



The Status of the Plethodontid Salamander Genera *Bolitoglossa* and *Magnadigitata*

Author(s): David B. Wake and Arden H. Brame, Jr.

Reviewed work(s):

Source: *Copeia*, Vol. 1963, No. 2 (Jun. 14, 1963), pp. 382-387

Published by: [American Society of Ichthyologists and Herpetologists \(ASIH\)](#)

Stable URL: <http://www.jstor.org/stable/1441357>

Accessed: 24/01/2012 13:18

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at

<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



American Society of Ichthyologists and Herpetologists (ASIH) is collaborating with JSTOR to digitize, preserve and extend access to *Copeia*.

<http://www.jstor.org>

the construction and maintenance of the field equipment; and to Dr. A. R. Main for his review of the manuscript.

LITERATURE CITED

- DAVIS, W. C. 1963. Comparative courtship of *Taricha*. *Copeia* (in press).
- PACKER, W. C. 1960. Bioclimatic influences on the breeding migration of *Taricha rivularis*. *Ecology* 41:509-17.
- . 1961. Feeding behavior in adult *Taricha*. *Copeia* 1961:351-2.
- . 1962. Aquatic homing behavior in *Taricha rivularis*. *Copeia* 1962:207-8.

- TWITTY, V. C. 1959. Field experiment on the biology and genetic relationships of the Californian species of *Triturus*. *J. Exp. Zool.* 129:129-48.
- . 1959. Migration and speciation in newts. *Science* 130(3391):1735-43.
- . 1961. Experiments on homing behavior and speciation in *Taricha*, pp. 415-59, *Vertebrate Speciation*, ed. W. F. Blair, U. of Texas Press xvi + 642 pp.

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF WESTERN AUSTRALIA, NEDLANDS, W. A., AUSTRALIA.

The Status of the Plethodontid Salamander Genera *Bolitoglossa* and *Magnadigita*

DAVID B. WAKE AND ARDEN H. BRAME, JR.

Critical reevaluation of the status of the tropical American salamander genera *Bolitoglossa* and *Magnadigita* shows that the diagnostic characters break down and that only a single natural group is represented. The older name, *Bolitoglossa*, is retained for the group. The genus is re-diagnosed and a list of names based on examples of *Bolitoglossa* is included.

REVISION of the nominal genus *Oedipus* Tschudi by Taylor (1944) resulted in the grouping of the many species previously referred to this taxon into seven genera. Two assemblages were recognized as the genera *Magnadigita* and *Bolitoglossa*. Although the two genera share many characters in common, Taylor stated that they differed in several features (see Table 1). No contrasting characters other than those presented in Table 1 can be found in his diagnoses, and it is evident that Taylor considered webbing (3) to be of prime importance in distinguishing between the two groups.

Many herpetologists have been reluctant to accept the conclusions of Taylor. As late as 1951, Schmidt and Inger referred Brazilian material to the preoccupied genus *Oedipus*. Other authors have encountered difficulties in allocating material to *Magnadigita* and *Bolitoglossa* and during the course of our studies of South American salamanders we have been unable to assign certain species to either genus. In some cases species closely related on the basis of many other characteristics must be placed in different genera on the basis of the distinguishing

features employed by Taylor. The two genera share many features in common and the species presently assigned to them appear to be members of a single natural group. All members of the two genera lack a sublingual fold in contrast to the other neotropical members of the family. In addition, the two genera are similar in throat myology and in the shape of hyoid elements, and in these characters differ from all other members of the composite genus *Oedipus* (Tanner, 1952). An intensive survey of the osteology of 22 species of the two genera, including the generic types, by the senior author has revealed no character, or combination of characters, which will separate the species along the lines of generic division proposed by Taylor (1944). On the basis of these data critical reevaluation of Taylor's separation of these salamanders into two genera seemed essential. Our analysis consisted of examination of 45 species of the group, including several undescribed species. Particular attention was given to Taylor's diagnostic characters.

