

ALYTES

INTERNATIONAL JOURNAL OF BATRACHOLOGY

December 2004

Volume 22, N° 1-2

Alytes, 2004, 22 (1-2): 1-14.

The higher nomenclature of recent amphibians

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The absence of rules in the *International Code of Zoological Nomenclature* for nomenclature of taxa above superfamily is a source of instability and confusion, especially with the recent increase in number of higher taxa following multiplication of phylogenetic analyses. A recent proposal concerning such rules, submitted elsewhere, is briefly presented here, and its consequences regarding nomenclature of higher taxa of recent amphibians are summarised. The class nomen AMPHIBIA should be credited to DE BLAINVILLE (1816) instead of LINNAEUS (1758). The nomen LISSAMPHIBIA Haeckel, 1866 is an invalid junior synonym of BATRACHIA Brongniart, 1800, that applies to one of the superorders of the subclass including all recent amphibians. The valid nomen of this subclass is NEOBATRACHI Sarasin & Sarasin, 1890. The three orders of recent amphibians should be known as ANURA Duméril, 1806, URODELA Duméril, 1806 and GYMNOPHIONA Rafinesque-Schmaltz, 1814. The nomina SALIENTIA Laurenti, 1768, CAUDATA Scopoli, 1777, APODA Oppel, 1811, ARCHAEOBATRACHIA Reig, 1958 and NEOBATRACHIA Reig, 1958 are invalid and should no longer be used.

To be able to study and designate living organisms, systematists have devised a system of scientific classification of these organisms into taxa (taxonomy) and a system of rules pertaining to designation of these taxa (nomenclature). The latter system allows any taxon to be universally designated by all biologists worldwide by a single scientific name or *nomen* (DUBOIS, 2000). However, the current *International Code of Zoological Nomenclature* (ANONYMOUS, 1999; cited below as “the *Code*”), only deals with nomina of some taxa, from subspecies to superfamily, excluding taxa of lower and higher ranks. Nomenclature of higher zoological taxa above superfamily (“class-series nomina” according to DUBOIS, 2000) should

be fixed by consensus among workers. However, in many zoological groups, no such consensus exists, even for well-known and non-controversial taxa, as is exemplified by the three orders of recent amphibians, for which the *Zoological Record*, in its recent editions, uses double denominations: “ANURA (= SALIENTIA)”, “CAUDATA (= URODELA)” and “GYMNO-**PHIONA** (= APODA)”. This absence of rules is a source of confusion and instability in scientific literature, especially given recent development of phylogenetic analyses and multiplication of higher zoological taxa. For this reason, a set of formal rules for this nomenclature, based on a detailed rationale, was recently proposed (DUBOIS, submitted). This proposal, which is much more precise and consistent than a previous one (DUBOIS, 1984b), still has to be considered and discussed by the international community of zoologists before its possible inclusion, most likely after some changes, in the *Code*. The major criteria on which the proposed system is based are as follows:

(C1) As requested in the *Preamble* of the *Code* (p. 2), the rules should respect “the freedom of taxonomic thought or actions”. This means that these rules should not tie nomenclature to any fixed classification of animals, and, more importantly, to any given philosophy of taxonomy (e.g., phylogenetic).

(C2) Just like those of the *Code* for other nomina, these rules should work automatically, without need of a permanent recourse to a committee, board or court, so that they allow any taxonomist worldwide to find the valid nomen of any given taxon under any taxonomic system.

(C3) Therefore, the *status* (taxonomic allocation) of any nomen should be based on the original *extension* (content) of the taxon to which this nomen was first applied, irrespective of the *intension* (definition) then provided for the taxon, and of subsequent uses of the nomen, except in a few exceptional cases, as explained under (C5) below.

(C4) Like those of all other taxa, nomina of higher taxa should have been *published* after 1757 and their validation should follow a rule of *priority* (i.e., among several nomina proposed for the same taxon, the first published should be the *valid* one) and a rule of *homonymy* (i.e., any nomen homonymous with a previously published nomen should be *invalid*).

(C5) However, in order to avoid unnecessary instability, *genuine* well-known nomina, i.e., *nomina widely used outside specialised scientific literature dealing with taxonomy and evolution*, should be protected and stabilised, even if they are junior synonyms or homonyms of other more obscure nomina. An objective criterion is proposed to recognize nomina that should be so protected, and this is presence of these nomina in a high number (100) of *titles* of non-taxonomic publications dealing with these animals after 1900. This is justified by the fact that use of a nomen in a title is relevant only if this nomen is well-known to most potential readers, and not only to specialists.

(C6) A number of criteria and rules need to be added to have a complete functional set of rules allowing automatic and universal *allocation* of nomina to taxa and *validation* of one of them among several competing nomina for the same taxon. In particular, whenever a couple or set of *sister-nomina* was proposed for taxa created in the process of splitting an earlier higher taxon (such as **GRADIENTIA-SALIENTIA-SERPENTIA**, **CAUDATA-ECAUDATA** or **ANURA-URODELA**), these sister-nomina should be validated or rejected together, instead of validating a mixture of nomina from two or more such different couples or sets.

Pending publication of this long work (DUBOIS, submitted), its discussion by the international community and its possible formal inclusion in the *Code*, a process which is likely to take years, it may be useful to provide all batrachologists with general data and conclusions concerning higher nomenclature of the most important groups of recent amphibians.

In the recent decades, various discussions have been published concerning phylogenetic relationships of recent amphibian groups (i.e., taxa represented by at least one species in the extant fauna: frogs, salamanders and caecilians), both among themselves and with other groups of fossil amphibians and other tetrapods. No consensual opinion has been reached on most of these questions, and further discussions, based on new information, can be expected in the future. Thus, higher taxonomy and nomenclature cannot be stabilised for the time being. The discussion below will be restricted to the few higher taxa which do not appear controversial and are likely to remain valid whatever the future developments of phylogenetic studies. Given this likely taxonomic stability, it is relevant to propose stabilisation of the nomina of these taxa for future works. Among higher taxa (above superfamily) that include recent amphibian groups, the taxa concerned are only those of the following ranks: class, subclass and orders. Although still controversial, the superorders will also be included in the discussion below.

