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Osteology and Evolution in Neotropical Bufo[1,2]

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ABSTRACT: Members of five species groups of Neotropical *Bufo* were examined osteologically. Representatives of the *guttatus* group possess broad frontoparietals which fuse with the pro-otics late in ontogeny; the neural spines of these species are greatly roughened. Affinity with the African *B. mauritanicus, B. superciliaris* and *regularis* species group and with the Asian *B. asper* is suggested. The *marinus* group displays broad frontoparietals in fusion with the pro-otics and cristation patterns similar to the Central American and Mexican *valliceps* group. Toads of the *granulosus* group possess "closed" orbits, intense dermal coossification, and frontoparietals of broad and intermediate width; these conditions are possibly secondarily derived. The *spinulosus* group comprises both broad and narrow frontoparietal types which may represent separate major evolutionary lines. The monotypic *variegatus* group appears closely related to the narrow frontoparietal members of the *spinulosus* group.

INTRODUCTION

Recently, much evolutionary research has been directed toward the genus *Bufo*. Baldauf (1955, 1958, 1959) has employed histological reconstruction in comparisons of cranial morphology. Evidence from paleontology and osteology has been utilized by Tihen (1960, 1962a,b; in press) toward systematic ends. Morphological and several biochemical approaches have been applied by Cei and various colleagues (1960, 1962, 1966) to South American species. Guttman (1967) has investigated blood proteins in *Bufo* using starch-gel electrophoresis, while Bogart (1968) has employed cytogenetic analysis in his research. The mechanics of vocalization of many bufonids have been compared by W. F. Martin (1967). During this time, Blair (1962, 1963, 1964, 1966; in press), utilizing artificial hybridization and other techniques, has developed a comprehensive evolutionary scheme for *Bufo*. Nevertheless, many opportunities for question and confirmation exist and provide stimuli for further investigation.

MATERIALS AND METHODS

This report presents and analyzes osteological data for five Neotropical species groups of *Bufo;* relevant species from other continents are also discussed in detail. Sample size is indicated in parentheses after the specific name. Debatable species status is indicated by question marks directly succeeding taxa. Species group assignation generally follows that of Blair (in press).

Skeletonization was by treatment with dilute sodium hypochlorite (Sanders, 1953) or by dermestid beetle larvae. Osteological details of

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major *Bufo* skull types are depicted in Figure 1. The three paired dermal elements which form much of the skull roof (nasals, anteromedial; frontoparietals, posteromedial; squamosals, lateral) may be cristate or smooth. When crests exist, two major patterns are evident: the *americanus* and *valliceps* types (Fig. 1). The nasal bones usually terminate anteriorly at approximately the line of the jaw; only marked deviations from this condition are noted. Considerable systematic importance has been focused (Tihen 1962a,b; Blair, 1963, 1964; R. F. Martin, 1964) upon the extent to which the frontoparietals project above the posteromedial corner of the orbit (Fig. 1). The degree to which the occipital canals are covered by elaborations of the frontoparietals varies interspecifically. Sutural contact of the frontoparietal and squamosal may be elaborate, partial or absent, and, within the orbit, fusion between pro-otic and frontoparietal elements may or may not occur. Surface texture varies among cranial elements from smooth to spiculate or cancellous. In occipital aspect, the suprapterygoid fenestrae may be large or occluded to varying degrees by flanges of the squamosal or pterygoid. Ventrally, the lateral wings (alae) of the parasphenoid may be overlapped by the medial arms of the pterygoid, merely tangent with them, or no contact may occur. The quadratojugal bone may be short and not contact the maxilla, or may extend more anteriorly from the angle of the jaw, overlapping the maxilla, and forming a large part of the lateral wall of the pterygoid fossa. Although discussed as a character of significance by Baldauf (1959), the location of the angle of the jaw in relation to the position of the jugular foramen is quite variable intraspecifically (R. F. Martin, 1964), and only extreme deviations from the condition in which they approximate the same transverse plane are noted.

