *Sanguinea*, eáque vel
  - *Pulmone reſpirantia*, corde ventriculis prædito,
    - *Duobus*,
      - *Vivipara*,
        - *Aquatica*; Cetaceum genus.
        - *Terreſtria*, Quadrupedia, vel, ut *Manati* etiam complectamur, piloſa. Animalia hujus generis amphibia terreſtribus annumeramus.
      - *Ovipara*, Aves.
    - *Unico*, Quadrupedia vivipara & Serpentes.
  - *Branchiis reſpirantia*, Piſces ſanguinei præter Cetaceos omnes.
- *Exanguia*.
  - *Majora*, quæ vel
    - *Mollia*, Μαλάκια, Polypus, Sepia, Lolligo.
    - *Cruſtacea*, Μαλακόστρακα, Locuſta, Aſtaeus Cancer.
    - *Teſtacea*, Ὀστρακόδερμα, quæ vel univalvia, vel bivalvia, vel turbinata.
  - *Minora*, Inſecta.

Fig. 15. From Ray (1693): First attempt to exhibit affinities or relationships in animals by a tree-like diagram; comprising also amphibians and reptiles.

authors without criticism. They made rather use of these earlier authors descriptions to identify the indigenous fauna. They began to understand the pedagogic function of images and the importanee of accuracy in representing the natural things in order to objeetively describe them. The most important collection of natural history coloured paintings, among them 50 tables with amphibians and reptiles, originates from Ulisse Aldrovandi (1522–1605), having been detected for science and described in the last years. "Their number and quality allow this collection of images to be considered as the first attempt to organize an ieonographic atlas of the Italian and Mediterranean fauna and, without any doubt, the first collection of herpetological images realized with relatively modern criteria" (Delfino, 2007; Delfino & Alessandro, 2008; Alessandrini & Ceregato, 2007). The laek of a species concept and the lack of the understanding of the animal organism, as well as the use of different engraving- and printing techniques (above all wood euts) eaused an excessive simplification in most contemporary publications and rendered the figures useless to represent the distinctive character of a species (cf. Gessner's figure; Fig. 2 hoc loco). The different insights of a painter and a mere engraver as well as the different qualities of a water colour and an engraving are shown by a comparison of an Aldrovandi water colour (Fig. 3).

It was about 250 years later, when the zoologist Hermann Sehlegel (see Schmidtler, 2007) delved into the theory of natural science images (German translation in Nissen,

20

4. *Familia.* Lacertini.

Lingua tenuis, furcata, protractilis, scuta abdominalia et caudalia lateralibus majora, haec omnia verticillata. Gula non dilatabilis.

Capitis
- squamae dorsalibus aequales; cauda bicarinata - Tupinambis.
- scuta, dorsalibus majora; collare
  - distinctum; cauda
    - quadricarinata - Dracaena.
    - rotundata - - Lacerta.
  - nullum - - - - - - Tachidromus.

Fig. 16. Diagram of the family "Lacertini" in Oppel (1811): Oppel (1811: 20) established the family "Lacertini" (now: Lacertidae), among six families within his order "Squamata". The "Lacertini" comprised four genera, two of them (*Tupinambis* and *Dracaena*) belonging now to other families, before Duméril (1806: No. 49-51) had established two families only ("Planicaudati" and "Tereticaudati") in his order "Saurii".– Similar trees or identification keys like this and Duméril's were the forerunners of an evolutionary view in herpetology (see Schmidtler 2009).