THE CLASS

Universal agreement currently exists among zoologists for recognising a class that includes all three groups of recent amphibians (frogs, salamanders and caecilians), as well as several all-fossil groups. Although some authors still used the nomen **BATRACHIA** for this class until the end of the 20th century, most current authors now use the nomen **AMPHIBIA** (see e.g. DUBOIS, 1984b: 10, tab. 1). In particular, this nomen was largely used in many *titles* of books and other publications, both in scientific and non-scientific literature, and should therefore be preserved according to criterion (C5).

The nomen **AMPHIBIA** was introduced in scientific literature by LINNAEUS (1758). However, Linnaeus's original taxon was quite different from the taxon now known under this nomen. It contained many more reptile and "fish" than amphibian species and genera: only 2 of the 16 genera originally included in the taxon (*Caecilia* and *Rana*) are currently considered to belong in it. It was split in three orders, two of which (**REPTILIA** and **SERPENTES**) included amphibians, but these two nomina were later historically associated with reptilian groups. The traditional division into two classes called respectively **AMPHIBIA** and **REPTILIA**, in the sense they have retained for about two centuries, was not immediate after LINNAEUS (1758). It was first established by DE BLAINVILLE (1816), and adopted progressively by subsequent authors. Probably the etymological meaning of the term **AMPHIBIA** ("animals with a double life") played a rôle in final stabilisation of this term to designate frogs, salamanders and caecilians. Since then, the nomen **AMPHIBIA** has been used in zoological taxonomy with various meanings, but always for a taxon including these three groups and excluding all groups of recent "reptiles" and "fishes". Pending consensus among authors on cladistic relationships between major vertebrate groups, the taxon **AMPHIBIA** is here used in the sense most often

found in the scientific literature, that of ZITTEL (1888), i.e., for the whole “batrachomorph” clade as recognized e.g. by TUDGE (2000). This is the sense of the term in thousands of publications, in most textbooks of biology and paleontology, and in all volumes of *Zoological Record* since 1927. Authorship of this nomen must however be credited to DE BLAINVILLE (1816), and the earlier homonymous nomen AMPHIBIA Linnaeus, 1758 must be rejected as invalid. This interpretation is not new, as it had already been proposed e.g. by KUHN (1965: 12), who however incorrectly cited LATREILLE (1825) instead of DE BLAINVILLE (1816) as the author of the current concept of the taxon.

THE SUBCLASS

Although phylogenetic relationships and taxonomy of entirely fossil groups of amphibians are still controversial (see e.g.: MILNER, 1988; TRUEB & CLOUTIER, 1991; LAURIN, 1998; SANCHÍZ, 1998; TUDGE, 2000), consensus exists among most current authors for allocation of all living amphibians, and their close relative fossil forms, into a single subclass including three orders (frogs, salamanders and caecilians). This subclass is not a taxon that can be considered well-known or widely used by authors who are not taxonomists or evolutionary biologists, as it was rarely mentioned in titles of non-systematic publications. Therefore its valid nomen should be established from original contents of taxa for which nomina were coined, not by any subsequent incorrect uses of these nomina by specialists.

For this subclass, some recent authors (e.g.: DUELLMAN & TRUEB, 1985; MILNER, 1988; TRUEB & CLOUTIER, 1991; LAURIN, 1998; TUDGE, 2000) used the nomen LISSAMPHIBIA Haeckel, 1866, whereas DUBOIS (1984*b*) supported use of the nomen **BATRACHIA** Brongniart, 1800. However, both opinions are unquestionably incorrect, as both nomina **BATRACHIA** and **LISSAMPHIBIA** were coined for a taxon including frogs and salamanders but expressly excluding caecilians. These two nomina are therefore available for a taxon of lower rank and will be considered below. So, what is the valid nomen of the subclass?

The first taxonomic recognition of a taxon encompassing the three current orders of the subclass containing all recent amphibians, and only them, was by OPPEL (1811*a-f*), under the nomen **NUDA**. However, this nomen is invalid, for several reasons, in particular as it is a junior homonym of **NUDI** Batsch, 1788.

The valid nomen for this subclass is **NEOBATRACHI** Sarasin & Sarasin, 1890, a nomen that was clearly mentioned by KUHN (1967: 30) and DUBOIS (1983: 272; 1984*b*: 12, 29) as a senior homonym of **NEOBATRACHIA** Reig, 1958, making the latter nomen invalid. The nomen **NEOBATRACHI** was proposed for a subclass including all recent amphibians (frogs, salamanders and caecilians) as opposed to the all-fossil amphibian groups, for which SARASIN & SARASIN (1890) used the nomen **STEGOCEPHALIA**. It should be used as the valid nomen for the taxon including all recent amphibians and closely related groups, for which the nomen **LISSAMPHIBIA** cannot be conserved.

THE SUPERORDERS

To designate the subclass of recent amphibians, the nomen **LISSAMPHIBIA** Haeckel, 1866 has had growing use in the last two decades (see DUBOIS, 1984*b*: 10), although almost exclusively in systematic publications. Few (if any) of the recent authors who used this nomen examined HAECKEL's (1866) book where it was first published, because if they had they would have realised that the original taxon designated under this nomen is different from that understood by recent authors.

HAECKEL (1866: cxxx-cxxxii) recognized a class **AMPHIBIA**, with two subclasses, for which he proposed the nomina **PHRACTAMPHIBIA** and **LISSAMPHIBIA**. The **PHRACTAMPHIBIA** were composed of three orders, two containing only fossil taxa (**GANOCEPHALA** and **LABYRINTHODONTA**) and one (**PEROMELA**) composed of the caecilians. The **LISSAMPHIBIA** contained three orders of living taxa, two of which (**SOZOBANCHIA** and **SOZURA**) embraced the current tailed amphibians, whereas the third one, **ANURA**, contained the tailless amphibians. Therefore, HAECKEL's (1866) **LISSAMPHIBIA** were exactly equivalent to BRONGNIART's (1800*a*) **BATRACHIA**, and not to the latter plus the **GYMNOPHIONA**, as stated by several recent authors. This remained the opinion of Haeckel apparently for his entire life, as in all his subsequent works (e.g., HAECKEL, 1868, 1870, 1872, 1873, 1902) the **LISSAMPHIBIA** always only contained the current **ANURA** and **URODELA**, whereas the **GYMNOPHIONA** were classed in the **PHRACTAMPHIBIA**.