Taylor's diagnostic characters.—Taylor (1944) was not explicit in regard to two of the three characters that differed in his

TABLE 1. GENERIC CHARACTERS OF *Magnadigita* AND *Bolitoglossa* USED BY TAYLOR (1944)

<i>Magnadigita</i>	<i>Bolitoglossa</i>
(1) Maxillary teeth present.	(1) Maxillary teeth not typically pleurodont but arising from flat surface of bone and not at the edge, with two forms lacking teeth.
(2) Metatarsals, metacarpals, and phalanges poorly ossified with phalanges compressed, flattened, with some evidence of lateral bony web.	(2) Metatarsals, metacarpals, and phalanges compressed, hourglass-shaped with lateral bony webs (some of the terminal phalanges may be represented by cartilage only).
(3) Digits wide, more or less truncate, the outer one or two phalanges greatly shortened and free.	(3) Feet and hands palmate, none or only tips of digits free.

diagnoses of *Bolitoglossa* and *Magnadigita* [see (1) and (2), Table 1]. Let us examine these characters in more detail. No significant or consistent difference between placement or type of maxillary dentition in species presently assigned to the two genera can be found. In certain of the more completely webbed species (*rufescens*, *occidentalis*, *colonnea*, *altamazonica*, for example) greatly reduced numbers of maxillary teeth (or absence of teeth) are found. Tooth loss is an obvious specialization in plethodontids and these species are also specialized in other ways. Other species having similar hands and feet (*alvaradoi*, *borburata*, *striatula*, for example) have relatively large numbers of maxillary teeth.

As is evident from Table 1, Taylor was vague concerning differences associated with the shape of the metatarsals, metacarpals, and phalanges in the two genera. We found no consistent differences that correlate with Taylor's generic division, or with a division based on any other characters. The distal phalanges of forms with truncate, relatively slightly webbed digits are often larger than the distal phalanges of fully webbed species, but intermediates occur in correlation with intermediate amounts of webbing. A general trend seems to prevail in which the amount of reduction in size of the phalanges from proximal to distal is greater as the webbing increases, but no obvious break in this continuum is evident.

Two extremes of hand and foot types are seen among species currently assigned to the genera *Bolitoglossa* and *Magnadigita*. One is typified by the foot of *robusta* (Fig.

1, B), a form that fits Taylor's diagnosis of *Magnadigita* [see character (3), Table 1]. The other, typified by the foot of *mexicana* (Fig. 1, L), fits his diagnosis of *Bolitoglossa*. The foot of *robusta* is virtually webless and generalized, and is similar to what might be considered a primitive plethodontid foot. On the other hand, that of *mexicana* is fully webbed and in that characteristic is specialized and, presumably, advanced compared to the foot of *robusta*. On the basis of these very different foot structures, it appears that Taylor's webbing character divides the group into fully webbed species (his *Bolitoglossa*) and webless or slightly webbed species (his *Magnadigita*). This division is not valid, however, since intermediates of many different types are found. When all species of both nominal genera are considered, a gradual transition from no webbing to complete webbing is evident. Since the shape of the digits and amount of digit webbing are the characters emphasized by Taylor in his original diagnosis of the groups, they are discussed in some detail below.

The feet of *nigroflavescens* (Fig. 1, A; all figures drawn from actual specimen through use of an opaque projector), the genotype of *Magnadigita*, and of *robusta* (Fig. 1, B) are examples that fit Taylor's diagnosis of *Magnadigita*. The truncate digits of *robusta* are virtually webless, while the slightly less truncate digits of *nigroflavescens* are only slightly webbed. The outer one or two phalanges of these two species, based on examination of cleared and stained specimens, are no more greatly shortened than are those of species assigned by Taylor to