Mensuration was with vernier calipers or ocular micrometer, recorded to the nearest 0.1 mm. The characters measured were:

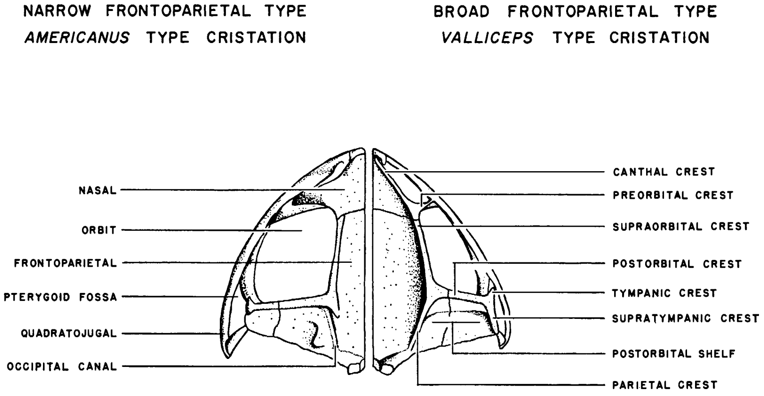

Fig. 1.—Nomenclature of cranial characters of *Bufo*

Skull length.—Distance from posterior end of the occipital condyles to tips of nasal bones.

Skull width.—Distance between lateral edges of maxillae (or quadratojugals) at greatest breadth.

Skull height.—Perpendicular distance between a plane upon which ventral surfaces of a skull are tangent and a parallel plane including most dorsal midline point of frontoparietal bones.

Transorbital width.—Distance between posteromedial corners of orbits measured at dorsal skull roof. If an arc of bone rather than a corner existed in this area, measurement was taken at a point (subjectively) judged to be its midpoint.

Occipital canal width.—Distance between centers of anterior openings of occipital canals (or grooves).

Neurocranial height.—Skull was viewed in occipital aspect along a line determined by lowest anterior and posterior points of parasphenoid bone. Neurocranial height was the distance between this line and most dorsal median point of frontoparietal bones.

Vertebral column length.—Distance from the most anterior edge of the articular facets of the first to the most posterior edge of the articular facets of the ninth vertebral centrum.

Vertebral column width.—Greatest width of the anterior end of the centrum of the fourth vertebra.

Humeral length.—Greatest length of humerus.

Humeral width.—Width of the humerus at most elevated portion of and including humeral crest.

Femoral length.—Greatest length of femur.

Femoral width.—Width of femur at midpoint of and including femoral crest.

Tibiofibula length.—Greatest length of the tibiofibula.

Tibiofibula width.—Shortest distance across neck of tibiofibula taken parallel to broadest plane of the bone.

Indices were constructed from the previous measurements. Underhill (1961) has indicated an isometric relationship of nonskeletal characters in certain ratios constructed for adult *B. woodhousei.* In the present study, the assumption of isometry was made for the following:

Skull length/width x 1000(Fig. 3). Samples with means between 775 and 885 were considered of average proportions.

Occipital canal width/transorbital width x 1000 (Fig. 4). This index attempts to quantify the width of the frontoparietal bones. In this research (and general usage) these terms apply not to the actual width of the bones at any point, but to the amount of their horizontal projection above the dorsal posteromedial corner of the orbit (and projection beyond the dorsolateral portion of the braincase at the rear of the orbit). Samples with means between 855 and 955 were considered of average proportions.

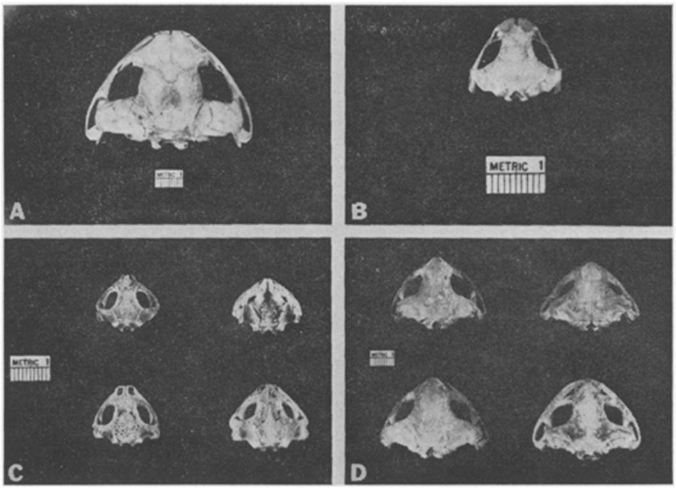

Fig. 2.—Crania of *Bufo*. (A) *B. blombergi*. (B) *B. haematiticus*. (C) top: *B. fernandezae*, *B. d'orbignyi;* bottom: *B. humboldti*, *B. major*. (D) top: *B. marinus*, Colombia; *B. paracnemis;* bottom: *B. marinus*, Mexico; *B. ictericus*