The recent confusion traces back to PARSONS & WILLIAMS (1963: 27), who resurrected the long-forgotten nomen **LISSAMPHIBIA** for a new taxon they erected for all living amphibians. Although they acknowledged that HAECKEL (1866) had clearly excluded the **GYMNOPHIONA** from his **LISSAMPHIBIA**, they stated that they were following GADOW's (1901) use of the latter nomen for all recent amphibians, a significant change for which GADOW (1901: xi, 10, 84-274) did not provide any explanation. As GADOW (1901: 9-10) was clearly aware of the original content of the **LISSAMPHIBIA**, as well as of existence of the nomen **NEOBATRACHI**, his choice of the former for the taxon may be explained only by its etymological meaning ("smooth amphibians"). He may have considered it more appropriate to designate a taxon for which he provided the following diagnosis: "Amphibia without dermal armour" (GADOW, 1901: 84). KUHN (1967: 27) did not recognize **LISSAMPHIBIA** as a valid taxon but wrote incorrectly about it: "für Caudata, Gymnophiona und Salientia; heterogen". Most other subsequent authors seem to have simply followed PARSONS & WILLIAMS (1963) in accepting this nomen. It was used by ROMER (1966: 364), and adopted since then by several authors for a subclass containing all three recent orders of amphibians, but, as first noted by DUBOIS (1983, 1984*b*) it should be treated as a strict junior synonym of **BATRACHIA** Brongniart, 1800, which furthermore has had a dramatically larger use in zoology. This latter nomen thus deserves a detailed discussion.

Contrary to the statement by STEJNEGER (1904), and as shown by DUBOIS (1984*b*: 11, 24), the familial nomen **BATRACHI** Batsch, 1788 is not available in the class-series, and BRONGNIART (1800) must be credited with authorship of the class-series nomen **BATRACHIA** (as **BATRACIENS**). The first post-1757 published use of this widespread nomen, based on the Greek term

batrachos (“frog”), under the spelling *BATRACHI*, was by BATSCH (1788), who gave family rank to this taxon. BATSCH (1788) was the first author to use the category family in classification of the amphibians. This was a high category in his taxonomic system, between order and genus. He recognized families throughout the entire animal kingdom. Some nomina he coined for these families were based on stems of available generic nomina, whereas others were not. In his class **AMPHIBIA**, BATSCH (1788) recognized four families, three of which (*BATRACHI*, *LACERTAE* and *SERPENTES*) contained amphibians. The nomen *TESTUDINES* has long been recognized, under the form *TESTUDINIDAE* Batsch, 1788, as the valid nomen of the family of land turtles including the genus *Testudo* Linnaeus, 1758 (e.g.: BOUR & DUBOIS, 1985; IVERSON, 1992; ROGNER, 1996; MERCHAN FORNELINO & MARTINEZ SILVESTRE, 1999; LAPPARENT DE BROIN, 2001; VETTER, 2002). The same should be done for the family nomen *LACERTIDAE*, erroneously credited in recent herpetological literature either to OPPEL (1811*e*) (e.g., PÉREZ-MELLADO, 1998), to GRAY (1925) (e.g., ESTES et al., 1988: 211; CEI, 1993: 58; ZHAO et al., 1999: 219) or to COPE (1864) (e.g., TAYLOR, 1963: 928; DOWLING & DUELLMAN, 1978: 84.1). However, the nomina *BATRACHI* and *SERPENTES*, not based on available generic nomina, are incorrectly formed as family-series nomina according to the *Code*, and are therefore nomenclaturally unavailable.

The nomen *BATRACHI* Batsch, 1788 being unavailable, the author who made this nomen available, as a nomen of order, was BRONGNIART (1800*a*). He created four orders in the class **REPTILES**: **BATRACIENS**, **CHÉLONIENS**, **OPHIDIENS** and **SAURIENS**. These four nomina were latinized the same year by LATREILLE (1800: xxxvii, xi, xviii, xiii), respectively as **BATRACHII**, **CHELONII**, **OPHIDII** and **SAURII** (spellings that soon became unused, except for **CHELONII**), and shortly after by ROSS & MACARTNEY (in CUVIER, 1802: tab. 3), respectively as **BATRACHIA**, **CHELONIA**, **OPHIDIA** and **SAURIA**. Except for **CHELONIA**, these latter spellings have been universally used by later authors and should be retained as correct spellings of these nomina. BRONGNIART (1800*a*) was the first author to remove the salamanders from the lizards, where they had been placed by all his predecessors. He grouped them with the frogs in his new order **BATRACIENS**. He also expressed doubts (BRONGNIART, 1800*b*: 91) about the caecilians being properly referred to the order which he called **OPHIDIENS** (that included snakes, limbless lizards and amphisbaenians), but he kept them unallocated to order and did not refer them formally to his **BATRACIENS**, so that the latter taxon is less inclusive than the **NEOBATRACHI** of SARASIN & SARASIN (1890).

The nomen **BATRACHIA** has been long used in zoology, but in an ambiguous sense, as it has been employed to designate the class of amphibians (e.g., BOULENGER, 1910), or its subclass containing all recent amphibians (e.g., DUBOIS, 1983, 1984*b*), or a superordinal taxon including only the two orders of frogs and salamanders, considered sister-taxa (e.g.: MILNER, 1988; TRUEB & CLOUTIER, 1991; ZARDOYA & MEYER, 2001). The latter opinion is correct, as the original extension of the taxon covered only our current frogs and salamanders. TRUEB & CLOUTIER (1991: 295) wrote about **BATRACHIA**: “we restrict it to include only the Urodela and Salientia”. Actually this is not a restriction, but a return to the original definition of the taxon. There currently exists no general consensus on the validity of this taxon, although recent data, both morpho-anatomical (TRUEB & CLOUTIER, 1991) and molecular (ZARDOYA & MEYER, 2001) strongly support it. Under this interpretation, adopted here, the nomen **BATRACHIA** is the valid nomen of a superorder including frogs and salamanders, and the superorder containing the caecilians should bear the nomen **GYMNOPHIONA** (see below). Under an

alternative interpretation where the salamanders and caecilians are sister-taxa (e.g., FELLER & HEDGES, 1998), the nomen **BATRACHIA** should be kept as the valid nomen of the subclass including all recent amphibians. The nomen **NEOBATRACHI** Sarasin & Sarasin, 1890 would then become its junior synonym. In such an arrangement, the superorders should be known respectively as **ANURA** Duméril, 1806 for frogs (see below) and **UROPHORA** Hogg, 1839 (senior synonym of the unnecessary nomen **PROCERA** Feller & Hedges, 1998) for the order containing the **URODELA** and **GYMNOPHIONA**.