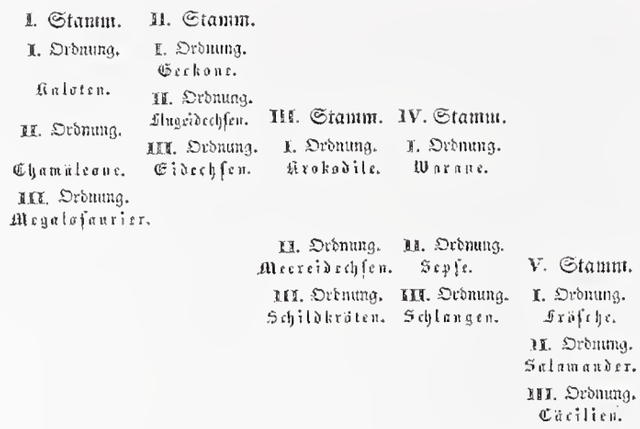


Fig. 17. Diagram from Kaup (1836): His "III. Ordnung Eidechsen" („Lacertae", text p. 26) corresponds to the rank of the present day family Lacertidae, comprising several genera like the "eigentliche Eidechsen" = *Lacerta*. His "Stamm" corresponds nearly to a current order. In this diagram there is exhibited the famous and strange dead end of "natural philosophy"; displaying more a mysticism of numbers than a concept of natural science: Like in birds, mammals and amphibians as well, there exists in Kaup only a strict number of **five** "Stämme" and in each there are enclosed strictly **three** "Ordnungen"! See chapter 3.4. This mysticism does not procced in the number of lacertid genera. See also Fitzinger (1843) and the critique in Mertens (1973).

1978: 231). According to him it is the function of such a figure to supersede the subjects difficult to be seen or examined in nature, in order to recognize them after the depiction and to be able to derive their shape, colours, proportions and other features as exact as possible. The perfection of this claim calls for a full interaction of text and illustration in the scientific, artistic and technical aspects – in this article being demonstrated on the basis of the Linnean genus *Lacerta*.

When the taxonomic importance of the different structures, like scales, spotting and colouration had been recognized about 1800, there originated also the need to display them separately from each other. The joint – naturalistic – appearance interfered with their independant perceptibility, for instance because of their poor visibility (e.g. sutures of scutes), overlapping with spotting, light reflection (Figs 8, 9), etc. At the same time abstracted figures (diagrams) were also used to exhibit relationships and / or identification keys, etc. (Figs 15–20).