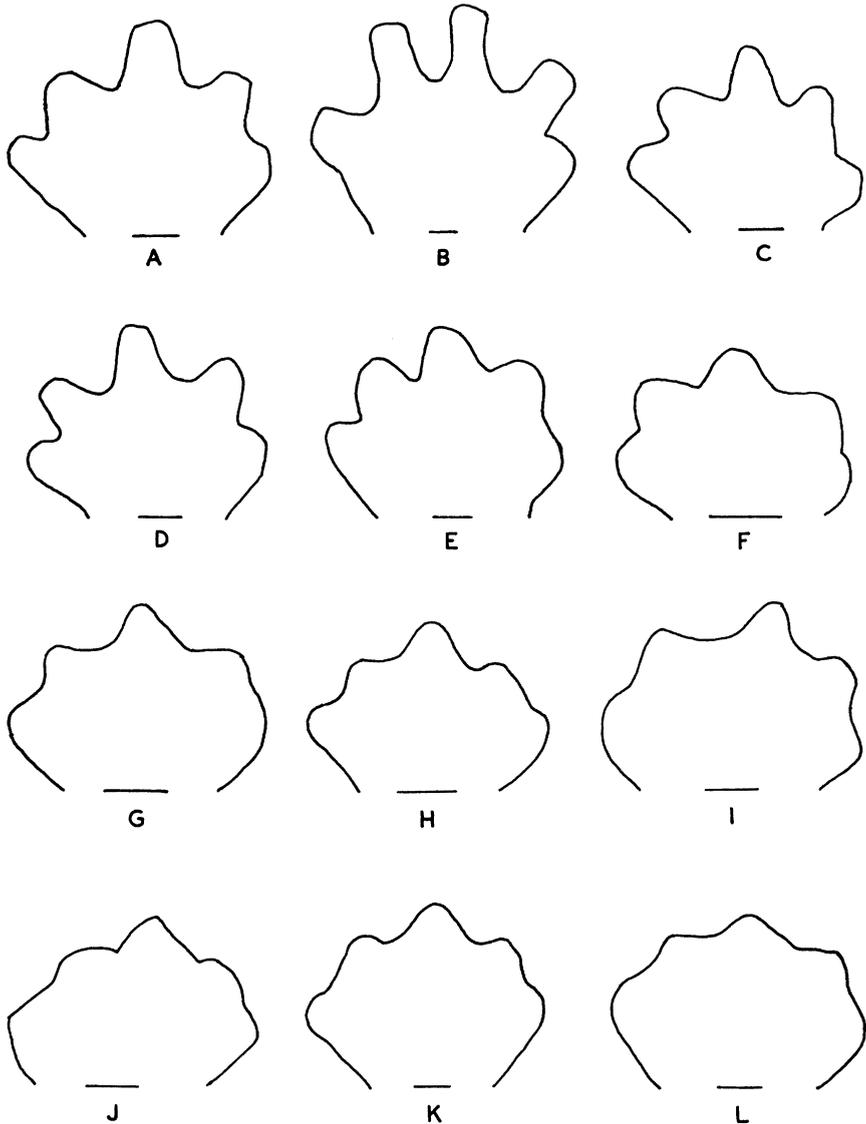


Fig. 1. Variation of left hind feet in *Bolitoglossa* (outlines made with an opaque projector).

- A. *B. nigroflavescens*, UMMZ 88216, México, Chiapas: Cerro Ovando.
- B. *B. robusta*, Univ. So. Calif. (CRE 192), Costa Rica, Cartago: Cienaga de Colorado, east of Juan Viñas.
- C. *B. flavimembris*, CNHM 20322, Guatemala, San Marcos: Volcán Tajumulco.
- D. *B. adspersa*, ICNB no number, Columbia, Cundinamarca: Páramo Crus Verde, vicinity of Bogotá.
- E. *B. adspersa*, ANSP 24101, Colombia, Cundinamarca: Aguadita, south of Bogotá.
- F. *B. orestes*, BM 1905.5.31.101, Venezuela, Mérida: Culata.
- G. *Bolitoglossa* sp., MLaS 4, Colombia, Santander: San Gil.
- H. *B. helmrichi*, UMMZ S-1597, Guatemala, Alta Verapaz.
- I. *B. borburata*, UMMZ 113870 (4088), Venezuela, Aragua: Rancho Grande.
- J. *B. borburata*, UMMZ 113870 (4086), same locality as I.
- K. *Bolitoglossa* sp., MLaS 1a, Colombia, Cundinamarca: Hacienda La Victoria.
- L. *B. m. mexicana*, CNHM 91457, México, Chiapas: Palenque.