THE ORDERS

In the second half of the 20th century, a few authors (e.g., GOIN & GOIN, 1962) still recognized an order (**TRACHYSTOMATA** Cope, 1866) for the single family *SIRENIDAE* Gray, 1825. Currently, there seems to be general consensus to recognize only three orders (frogs, salamanders and caecilians) among recent amphibians, and the *SIRENIDAE* are now universally included among the salamanders (DUELLEMAN & TRUEB, 1985; FROST, 1985; LAURENT, 1986; DUBOIS, 1985; ZUG, 1993).

A few words only will be devoted here to the suborders of frogs and salamanders. No consensus currently exists among authors regarding these taxa. Furthermore, the nomenclature of these suborders raises a number of complex problems, the discussion of which would require too much space here. These problems will be discussed at length in the forthcoming publication (DUBOIS, submitted). Let us just stress again here (after e.g. KUHN, 1967, and DUBOIS, 1984*b*) that, anyway, the nomina **ARCHAEOBATRACHIA** Reig, 1958 and **NEOBATRACHIA** Reig, 1958 cannot be retained as valid for two suborders of **ANURA**, being junior homonyms of **ARCHAEOBATRACHI** Sarasin & Sarasin, 1890 and **NEOBATRACHI** Sarasin & Sarasin, 1890, respectively. Reig's nomina have never been used outside systematic literature, and therefore cannot be protected on the basis of usage. Pending the publication of the detailed analysis of this case, the best solution for authors who wish to recognise these two suborders (a still controversial matter) may be to use the nomina **DISCOGLOSSOIDEI** and **RANOIDEI** proposed for them by SOKOL (1977), followed and expanded by DUBOIS (1984*b*, 1985).

CAECILIANS

The first available nomen for an order including only the caecilians is **APODA** Oppel, 1811. In his order **NUDA**, OPPEL (1811*a-f*) recognized three taxa: **APODA**, **CAUDATA** and **ECAUDATA**. The last two will be discussed below. Because of its priority, the nomen **APODA** has been used by a number of subsequent authors to designate the order of caecilians or another higher taxon containing the caecilians. However it cannot be valid for this taxon, being a junior homonym. This nomen is preoccupied by several earlier nomina: an ordinal nomen of fish of LINNAEUS (1758: 241); three identical nomina proposed by LATREILLE (1804: 73, 75, 103) for three different orders of fishes; and several ordinal nomina proposed by FISCHER (1808: [13, 25, 28]), including one as a replacement nomen for **OPHIDIA** Brongniart,

1800 (i.e., a taxon that did not include caecilians). Therefore the nomen **APODA** cannot be used for an order containing only caecilians. OPPEL's (1811c: 409) use of **APODA** for an order containing the single genus *Caecilia* must be considered as a new nomen for a new taxon, and therefore an invalid junior homonym. This nomen was not used enough in non-systematic works to qualify for conservation under criterion (C5). It should therefore be definitively abandoned in the higher taxonomy of amphibians, and cannot be retained, even as a subdivision of the **GYMNOPHIONA**, as suggested e.g. by TRUEB & CLOUTIER (1991: 296).

The nomen **GYMNOPHIONA** should be retained for the order of caecilians. This nomen was first used under this spelling by MÜLLER (1831), but, as established by DUBOIS (1984a), this should be considered an emendation of the nomen **GYMNOPHIA** proposed by RAFINESQUE-SCHMALTZ (1814b: 104). The latter author proposed many new nomina for higher taxa of vertebrates, especially reptiles and amphibians (RAFINESQUE-SCHMALTZ, 1814a-b; RAFINESQUE, 1815), which he divided in 5 orders and 15 families. His order **GYMNOPHIA** contained a single genus, *Cecilia* Rafinesque-Schmaltz, 1814, an emendation of *Caecilia* Linnaeus, 1758. MÜLLER's (1831: 198) spelling **GYMNOPHIONA**, which has been used by many subsequent authors, must be kept as the valid spelling of this taxon.

Finally, within the frame of the taxonomy of recent amphibians presented below, and as a result of the rule of coordination adapted to class-series nomina (for details, see DUBOIS, submitted), the nomen **GYMNOPHIONA** Rafinesque-Schmaltz, 1814 is also the valid nomen for the superorder including this single order.

FROGS AND SALAMANDERS

Whereas many current authors agree on use of **GYMNOPHIONA** for the order of caecilians, consensus is not as good for the other two orders of extant amphibians, salamanders and frogs, which have received many different nomina. The most frequently used ones are respectively **CAUDATA** and **URODELA**, and **SALIENTIA** and **ANURA**. Considerable usage of each of the alternative nomina in non-purely systematic literature can be documented, so that none of these four nomina can be protected against one another, and original contents of the taxa must be used as the criterion for allocation of these nomina to our current taxa.

Most authors have long been aware that limbed amphibians were composed of two different groups, tailed salamanders and tailless frogs, and accordingly several early authors proposed couples of nomina for these groups. The three most noteworthy of these couples of nomina were proposed by LAURENTI (1768), SCOPOLI (1777) and DUMÉRIL (1806a). According to the rules proposed (DUBOIS, submitted), two such nomina can be validated together, but a combination of nomina from different couples is not acceptable.