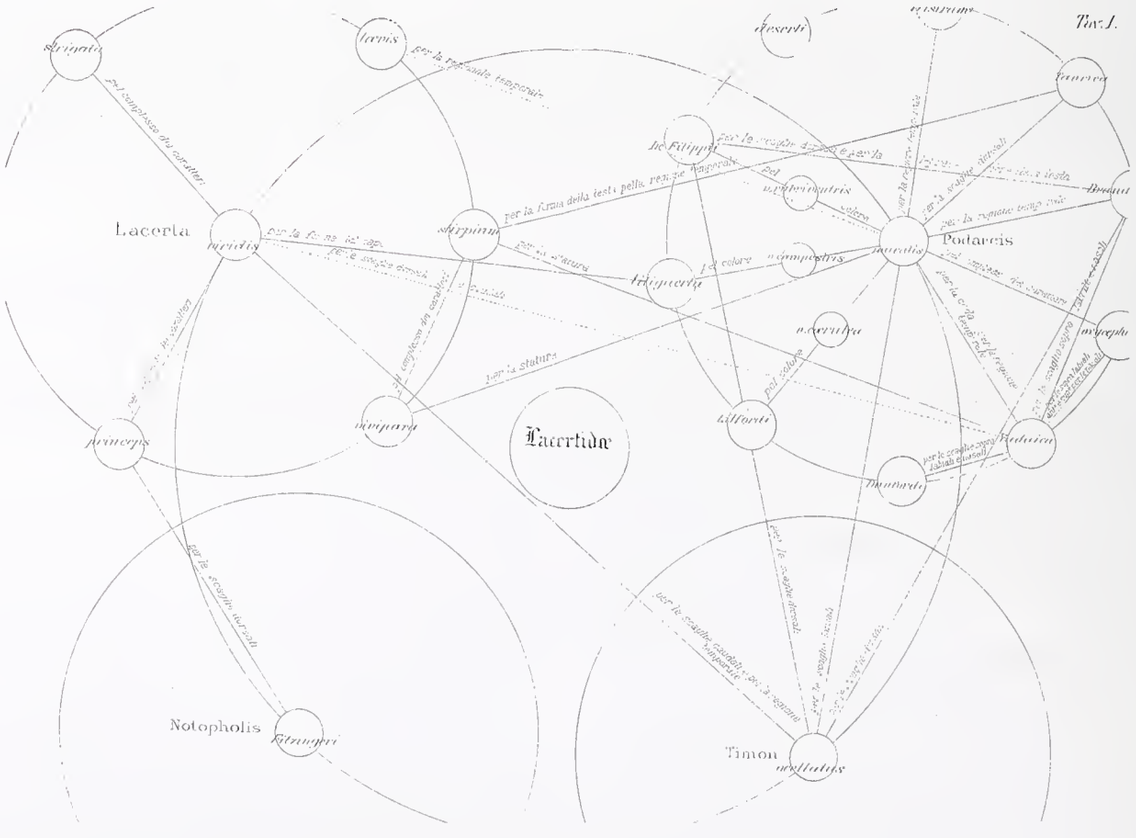


Fig. 18. From Camerano (1877: Tav. I, excerpt): Another rather popular kind of diagram displaying the relations between taxa. The small circles within the large circles symbolise related taxa of the four lacertid genera (*Lacerta, Podarcis, Notopholis, Timon*). The lines between such encircled taxa designate important morphological resemblances.

The first engraving – and printing – techniques were wood cuts (15th century), and shortly later, copper engravings. Around 1800 copper engraving was refined (etchings) and the first very expensive and rare colour prints in herpetology were based upon them (Daudin 1802; see Schmidtler 2007) after centuries of hand colouring. Lithography (the first lizards in Schmid 1819) was invented and improved more and more up to the time of chromolithography (see Fig. 8). Bewick (e.g. 1809–1816; Fig. 7) renewed the wood cuts ("Wood engraving"). In the second half of the 19th century the first photographs appeared (see Niekisch, 2010; Fig. 9 hoc loco) and revolutionised the book-illustration also in natural science and herpetology together with new letterpress printing techniques. These technical advances were attended by the expansion of some zoological / herpetological disciplines – or facilitated their proliferation – like ethology, husbandry, ecology.

It is noteworthy to emphasize that each of the engraving- and printing techniques displays its technical, artistic and economical strengths and weaknesses as measured by the different requirements they have to satisfy (see Schmidtler, 2007). Book illustrations were always expensive and this was the most important reason why the informative value of many important works had to suffer immensely.

3.2 Naturalistic figures

As was explained above, the lack of species recognition was especially responsible for rendering many figures useless in representing distinctive characters. This was especially the case for many of the reptiles, being regarded as abhorrent or less important (except the venomous snakes), compared to mammals or birds – up to the Linnean times and later.

A good example is Gessner`s fabulous creature (Fig. 1), called "*Lacertus viridis*", and typically attended with a poem advertising a medical and cosmetic prescription. It is only the indentations across the tail which suggests the possible belonging to the current Lacertidae.

Shortly before Linnaeus, the "Thesaurus" of the wealthy pharmacist Seba (1735) described many exotic animals from Seba's "Wunderkammer". This voluminous work depicted also many mythical creatures – besides some indigenous reptiles, e.g. the male of a "*Lacerta viridis*" (= *Lacerta agilis*), being identifiable only by means of the distinctive dorsal pattern and the green and brown colours (see Schmidtler, 2004: Abb. 1).