Bolitoglossa, and in fact are considerably larger than those of many *Bolitoglossa*. Several other species have feet similar to *robusta* and *nigroflavescens*, including *dunni*, *subpalmata*, *marmorea*, *hypacra*, and *cerroensis*. A number of species have a foot that is similar to that of *nigroflavescens*, but with more webbing. The feet of *flavimembris* (Fig. 1, C), and *omniumsantum* have more webbing and the digits are slightly less truncate than those of *nigroflavescens*, while the digits are rounded or even slightly pointed at the tips.

Intraspecific variation is seen in the shape of the hands and feet in *adpersa*, some individuals having feet with little webbing and truncate digits (Fig. 1, D) very similar to those of *nigroflavescens*, others having more fully webbed feet with less truncate and rounded or slightly pointed digits (Fig. 1, E). Generic allocation of *adpersa* has long been in question and Taylor (1944) included it in *Magnadigita* with a query. Later in the same paper, Taylor assigned another specimen of *adpersa* to *Bolitoglossa* sp. with a query.

The foot of *orestes* (Fig. 1, F) has broadly flattened, round tipped digits that are not truncate and are visible as discrete structures united to one another for much of their length by a narrow thin web. The foot of *palmata* (Brame and Wake, 1962: 172, Fig. 2, A) is similar to that of *orestes* but the digits have more webbing. Another species with an intermediate foot type is an undescribed species from San Gil, Departamento de Santander, Colombia, which has digits that are not truncate and have somewhat pointed tips (Fig. 1, G). The webbing between the first and second, and the fourth and fifth digits is increased over that of *orestes*, but the longest fingers and toes remain relatively free of webbing.

Flattened feet and pointed indistinct digits are present in *helmrichi* (Fig. 1, H), but the webbing is incomplete. Taylor (1944) considered *helmrichi* to be a *Bolitoglossa*, but Stuart (1952) considered it to be closely related to other *Magnadigita* and placed it in that genus. Some *helmrichi* have less webbing than in the specimen illustrated. The feet on *cuchumatana* are similar to those of *helmrichi*.

Another variable species is *borburata*, some individuals of which have flattened feet with rounded, discrete toe tips and

small amounts of webbing (Fig. 1, I), while others have flattened feet and indistinct digits with rounded tips and more webbing (Fig. 1, J).

A new species from Hacienda La Victoria, Departamento de Cundinamarca, Colombia, has a flattened foot with rounded toe tips, but the webbing is not complete and one phalanx in several toes is free from the web (Fig. 1, K).

The genotype of *Bolitoglossa mexicana* (Fig. 1, L), as well as *alvaradoi*, *altamazonica*, *striatula*, and others, are examples of forms that have virtually fully webbed feet with flattened digits that are broadly united by an extensive web. In these forms it is difficult to recognize the toes as discrete structures and the tips extend from the web as broad-based points.

It is clear that a gradual transition occurs in all of the characters associated with digit shape and amount of webbing of digits which were used by Taylor in erecting the genera *Bolitoglossa* and *Magnadigita*. It is impossible to separate the species of the nominal genera on the basis of these or other characters.

Discussion.—In the light of the above information it becomes necessary to state our definition of a genus. We think of the genus as a taxonomic and phylogenetic category consisting of one or more species that have a uniformity of characters indicating that the species are members of a single phylogenetic sequence—a natural group. The genus is distinguishable from related genera by characters that are roughly equivalent (in a phylogenetic sense) to those separating other genera within the same family. Obviously the genus is a subjective category and it falls to the systematist to evaluate the importance of a character or combination of characters. The old genera *Magnadigita* and *Bolitoglossa* are not natural groups and thus, according to our definition, are not valid genera. The revised genus *Bolitoglossa*, containing all species of the former genera, fits the definition because the species illustrate a uniformity that indicates all are members of a single large natural group. The genus *Bolitoglossa* is distinguished from all other genera of plethodontid salamanders by a combination of myological, osteological, and superficial characters. Several subgroups, none achieving generic rank, are recognizable and will

be discussed in forthcoming publications.

The name *Bolitoglossa* Duméril, Bibron, and Duméril, 1854, has a priority over *Magnadigita* Taylor, 1944.

Diagnosis.—The genus *Bolitoglossa* includes those plethodontid salamanders with a boletoid tongue, no sublingual fold, 5 toes, a single premaxilla, 14 amphicoelous trunk vertebrae (13 costal grooves), variable amounts of hand and foot webbing, ceratohyals terminating in a bluntly rounded end, and operculum with columella absent or tiny and vestigial.