In his class **REPTILIUM**, LAURENTI (1768) recognized three orders, two for which he provided new nomina (**SALIENTIA** and **GRADIENTIA**) and one (**SERPENTIA**) for which he used a nomen from LINNAEUS (1758). All three orders included amphibians, but only the first was homogeneous in this respect. LAURENTI's (1768) nomen **SALIENTIA** was proposed for the order including frogs, and its sister-nomen **GRADIENTIA** for the order including salamanders. However, both taxa were heterogeneous in this original work, especially as one genus (*Proteus*) was straddling both orders, a very exceptional situation indeed in taxonomy,

contradictory to the principles of dichotomy and hierarchy used in Linnaean taxonomy. The **SALIENTIA** were almost homogeneous, as they contained four genera of frogs (*Bufo*, *Hyla*, *Pipa*, *Rana*), but also a single species that was referred to the genus *Proteus*. Two other species of the latter genus were referred to the **GRADIENTIA**, along with two other genera of salamanders (*Salamandra*, *Triton*) and one of frogs (*Caudiverbera*), but also with one of crocodylians (*Crocodylus*) and nine of lizards. Probably because of this heterogeneity, the nomen **GRADIENTIA**, apart from limited use in the 19th century (e.g., MERREM, 1820; GRAY, 1850; BOULENGER, 1882), was rejected by most subsequent authors, and was never used as valid since 1900, whereas the nomen **SALIENTIA** was continually considered valid by many authors. Because of the original extension of the taxon it designated (including both reptiles and amphibians), the nomen **GRADIENTIA** cannot be the valid nomen for the order of salamanders. Consequently, its sister-nomen **SALIENTIA** also cannot be retained as the valid nomen for the order of frogs. Furthermore, as the taxon **SALIENTIA** Laurenti, 1768 included (although in part only) the genus *Proteus*, the nomenclatural status of which is fixed by its type-species (*Proteus anguinus* Laurenti, 1768, a salamander), the nomen **SALIENTIA** applies to the taxon of rank superorder for which the valid nomen is **BATRACHIA** Brongniart, 1800 (see above). Therefore, the nomen **SALIENTIA** should not be used as valid for frogs, as suggested e.g. by TRUEB & CLOUTIER (1991).

SCOPOLI (1777) published a classification of the animal kingdom in 12 “tribus”, corresponding mostly to taxa proposed by LINNAEUS (1758) either for classes or orders. Each “tribus” could be divided in several taxa of rank “gens”, the latter in taxa of rank “divisio”, the latter in taxa of rank “ordo” and the latter in taxa of rank “genus”. Within the divisio **REPTILIA** of his gens **LEGITIMA**, SCOPOLI (1777) recognized two new orders: **CAUDATA** for the genera *Draco*, *Lacerta*, *Siren* and *Testudo*, and **ECAUDATA** for the single genus *Rana*. Only the second of these taxa corresponds to a group now considered homogeneous. However, only the first of these nomina was retained by subsequent authors, while the second was forgotten almost entirely shortly after the introduction by DUMÉRIL (1806a) of two replacement nomina for the two nomina of SCOPOLI (1777) (see below). Despite its subsequent use for the order of salamanders by several authors, the nomen **CAUDATA** Scopoli, 1777 does not apply to this taxon according to criterion (C3), as the least inclusive taxon that contains all its originally included genera covers both reptiles and amphibians.

The first author who clearly separated salamanders from lizards, and classified them with frogs, was BRONGNIART (1800a-b). As mentioned above, he created an order **BATRACIENS** for the genera *Bufo*, *Hyla*, *Rana* and *Salamandra*. Shortly thereafter, DUMÉRIL (1806a) adopted this order (as **BATRACHII**) and divided it in two taxa, **ANOURES** and **URODÈLES**, corresponding to tailless and tailed amphibians. This was the first couple of taxa clearly created to separate, within the order of living amphibians, salamanders, and only them (excluding the lizards), from frogs, which was not the case with **GRADIENTIA** and **CAUDATA**. DUMÉRIL (1806a) introduced his two new nomina as French translations of the Latin nomina **ECAUDATI** and **CAUDATI** which he also mentioned for the same taxa. The question may be posed, whether DUMÉRIL’s (1806a) nomina **ECAUDATI** and **CAUDATI** were new nomina, and therefore invalid junior homonyms of **ECAUDATA** and **CAUDATA** proposed earlier by SCOPOLI (1777), or new acceptations and spellings (aponyms, sensu DUBOIS, 2000) for the latter nomina. In the first four texts published by DUMÉRIL (1806a-b, 1807a-b) where this author used the nomina **ECAUDATI** and **CAUDATI**, he did not mention SCOPOLI’s (1777) text and nomina, but he did so

in later works (DUMÉRIL, 1808: 312; DUMÉRIL & BIBRON, 1834: 242), so there is little doubt that he simply used Scopoli's nomina but provided new definitions and contents for the taxa designated by them.

The taxon **ECAUDATI** as used by DUMÉRIL (1806*a*) included four genera, *Bufo*, *Hyla*, *Pipa* and *Rana*. The last was the only genus originally mentioned by SCOPOLI (1777) as a member of his **ECAUDATA**, a nomen of which Duméril's **ECAUDATI** must therefore be considered as an emendation. However, the situation is different concerning **CAUDATI**. As used by DUMÉRIL (1806*a*), this taxon included four genera: *Proteus* (as *Protoeus*), *Salamandra*, *Triton* and *Siren*. Only the last of these genera was part of the genera originally included in the **CAUDATA** Scopoli, 1777, which also included reptiles, so **CAUDATI** Duméril, 1806, which applies to a distinct taxon, must be considered a junior homonym created for a different taxon.

Whatever the interpretation chosen for the status of Duméril's nomina with respect to those of Scopoli, the nomina of the latter cannot be validated for the orders of frogs and salamanders: (1) if Duméril's nomina are considered as two new nomina, both are invalid, being junior homonyms of Scopoli's nomina; (2) if, as supported here, they are interpreted as subsequent uses of Scopoli's nomina, only the nomen **ECAUDATI**, as an emendation of **ECAUDATA**, could possibly be considered valid, whereas **CAUDATI** Duméril, 1806, designating a distinct new taxon, is an invalid junior homonym of **CAUDATA** Scopoli, 1777. But then, because they are sister-nomina, **ECAUDATI** also must be rejected as invalid.