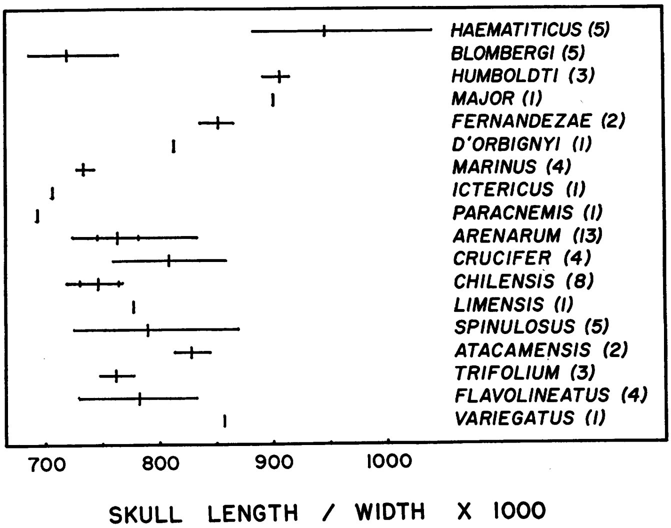

Fig. 3.—Skull length/skull width X 1000. The horizontal line indicates the range; the long vertical line intersecting it, the mean. For samples exceeding five, the 95% confidence intervals are indicated by short vertical lines bracketing the mean. Sample size is indicated in parentheses

Neurocranial height/occipital canal width x 1000 (Fig. 5). This index describes the shape of the braincase: elevated, depressed or intermediate. Samples with means between 670 and 750 were considered of average dimensions.

Total height-neurocranial height/neurocranial height x 1000 (Fig. 6). This index indirectly describes the degree of elevation of the base of the braincase above the most ventral portion of the skull and is a function of the length of

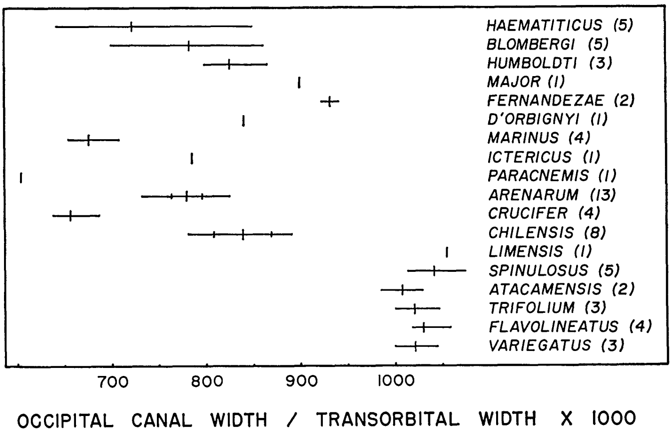

Fig. 4.—Occipital canal width/transorbital width X 1000. The horizontal line indicates the range; the long vertical line intersecting it, the mean. For samples exceeding five, the 95% confidence intervals are indicated by short vertical lines bracketing the mean. Sample size is indicated in parentheses

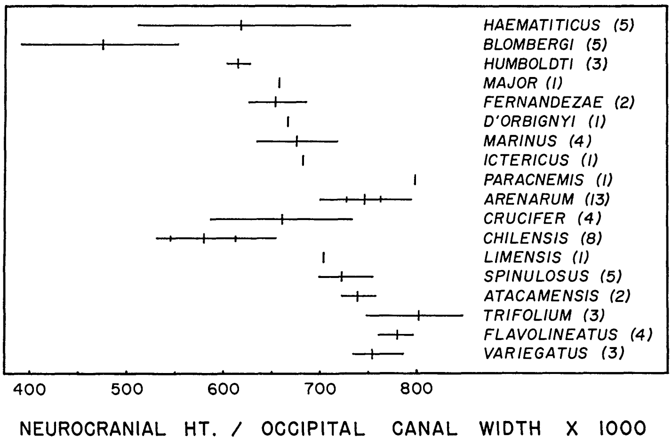

Fig. 5.—Neurocranial height/occipital canal width X 1000. The horizontal line indicates the range; the long vertical line intersecting it, the mean. For samples exceeding five, the 95% confidence intervals are indicated by short vertical lines bracketing the mean. Sample size is indicated in parentheses

the descending arm of the squamosal and also the angle this arm forms with the vertical. Samples with means between 560 and 900 were considered of average proportions.