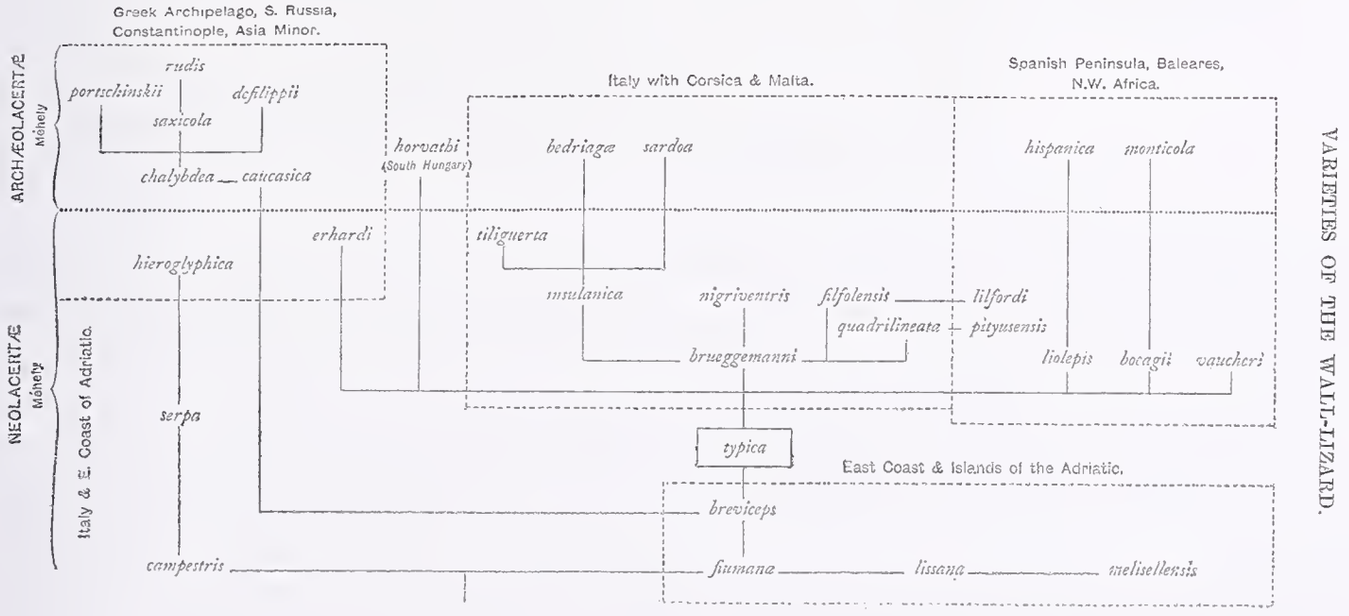


Fig. 19. From Boulenger (1913: 205–206): Linear diagram of the forms of *Lacerta muralis*: Citation: "The preceding diagram expresses their affinities, as I conceive them, and also their distribution. It will also enable the reader to see at a glance how my views on the possible derivation of these forms differ from those advocated by Prof. Méhely." The "varieties" of Boulenger's only species "*Lacerta muralis*" comprise four current genera (*Podarcis, Darevskia, Iberolacerta, Archaeolacerta*) with at least 17 current species and some more subspecies.