Let us finally consider DUMÉRIL's (1806*a*) new nomina **ANOURES** and **URODÈLES**. They were proposed as replacement nomina of **ECAUDATI** and **CAUDATI**, thus having the same original definitions as the nomina **ECAUDATA** Scopoli, 1777 and **CAUDATI** Duméril, 1806. These two nomina were later latinized, as **ANURA** and **URODELA**, and used as valid nomina by many authors. As both these nomina have remained in wide use by many biologists since their creation, they fully qualify for validation for the two orders of batrachians. However, their retention as valid nomina imposes rejection of the nomina **ECAUDATA** Scopoli, 1777 (of which **ANURA** is a replacement nomen) and **CAUDATI** Duméril, 1806 (already rejected as a junior homonym). It is therefore not possible to maintain uses of both **CAUDATA** and **URODELA** as valid taxa, with the former including the latter or the contrary, as was done by some recent authors (e.g., respectively: MILNER, 1988; TRUEB & CLOUTIER, 1991). Similarly, the nomen **SALIENTIA** cannot be used for a taxon including the **ANURA**, as done also by several authors (e.g.: MILNER, 1988; TRUEB & CLOUTIER, 1991). Validation of both nomina **ANURA** and **URODELA** definitively rejects the couples of sister-nomina **SALIENTIA-GRADIENTIA** and **ECAUDATA-CAUDATA**. These last four nomina should no longer be used in higher nomenclature.

HIGHER NOMENCLATURE OF RECENT AMPHIBIANS

This review of amphibian nomenclature is but one example of the difficulties arising from lack of rules governing nomenclature of higher taxa. Hopefully, the new proposed rules (DUBOIS, submitted) will remedy this chaos. On the basis of this analysis, the nomenclature of the major taxa of recent amphibians is as follows:

- Classis **AMPHIBIA** De Blainville, 1816
 Subclassis **NEOBATRACHI** Sarasin & Sarasin, 1890
 Superordo **BATRACHIA** Brongniart, 1800
 Ordo **ANURA** Duméril, 1806
 Ordo **URODELA** Duméril, 1806
 Superordo **GYMNOPHIONA** Rafinesque-Schmaltz, 1814
 Ordo **GYMNOPHIONA** Rafinesque-Schmaltz, 1814

ACKNOWLEDGEMENTS

For bibliographic information and constructive comments on the manuscript of this paper, I am grateful to Roger Bour, Lauren E. Brown, Patrick David, Darrel R. Frost, W. Ronald Heyer, Annemarie Ohler, Don Shepard and an anonymous reviewer.

LITERATURE CITED

- ANONYMOUS [International Commission on Zoological Nomenclature], 1999. – *International code of zoological nomenclature*. Fourth edition. London, International Trust for zoological Nomenclature: i-xxix + 1-306.
- BATSCH, A. J. G. C., 1788. – *Versuch einer Anleitung, zur Kennniss und Geschichte der Thiere und Mineralien*. Erster Theil. Jena, Akademische Buchhandlung: i-viii + 1-528, pl. 1-5.
- BOULENGER, G. A., 1882. – *Catalogue of the Batrachia Gradientia s. Caudata in the collection of the British Museum*. Second edition. London, Taylor & Francis: i-ix + 1-127, pl. 1-9.
- 1910. – *Les Batraciens, et principalement ceux d'Europe*. Paris, Doin: i-ix + 1-305 + i-xii.
- BOUR, R. & DUBOIS, A., 1985. – Nomenclature ordinale et familiale des Tortues (Reptilia). *Studia geologica salmanticensia*, “1984”, vol. especial 1, *Studia palaeocheloniologica*, 1, Salamanca, Ediciones Universidad: 77-86.
- BRONGNIART, A., 1800a. – Essai d’une classification naturelle des reptiles. I^{ere} partie. Etablissement des ordres. *Bull. Sci. Soc. philom.*, 2 (35): 81-82.
- 1800b. – Essai d’une classification naturelle des reptiles. II^e partie. Formation et disposition des genres. *Bull. Sci. Soc. philom.*, 2 (36): 89-91, pl. 6.
- CEI, J. M. 1993. – *Reptiles del noroeste, nordeste y este de la Argentina. Herpetofauna de las selvas subtropicales, puna y pampas*. Torino, Museo regionale di Scienze naturali, Monogr. 14: 1-949, pl. 1-126.
- COPE, E. D., 1864. – On the characters of the higher groups of Reptilia Squamata – and especially of the Diploglossa. *Proc. Acad. nat. Sci. Philadelphia*, 16: 224-231.
- 1866. – On the structure and distribution of the genera of the arciferous Anura. *J. Acad. nat. Sci. Philadelphia*, (2), 6: 67-112.
- CUVIER, G., 1802. – *Lectures on comparative anatomy*. Translated from the French of G. CUVIER (. .) by William Ross, under the inspection of James MACARTNEY (. . .). Vol. 1. *On the organs of motion*. London, Longman & Rees: i-xl + 1-542, tab. 1-9.
- DE BLAINVILLE, H., 1816. – Prodrome d’une nouvelle distribution systématique du règne animal. *Bull. Sci. Soc. philom. Paris*, juillet 1816: “105-112” [actually 113-120] + 121-124.
- DOWLING, H. G. & DUELLMAN, W. E., 1974-1978. – *Systematic herpetology: a synopsis of families and higher categories*. New York, HISS Publications, Publications in Herpetology, 7: i-vii + 1.1-118.3 + i-viii.
- DUBOIS, A., 1983. – Classification et nomenclature supragénérique des Amphibiens Anoures. *Bull. mens. Soc. linn. Lyon*, 52: 270-276.
- 1984a. – Miscellanea nomenclatorica batrachologica (V). *Alytes*, 3: 111-116.