Vertebral column length/width x 1000. Samples with means between 890 and 1010 were considered of average proportions; below 890, short; above 1010, long.

Humeral width/length x 1000. Samples with means between 183 and 209 were considered average; below 183, thin; above 209, thick.

Femoral width/length x 1000. Samples with means between 860 and 990 were considered of average proportions.

Tibiofibula width/length x 10,000. Samples with means between 670 and 800 were considered of average proportions.

Categorizations of ratios (long, average, etc.) apply only to *Bufo* described in the present study. The range, sample mean, standard deviation, standard error and 95% confidence intervals of the mean were calculated for each ratio in the species examined and were incorporated in Figures 3-6.

RESULTS

Guttatus group.—*B. haematiticus* (7). The skull is narrow (Figs. 2, 3); the frontoparietals, broad (Fig. 4). In larger specimens, supra- and postorbital crests are present. Low supratympanic crests are borne on the lateral edges of the squamosals. The dorsal surfaces of the nasals bulge slightly above those of the frontoparietals, imparting to the bones an inflated appearance. The dorsal margins of the nasals

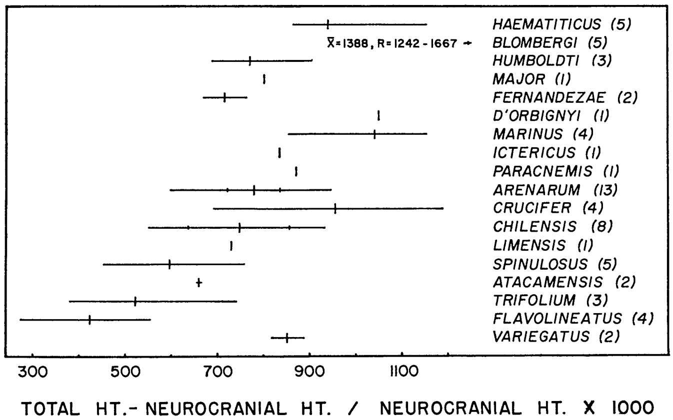

Fig. 6.—Total height — neurocranial height/neurocranial height x 1000. The horizontal line indicates the range; the long vertical line intersecting it, the mean. For samples exceeding five, the 95% confidence intervals are indicated by short vertical lines bracketing the mean. Sample size is indicated in parentheses

are rounded, contrasting sharply with the acuminate margination exemplified by the *valliceps* and *melanostictus* groups (R. F. Martin, in press). The dorsal surfaces of the frontoparietals and nasals are only lightly ornamented; the lateral edges of the squamosals are ornamented to a greater degree. Parietal crests are absent. The occipital canals are roofed. Frontoparietal-pro-otic fusion is present. The otic plate of the squamosal is extensive and trapezoidal in shape. The neurocranium is relatively platybasic (Fig. 5), but the squamosal shafts are long (Fig. 6). The quadratojugals are thin, but moderately extensive, projecting anteriorly from the angle of the jaw for approximately half the pterygoid fossae. The wings of the parasphenoid are only slightly overlapped by the medial arms of the pterygoids. The medial arms of the pterygoids also bear thin dorsal flanges which slightly occlude the suprapterygoid fenestrae. The vertebral centra are elongate. The transverse processes of vertebrae 5, 6, 7 and 8 are long and bear prominent horizontal flanges; the neural spines of all vertebrae are flattened into horizontal plates. The limb bones are long and slender. Tihen (1962a) has erected a monotypic group for this species. Unquestionably, it possesses several peculiar specializations; however, some of the features described by Tihen are not characteristic of my specimens. Only one of my specimens displays the extremely narrow maxillary ellipse shown by Tihen. The largest of my specimens does not display the poorly ossified sphenethmoid characteristic of