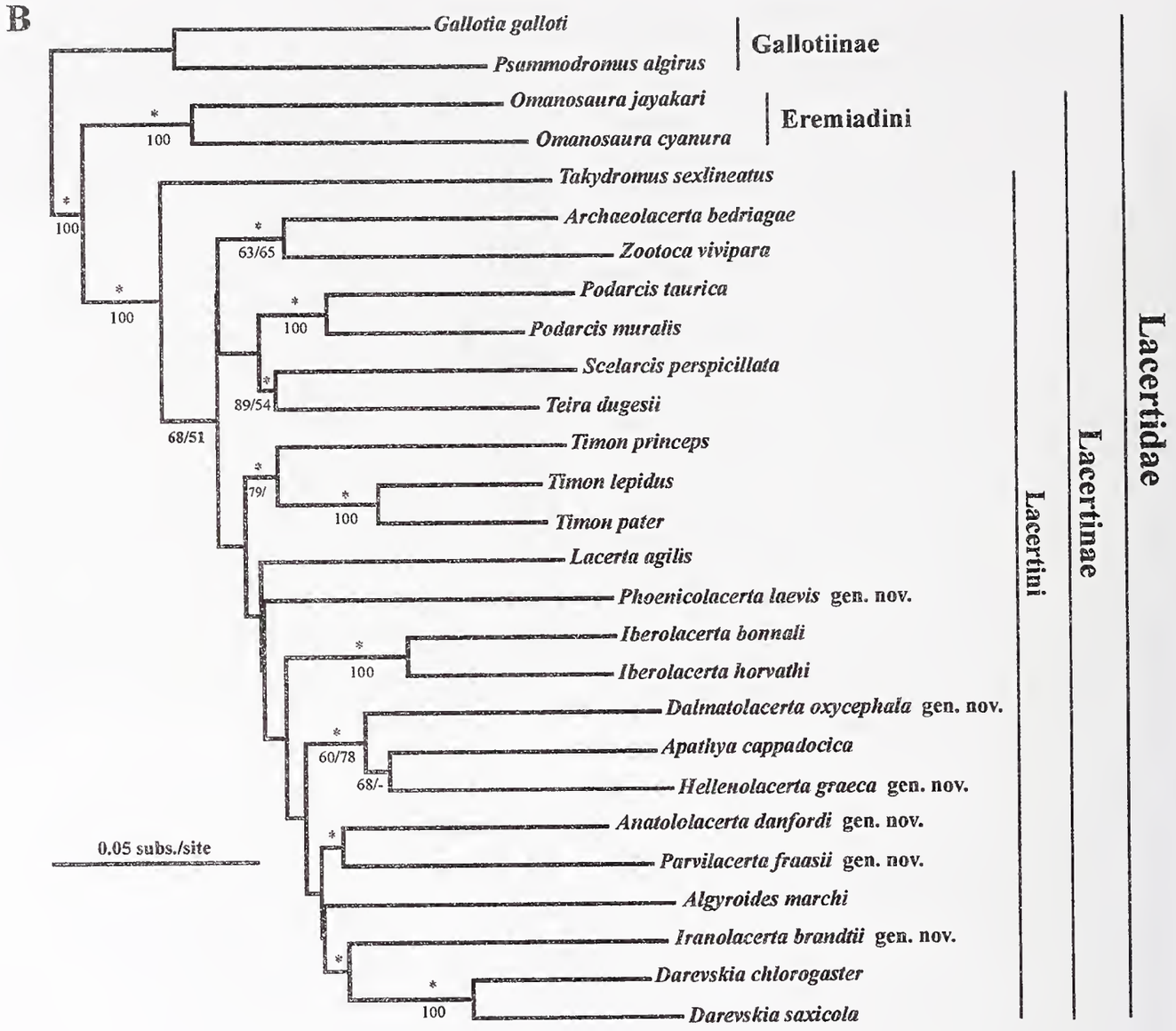


Fig. 20. From Arnold et al. (2007: Fig. 1B): The most actual phylogenetic tree of the Lacertidae comprising in detail the tribe Lacertini (among them *Lacerta* and the new genera *Phoenicolacerta, Dalmatolacerta, Hellenolacerta, Anatololacerta, Iranolacerta*), having been broken up from it). The relationships are indicated by DNA sequences (ML tree from a reanalysis of the mt DNA data set of Harris et al. (1998) based on cytochrome b, 12 S RNA and 16 S RNA). Different probability values resulting from Bayesian analysis are indicated.

The changes in scientific insight are visible by the differences of the carlier drafts and the final hand coloured engraving in Rösel v. Rosenhof's (1758) famous frontispiece (see Fig. 4).

Garsault (1764: pl. 688; fig. 5 hoc loco), a forerunner of Laurenti (1768), and a splitter like him (Chapter 2), moved an almost correct drawing of lacertids forward. In contrast to this figure, Laurenti's (1768: Tab.I, Fig.III) *Seps caerulescens* (= *Lacerta agilis*) has accomplished perfection for the first time in the history of a lacertid drawing. Laurenti's (1768) image remained unique for some decades. Even the excellently hand coloured copper engravings of male and female specimens of *Lacerta agilis* in Wolf in Sturm (1799) and Bechstein (1800) display some deficiencies in pileus scutellation (cf. also Schmidtler 2004). The black / white and coloured engravings in Daudin (1802) are comparably of a very different quality. The colours of his excellently drawn shape of *L. ocellata* (1802: pl. XXXIII; without the blue ocellae) reveals that he did not see a live specimen. But the shape of the adult male is to the point. In Daudin (1801–1803), part of the so called Sonnini edition, for the first time the progressive but extremely expensive technique of colour printing was used in herpetology (see Schmidtler 2007).

On the contrary, the hand coloured engravings in Sonnini & Latreille (1801) are very small – and bad; likewise the figures in the numerous popular editions of the French natural histories, named "Buffon – Cuvier – Lacepède", are out of the question. Their images were cribbed permanently and often lost their quality step-by-step up to an unrecognisable condition.

In the second half of the 19th century research on colours and patterns, the biological reasons and causes of their adaptation, became important for the evaluation of infraspecific variation and biology in general (Eimer, 1881: Taf. XIII–XV). Subsequently, many subspecies, especially within the current genus *Podarcis* (then mostly "*Lacerta lilfordi, Lacerta melisellensis, Lacerta muralis, Lacerta sicula*"), were based upon minute differences in scale counts, colouration and pattern (see Mertens & Wermuth 1960). As a result of the genetic revolution in the last years the importance of naturalistic figures in lacertid systematics is on the decline. At the same time top-quality photos (Fig. 10) have gained in importance especially in popular vivaristic publications.