- 1984b. – La nomenclature supragénérique des Amphibiens Anoures. *Mém. Mus. natn. Hist. nat.*, (A) **131**: 1-64.
- 1985. – Miscellanea nomenclatorica batrachologica (VII). *Alytes*, **4** (2): 61-78.
- 2000. – Synonymies and related lists in zoology: general proposals, with examples in herpetology. *Dumerilia*, **4** (2): 33-98.
- submitted. – Proposed Rules for the incorporation of nomina of higher zoological taxa in the *International Code of Zoological Nomenclature*, with the example of the higher nomina of recent Amphibia.
- DUELLMAN, W. E. & TRUEB, L., 1985. – *Biology of amphibians*. New York, McGraw-Hill, "1986": i-xix + 1-670.
- DUMÉRIL, A. M. C., 1806a. – *Zoologie analytique, ou méthode naturelle de classification des animaux, rendue plus facile à l'aide de tableaux synoptiques*. Paris, Allais: i-xxxiii + 1-544.
- 1806b. – *Analytische Zoologie*. Aus dem Französischen, mit Zusätzen von L. F. FRORIEP. Weimar, Landes-Industrie-Comptoir: [i] + i-vi + 1-346.
- 1807a. – *Traité élémentaire d'histoire naturelle*. Seconde édition. Tome 2. Paris, Deterville: i-xii + 1-360, 20 pl.
- 1807b. – Sur la division des Reptiles Batraciens en deux familles naturelles. *Nouveau Bulletin des Sciences, par la Société philomathique*, **1** (3): 62-63.
- 1808. – Mémoire sur la division des Reptiles Batraciens en deux familles naturelles. *Magasin encyclopédique, ou journal des Sciences, des Lettres et des Arts*, **1808** (2): 308-329.
- DUMÉRIL, A.-M.-C. & BIBRON, G., 1834. – *Erpétologie générale ou histoire naturelle complète des Reptiles*. Tome 1. Paris, Roret: i-xxiv + 1-447.
- ESTES, R., DE QUEIROZ, K. & GAUTHIER, J., 1988. – Phylogenetic relationships within Squamata. In: R. ESTES & G. PREGILL (ed.), *Phylogenetic relationships of the lizard families*, Stanford, Stanford Univ. Press: 119-281.
- FELLER, A. E. & HEDGES, S. B., 1998. – Molecular evidence for the early history of living amphibians. *Mol. Phyl. Evol.*, **9** (3): 509-516.
- FISCHER, G., 1808. – *Tableaux synoptiques de zoognosie*. Moscou, Imprimerie de l'Université Impériale: [1-60] + 1-186, 6 pl.
- FROST, D. R. (ed.), 1985. – *Amphibian species of the world*. Lawrence, Allen Press & Assoc. Syst. Coll.: [i-iv] + i-v + 1-732.
- GADOW, H., 1901. – *Amphibia and reptiles*. London, Macmillan & Co.: i-xiii + 1-668, 1 pl.
- GOIN, C. J. & GOIN, O. B., 1962. – *Introduction to herpetology*. San Francisco & London, Freeman & Co.: i-ix + 1-341.
- GRAY, J. E., 1825. – A synopsis of the genera of Reptiles and Amphibia, with a description of some new species. *Ann. Philos.*, (2), **10**: 193-217.
- 1850. – *Catalogue of the specimens of Amphibia in the collection of the British Museum*. Part II. *Batrachia Gradientia, etc.* London, Spottiswoodes & Shaw: 1-72, pl. 3-4.
- HAECKEL, E., 1866. – *Generelle Morphologie der Organismen*. Zweiter Band. *Allgemeine Entwicklungsgeschichte der Organismen*. Berlin, Georg Kramer: i-clx + 1-462, pl. 1-8.
- 1868. – *Natürliche Schöpfungsgeschichte*. Berlin, Reimer: i-xvi + 1-568, 11 pl.
- 1870. – *Natürliche Schöpfungsgeschichte*. Zweite, verbesserte und vermehrte Auflage. Berlin, Reimer: i-xxxii + 1-688, 15 pl.
- 1872. – *Natürliche Schöpfungsgeschichte*. Dritte verbesserte Auflage. Berlin, Reimer: i-xxviii + 1-688, 15 pl.
- 1873. – *Natürliche Schöpfungsgeschichte*. Vierte verbesserte Auflage. Berlin, Reimer: i-xxviii + 1-688, 15 pl.
- 1902. – *Natürliche Schöpfungsgeschichte*. Zehnte verbesserte Auflage. Zweiter Theil. *Allgemeine Stammes-Geschichte (Phylogenie und Anthropogenie)*. Berlin, Reimer: i-v + 371-832, 23 pl.
- HOGG, J., 1839. – On the classifications of the Amphibia. *Mag. nat. Hist.*, (n.s.), **3**: 265-274.
- IVERSON, J. B., 1992. – *A revised checklist with distribution maps of the turtles of the world*. Richmond, Earlham College: i-xiii, 1-363.
- KUHN, O., 1965. – *Die Amphibien*. Krailling bei München, Oeben: 1-102.
- 1967. – *Amphibien und Reptilien*. Stuttgart, Gustav Fischer: i-vii + 1-124.
- LAPPARENT DE BROIN, F. DE, 2001. – The European turtle fauna from the Triassic to the present. *Dumerilia*, **4** (3): 155-218.