Included taxa.—The following list includes all names known to be based on examples of *Bolitoglossa*. Valid names are in boldface type. Evidence for reference of certain names to synonymy and resurrection of others in the list below (in brackets) will be presented in subsequent papers. Initials following species names indicate country in which each is known to occur as follows: Br = Brazil, BH = British Honduras, B = Bolivia, C = Colombia, CR = Costa Rica, E = Ecuador, G = Guatemala, H = Honduras, M = México, N = Nicaragua, P = Panamá, Pr = Peru, S = El Salvador, V = Venezuela.

adspersa (Peters, 1863); C
ahli Unterstein, 1930 = *lignicolor*
altamazonica (Cope, 1874); Br, B, C, Pr
alvaradoi Taylor, 1954; CR
andicola Posada Arango, 1909 = *adspersa*
arborescendens Taylor, 1954; CR
attitlanensis Brocchi, 1883 = *salvinii*
biseriata Tanner, 1962; P
bocourti Brocchi, 1883 = *rostrata*
borburata Trapido, 1942; V
brevipes (Bumzahem and Smith, 1955); M
carbonarius Cope, 1860 = *platydactyla*
cerroensis (Taylor, 1952); CR
colonnea (Dunn, 1924); CR, P
copei Brocchi, 1883 = *mexicana mulleri*
cuchumatana (Stuart, 1943); G
dofleini (Werner, 1903); G
dunni (Schmidt, 1933); H
engelhardti (Schmidt, 1936); G, S
estheri Miranda Ribeiro, 1937 = *altamazonica*
flavimembris (Schmidt, 1936); G
foaventris (Schmidt, 1936); M
franklini (Schmidt, 1936); G
helmrichi (Schmidt, 1936); G
hypacra (Brame and Wake, 1962); C
lignicolor (Peters, 1873); CR, P

lincolni (Stuart, 1943); G
macrinii (Lafrentz, 1930); M
marmorea (Tanner and Brame, 1961); P
mexicana Duméril, Bibron, and Duméril, 1854 = *mexicana mexicana*; BH, G, H, M
mulleri (Brocchi, 1883) = *mexicana mulleri*; G
moreleti Smith, 1945 = *mexicana mexicana*
morio (Cope, 1869); G
nigrescens (Taylor, 1949); CR
nigroflavescens Taylor, 1941; M
occidentalis Taylor, 1941; G, M
odonelli (Stuart, 1943) = *mexicana odonelli*; G
omniumsanctorum (Stuart, 1952); G
orestes Brame and Wake, 1962; V
palmata (Werner, 1897); E
palustris Taylor, 1949 [= *lignicolor*]
paraensis Unterstein, 1930 [= *altamazonica*]
peruviana (Boulenger, 1883); Pr
pesrubra Taylor, 1952 [= *subpalmata*]
phalarosoma Wake and Brame, 1962; C
platydactyla (Gray, 1831); M
?punctatum Brocchi, 1883 = *platydactyla*
robusta (Cope, 1894); Cr, P
rostrata (Brocchi, 1883); G
rufescens (Cope, 1869); G, H, M
salvinii (Gray, 1869); G, M
schmidti (Dunn, 1924); H
[sima (Vaillant, 1911); E]
striatula (Noble, 1918); CR, H, N
subpalmata (Boulenger, 1896); CR, P
togata Duméril, Bibron, and Duméril, 1854 = *platydactyla*
torresi Taylor, 1952 [= *subpalmata*]
variegata Gray, 1831 = *platydactyla*
veracruzis Taylor, 1951; M
yucatanica (Peters, 1882); M

Smith and Taylor (1948) tentatively placed *Spelerpes sulcatum* Brocchi, 1883, in the genus *Magnadigita*. The holotype was recently examined by Brame and found not assignable to the revised genus *Bolitoglossa*.