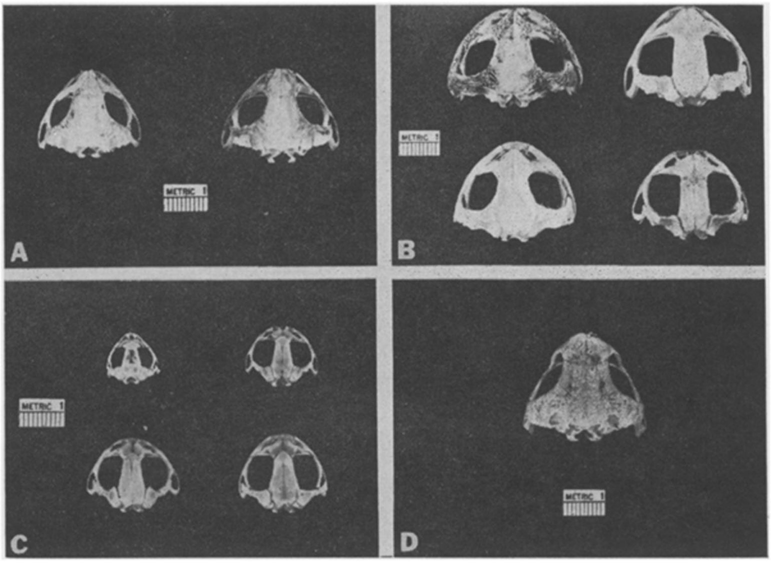

Fig. 7.—Crania of *Bufo*. (A) *B. crucifer, B. arenarum*. (B) top: *B. chilensis*, Til Til, Chile; *B. limensis;* bottom: *B. chilensis*, Zapallar, Chile; *B. spinulosus*. (C) top: *B. variegatus, B. flavolineatus;* bottom: *B. trifolium, B. atacamensis*. (D) *B. asper*

Tihen's specimens and my smaller individuals. Tihen also describes *B. haematiticus* as possessing unfused frontoparietal-pro-otic contact. In my specimens, this character varies with size, from absence of fusion in small specimens, to complete fusion in large individuals. Thus, as in other "fused" species, the condition varies ontogenetically, but differs from most in that the state of fusion appears to be reached later than usual in life of the individual.

B. blombergi (6). The skull is broad and short (Figs. 2, 3). The frontoparietals are broad (Fig. 4), their lateral edges roofing a considerable portion of the orbit, but not produced into definite crests. The postorbital shelves are subrectangular, their anterior edges forming obtuse angles with the lateral edges of the frontoparietals. The dorsal surface of the skull is moderately sculptured. Parietal crests are prominent but low. The occipital canals are roofed. Dorsal corners of the nasals are rounded. Although my specimens are adult, fusion of the frontoparietal and pro-otic is complete in only one, incomplete in three, and absent in one specimen. The size range of *B. blombergi* (Myers and Funkhouser, 1951) exceeds that of my sample and, since Tihen (1962a) describes the species as fused, it appears that, as in *B. haematiticus,* fusion occurs late in ontogeny. The neurocranium is very depressed (Fig. 5) and the descending arms of the squamosals, very long (Fig. 6). The quadratojugals are of moderate proportions, extending forward for slightly more than half the length of the pterygoid fossae. Prominent flanges borne upon the medial arms of the pterygoids markedly occlude the suprapterygoid fenestrae in three of the five specimens examined. The medial arms of the pterygoids broadly overlap the wings of the parasphenoid. The sphenethmoid bone is well ossified and extensive, projecting anteriorly beyond the medial arms of the palatines nearly as far as posteriorly. The foramen magnum is much broader than tall, its height-width ratio averaging 0.56. The vertebral centra are very long, as are the transverse processes. The neural spines of the vertebrae are flattened and roughened, but not to such an extent as in *B. haematiticus.* The limbs are of average proportions.

Granulosus group.—B. humboldti? (4), *B. major?* (2), *B. fernandezae?* (2), *B. d'orbignyi?* (1). Skull proportions of group members range from average to narrow (Figs. 2, 3). The frontoparietals are of broad or moderate width, their lateral edges produced into prominent supraorbital crests which continue anteriorly on to the nasals and bifurcate to form less pronounced antorbital and canthal crests. The supraorbital crests join conspicuous postorbital crests in smooth arcs. Supratympanic crests of variable development are present. Parietal crests are prominent in *B. major, B. fernandezae* and *B. d'orbignyi,* but vary from present to nearly absent in *B. humboldti.* The occipital canals are completely enclosed. Dorsal and lateral dermal elements are heavily ornamented and dermal ossification obscures many of the sutures. The nasals and ascending processes of the premaxillae are intimately united by dermal ossification and project forward beyond the line of the jaw in a pronounced snout. The postorbital shelf is extensive and rectangular or trapezoidal in shape; the otic plate of the squamosal is large. The frontoparietals and prootics are fused. The lateral and ascending arms of the squamosal are united into a single bar which joins the maxilla, and encloses the orbit. The braincase is moderately platybasic (Fig. 5). The squamosal shafts are of average length in *B. fernandezae, B. major* and *B. humboldti,* long in *B. d'orbignyi* (Fig. 6). The suprapterygoid fenestrae are occluded and the wings of the parasphenoid are overlapped anteroventrally for at least half their length by the medial arms of the pterygoids. The quadratojugal-maxillary suture is obscured by dermal ornamentation. The articulation of the jaw is anterior to the jugular foramen. The vertebral centra of *B. major, B. humboldti* and *B. fernandezae* are short and broad; those of *B. d'orbignyi,* long. The limbs of *B. fernandezae* and *B. d'orbignyi* are very short and broad; those of *B. humboldti* and *B. major* are of normal proportions.