- LATREILLE, P. A., 1800. – *Histoire naturelle des salamandres de France, précédée d'un tableau méthodique des autres reptiles*. Paris, Villier: i-xlvii + 1-63, pl. 1-6.
- 1804. – *Tableau méthodique des poissons*. In: *Tableaux méthodiques d'histoire naturelle*, [i] + 1-238, in: *Nouveau dictionnaire d'histoire naturelle*, Tome 24, Paris, Deterville: 71-105.
- 1825. – *Familles naturelles du règne animal*. Paris, Baillière: [i-v] + 1-570.
- LAURENT, R. F., 1986. – Sous-classe des Lissamphibiens (Lissamphibia). Systématique. In: P.-P. GRASSÉ & M. DELSOL (ed.), *Traité de Zoologie*, 14, *Amphibiens*, fasc. I-B, Paris, Masson: 594-796.
- LAURENTI, J. N., 1768. – *Specimen medicum, exhibens synopsis Reptilium emendatam cum experimentis circa venena et antidota Reptilium austriacorum*. Viennae, Joan. Thom. Nob. de Trattnern: i-ii + 1-215, pl. 1-5.
- LAURIN, M., 1998. – The importance of global parsimony and historical bias in understanding tetrapod evolution. Part 1. Systematics, middle ear evolution and jaw suspension. *Annales des Sciences naturelles, Zoologie*, (13), 19: 1-42.
- LINNAEUS, C., 1758. – *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata. Tomus I. Holmiae, Laurentii Salvii: [i-iv] + 1-824.
- MERCHAN FORNELINO, M. & MARTINEZ SILVESTRE, A., 1999. – *Tortugas de España*. Madrid, Antiquaria, 1-400.
- MERREM, B., 1820. – *Versuch eines Systems der Amphibien. Tentamen systematis amphibiorum*. Marburg, Johann Christian Krieger: (i-xv + 1-191) ×2, 1 pl.
- MILNER, A. R., 1988. – The relationships and origin of living amphibians. In: M. J. BENTON (ed.), *The phylogeny and classification of the tetrapods*, Oxford, Clarendon Press: 59-102.
- MÜLLER, J., 1831. – Beiträge zur Anatomie und Naturgeschichte der Amphibien. *Z. Physiologie*, 4: 190-275, pl. 18-22.
- OPPEL, M., 1811a. – *Ordre II. Reptiles à écailles. Section II. Ophidiens*. *Annales du Muséum d'Histoire naturelle*, 16 (94): 254-295.
- 1811b. – Suite du 1^{er} mémoire sur la classification des Reptiles. *Annales du Muséum d'Histoire naturelle*, 16 (95): 376-393.
- 1811c. – Second mémoire sur la classification des Reptiles. *Annales du Muséum d'Histoire naturelle*, 16: 394-418.
- 1811d. – *Sur la classification des Reptiles*. Paris: i + 1-84.
- 1811e. – *Die Ordnungen, Familien und Gattungen der Reptilien als Prodrom einer Naturgeschichte derselben*. München, Lindauer: i-xii + 1-87.
- 1811f. – *Sur la classification des Reptiles*. *Nouv. Bull. Sci., Soc. philom.*, 2 (46): 301-306.
- PARSONS, T. S. & WILLIAMS, E. E., 1963. – The relationships of the modern Amphibia: a re-examination. *Quart. Rev. Biol.*, 38 (1): 26-53.
- PÉREZ-MELLADO, V. 1998. – Familia Lacertidae Opper, 1811. In: A. SALVADOR (ed.), *Reptiles*, Madrid, Museo Nacional de Ciencias Naturales, CSIC, *Fauna Iberica*, vol. 10: 161-166.
- RAFINESQUE, C. S., 1815. – *Analyse de la nature ou Tableau de l'univers et des corps organisés*. Palerme, Jean Barravecchia: 1-124, 1 pl.
- RAFINESQUE-SCHMALTZ, C. S., 1814a. – O quadro del metodo sinottico di somiologia. *Specchio Sci., Giorn. encicl. Sicilia*, 1 (1): 11-15.
- 1814b. – *Principes fondamentaux de somiologie, ou les loix de la nomenclature et de la classification de l'empire organique, ou des animaux et des végétaux, contenant les règles essentielles de l'art de leur imposer des noms immuables et de les classer méthodiquement*. Palerme, Franc. Abate: 1-52.
- REIG, O., 1958. – Propositiones para una nueva macrosistemática de los Anuros (nota preliminar). *Physis*, 21: 109-118.
- ROGNER, M., 1996. – *Schildkröten*. 2. Hürtgenwald, Heidi-Rogner-Verlag. 1-265.
- ROMER, A. S., 1966. – *Vertebrate paleontology*. Third edition. Chicago & London, The University of Chicago Press: i-ix + 1-468.
- SANCHÍZ, B., 1998. – Saliencia. In: P. WELLNHOFER (ed.), *Handbuch der Paläoherpetologie*, Teil 4, München, Friedrich Pfeil: i-xii + 1-275.
- SARASIN, P. & SARASIN, F., 1890. – Zur Entwicklungsgeschichte und Anatomie der ceylonesischen Blindwühle *Ichthyophis glutinosus*, L. Vierter Theil. In: *Ergebnisse naturwissenschaftlicher Forschungen auf Ceylon*, Zweiter Band, Wiesbaden, Krieger: 151-263, pl. 15-24.

- SCOPOLI, I. A., 1777. – *Introductio ad historiam naturalem, sistens genera lapidum, plantarum, ed animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae*. Pragae, Gerle: [i-x] + 1-506 + i-xxxvi.
- SOKOL, O. M., 1977. – A subordinal classification of frogs (Amphibia: Anura). *J. Zool.*, London, **182**: 505-508.
- STEJNEGER, L., 1904. – Amphibia versus Batrachia. *Science*, (2), **20**: 924-925.
- TAYLOR, E. H., 1963. – The lizards of Thailand. *University of Kansas Science Bulletin*, **44** (14): 687-1077.
- TRUEB, L. & CLOUTIER, R., 1991. – A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli). In: H.-P. SCHULTZE & L. TRUEB (ed.), *Origins of the higher groups of tetrapods: controversy and consensus*, Ithaca, New York, Cornell Univ. Press: 223-313.
- TUDGE, C., 2000. – *The variety of life*. Oxford, Oxford University Press: i-xv + 1-684.
- VETTER, H., 2002. – *Tarralog – Turtles of the World*. Vol. 1. *Africa, Europe and Western Asia*. Frankfurt am Main, Chimaira. 1-96.
- ZARDOYA, R. & MEYER, A., 2001. – On the origin of and phylogenetic relationships among living amphibians. *Proc. nat. Acad. Sci. USA*, **98** (13): 7380-7383.
- ZHAO, E., ZHAO, K., ZHOU, K. et al. (ed.), 1999. – *Fauna sinica. Reptila*. Vol. 2. *Squamata Lacertilia*. Beijing, Science Press: i-xi + 394, pl. 1-8.
- ZITTEL, K. A., 1888. – Vertebrata (Pisces, Amphibia, Reptilia, Aves). In: *Handbuch der Palaeontologie*, III. Band, [third installment], München & Leipzig, R. Oldenbourg: 257-436.
- ZUG, G. R., 1993. – *Herpetology*. San Diego, Academic Press: i-xv + 1-527.

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