Acknowledgments and abbreviations.—We are deeply indebted to Robert F. Inger, Chicago Natural History Museum (CNHM); Charles F. Walker and Norman E. Hartweg, University of Michigan Museum of Zoology (UMMZ); Alice G. C. Grandison, British Museum of Natural History (BM); Neil T. Richmond, Carnegie Museum; Charles M. Bogert and Richard G. Zweifel, American Museum of Natural History

(AMNH); Ernest E. Williams, Museum of Comparative Zoology (MCZ); L. Forcart, Naturhistorisches Museum, Basel; L. D. Brongersma, Rijksmuseum van Natuurlijke Historie, Leiden; J. Eisel, Naturhistorisches Museum, Wien; Fredrico Medem, Instituto Ciencias Naturales, Bogotá (ICNB); Alan E. Leviton, California Academy of Sciences; Werner Ladiges, Zoologisches Staatsinstitut und Museum, Hamburg; Doris M. Cochran, United States National Museum; Jean Guibe, Museum National de Histoire Naturelle, Paris; and Heinz Wermuth, formerly of Zoologisches Museum Berlin, for allowing us to examine valuable material from Mexico, Central America, and South America. We greatly appreciate the assistance of Hermano Nicéforo María of the Museo del Instituto de La Salle (MLaS), Bogotá, Colombia, who graciously loaned us his important salamander material. We appreciate helpful criticisms and review of the manuscript by Jay M. Savage. The junior author initiated his study of southern Central and South American urodeles under the sponsorship of the National Science

Foundation (G-6089). The research was completed while the senior author held a National Science Foundation Cooperative Graduate Fellowship.

LITERATURE CITED

- BRAME, A. H., JR. AND D. B. WAKE. 1962. A new salamander (Genus *Bolitoglossa*) from Venezuela with redescription of the Ecuadorian *B. palmata* (Werner). *Copeia* 1962:170-7.
- DUMÉRIL, A. M. C., G. BIBRON, AND A. DUMÉRIL. 1854. *Erpétologie générale ou histoire naturelle complète des reptiles* 9:v-xx, 1-440.
- SCHMIDT, K. P. AND R. F. INGER. 1951. Amphibians and reptiles of the Hopkins-Branner Expedition to Brazil. *Fieldiana, Zool.* 31: 439-65.
- STUART, L. C. 1952. Some new amphibians from Guatemala. *Proc. Biol. Soc. Washington* 65:1-12.
- TANNER, W. W. 1952. A comparative study of the throat musculature of the Plethodontidae of Mexico and Central America. *Univ. Kansas Sci. Bull.* 34, Pt. 2, 583-677.
- TAYLOR, E. H. 1944. The genera of plethodontid salamanders in Mexico. *Univ. Kansas Sci. Bull.* 30, Pt. 1, 189-232.
- DEPARTMENT OF BIOLOGY, UNIVERSITY OF SOUTHERN CALIFORNIA, LOS ANGELES 7, CALIFORNIA.

Body Temperature, Activity, and Behavior of the Agamid Lizard, *Amphibolurus barbatus*

ANTHONY K. LEE AND JUDITH A. BADHAM

Semicontinuous records of diurnal body temperatures of the 250- to 500-g agamid, *Amphibolurus barbatus*, were obtained with a deep esophageal thermocouple. The lizard is a heliotherm with a preferred range of body temperatures between 30 and 40°C, which includes 94 per cent of all activity observed. The rate of activity appears to be independent of body temperature within the preferred range. Heat storage, achieved by virtue of the mass of the lizard and opportunistic basking to temperatures approaching the maximum voluntary tolerance, permits the lizards to retain preferred temperatures when conditions favor heat loss. Relative independence of temperature and certain behavior patterns, such as feeding and threat display, are advantageous where the lizards spend long periods basking to preferred temperatures in the morning.

THE role of heliothermy in temperature regulation of reptiles was demonstrated by Cowles and Bogert (1944) and Bogert (1949a, 1959a). These authors were able to show that many active diurnal lizards maintain body temperatures within narrow limits (the preferred or ecritic temperatures), usually between 30 and 40°C, and largely independently of the temperatures of the

adjacent air and substratum. Behavioral regulation of the body temperature of active lizards was considered to endow lizards with the advantages of a relatively constant body temperature as found among mammals and birds.

The majority of studies has been concerned with the frequency of the phenomena of heliothermy and thigmothermy