3.3 Schematic figures

The abstraction of systematically important features, being more or less hidden to the unprejudiced observer, is a condition for successful species recognition. The first noteworthy attempts towards a schematisation of zoological / herpetological features were displayed by Linnaeus in his earlier editions of the "Systema Naturae" (Fig. 11). It is above all the scale counts of ventrals and subcaudals in snakes which are explained in his table III (Linnaeus 1756). Only these scale counts are given in the diagnoses of snakes (see also Linnaeus 1758 and 1766).

The decisive step forward in lizards was made by Merrem (1820). Based upon his similar system in snakes (Merrem 1790, 1820; see Schmidtler 2006) he gave names to the pileus shields of an adult *Lacerta ocellata* (now: *Timon lepidus*; see his page XII and XIII) and depicted their abbreviations in this figure. This description (see Fig. 12) covered seven types of scutes with the letters A (Wirbelschilder – Scuta vertebralia), B (Hinterhauptschilder – Scuta occipitalia), C (Augenbrauenschilder – Scuta superciliaria), E (Stirnschilder – Scuta frontalia posterioria), F (Schnautzenschilder – Scuta frontalia anterioria), G (Rüsselschild – Scutum rostrale, L (Nasenlöcherschilder – Scuta nasalia). This system was later on differentiated and improved by Milne Edwards (1829: pls. 5–8) who depicted and described also the shields of the lower sides of head, body and limbs. The concept of Merrem (1820) and Milne Edwards is valid up to now.

In the middle of the 19th century important osteological investigations also were executed in lacertids. They allowed taxonomic research in the higher categories but also within lacertid genera and species, after a reasonable schematization in osteology, above all in skull terminology, had been found (Fig. 13 from Méhely). They brought about the famous and interminable controversy of L. v. Méhely ("splitter") and G.A. Boulenger ("lumper") on the then intractable "Muralis-Frage" (see Méhely 1909; Boulenger 1920; among others).

It was the research since the middle of the 18th century which revealed the crucial importance of the dorsal pattern especially in the specific and infraspecific taxonomy of the current genus *Podarcis*. Eimer (1881: Taf. XIII; Fig. 14 hoc loco) named the different longitudinal zones ("I bis VI erste bis sechste Zone") which usually exhibit a system of n narrow longitudinal light streaks (nrs. I and III, "Grenzlinien") and dark bands (nrs. II," inneres / äußeres Band"). Méhely (1909: Fig. 1) eased his terminology and gave it the presently valid content. The seven light streaks and dark bands were named after their initial points at the pileus shields (like "Supraciliarstreifen" and "Occipitaband"); see also Schreiber (1912: Fig. 68; p. 333–335) and Mertens (1915: Fig. 3).

Admittedly, morphological schemata (scutellation, dorsal pattern) like these have lost their crucial taxonomic importance in the 19th and 20th centuries during the last two decades because of the reasons given above (see Section 2.2).

3.4 Diagrams

Semi-verbal depictions known in many different shapes (concerning biology as a whole) are book illustrations in broader terms. Contrary to naturalistic figures or the schemata discussed above, phylogenetical trees, based upon genetic research, have become indispensable parts of comprehensive taxonomic work in the last years (Fig. 20). In many analyses the genetic distances currently have totally replaced the traditional taxonomic decisions based upon morphology and reproduction biology – be it appropiate or not.

Tree-like diagrams, comprising also reptiles, trace back to Ray (1693) (see Fig. 15). They have an enormous importance in the history of general biology, not only in lizards. In the field of herpetology, lizards included, they became common practice since the basic works of Duméril (1806) and Oppel (1811; Fig. 16 hoc loco; see also Schmidtler 2009) and Cuvier in Cloquet (1819). Strange to say, it was not clear in those pre-evolutionary times, if the trees should represent identification keys only, or if

they should depict relationships (too) when illustrating the Linnean hierarchical system by diagrams. Gould (2003: 105) explained the secret of the then triumph of the Linnean categories (from species to class) being nested into one another, by the circumstance that this system later on was capable of being converted into a phylogenetic interpretation (see also Schmidtler 2009: 500, Figs 7a–d).

The subsequent diagrams are not yet phylogenetic trees in a strict sense; especially the one by Kaup (see Fig. 17), who was a follower of the fanciful "natural philosophy". Similar is the quality of Camerano`s diagram (Fig. 18 hoc loco) with its differently sized circles including the phenomenon of resemblances due to morphology.

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