Marinus group.—*B. marinus* (6), *B. poeppigi* (1; not figured), *B. paracnemis* (2), *B. ictericus* (1), *B. arenarum* (13), *B. crucifer* (5). The skull is short and broad except in *B. crucifer* (Figs. 2, 3, 7). The frontoparietals are broad (Fig. 4) and bear pronounced supraorbital crests which join posteriorly in an arc with the anteriorly projecting postorbital crests. The nasal bones contribute extensively to the supraorbital crests, which are met anteriorly by antorbital and canthal cristation. In *B. poeppigi,* the canthal crests are reduced. Laterally, the postorbital crests join with tympanic and supratympanic crests. The frontoparietal-nasal suture is nearly transverse. In *B. ictericus,* the anterior edges of the premaxillae extend beyond the anterior ends of the nasals, but in other members of this group, these bones terminate in approximately the same transverse plane. Nasals, frontoparietals and squamosals are generally heavily striated and granulated. Distinct parietal crests are absent, but the area they usually occupy is elevated by parallel ridges of bone. The postorbital shelves are extensive and trapezoidal in shape; the otic plates of the squamosals, large. Frontoparietal-pro-otic fusion is present. The occipital canals are completely roofed. Braincases vary among species from moderately depressed to moderately elevated (Fig. 5). The shafts of the squamosals are of average or greater than average length (Fig. 6). The alae of the parasphenoid are overlapped by the medial arms of the pterygoids for over half their length. The suprapterygoid fenestrae are nearly completely occluded by flanges borne on the shafts of the squamosals and the medial arms of the pterygoid in all group members but *B. crucifer,* whose fenestrae are only moderately occluded. Postcranial morphology was not examined in *B. poeppigi.* The vertebral columns of *B. paracnemis* and *B. ictericus* are short and broad, those of the remaining members of average proportions. The limbs of *B. crucifer* are slender. The femora of *B. ictericus, B. marinus, B. paracnemis* and *B. arenarum* are short and thick, as are the tibiofibulae of *B. paracnemis* and *B. arenarum*. Other limb bones are of average proportions.

Spinulosus group.—B. spinulosus, B. chilensis, B. limensis, B. achalensis, B. atacamensis, B. trifolium, B. flavolineatus.

B. chilensis? (6). The skull is broad (Figs. 3, 7). The horizontal laminae of the relatively broad frontoparietals are produced upward to form supraorbital crests which meet with the anterior edges of the postorbital shelves in a smooth arc (Figs. 4, 7). Low parietal, supratympanic and antorbital crests are present. The surfaces of dorsal and lateral dermal elements are heavily ornamented. The occipital canals are completely roofed in some specimens, uncovered posteriorly in others. The nasals terminate anteriorly posterior to the anterior ends of the premaxillae. The otic plate of the squamosal is large; the postorbital shelf large and subrectangular in shape. The frontoparietals are fused with the pro-otics. The lateral arms of the squamosals are long, broad, and cancellous; the descending arms, of average length (Fig. 6). The braincase is platybasic (Fig. 5). The suprapterygoid fenestrae are not occluded. The medial arms of the pterygoids overlap the anteroventral portions of the parasphenoid alae for one third to one half their lengths. The quadratojugal extends forward for at least three fourths the length of the pterygoid fossa. Vertebral centra are of average proportions. The humeri are short and broad; other limb proportions are average.

B. limensis? (1). The skull is of average proportions (Figs. 3, 7). The lateral edges of the narrow frontoparietals join with the anterior margins of the postorbital shelves in right angles (Figs. 4, 7). Cristation is absent. The anterior edges of the nasals terminate slightly posterior to the bases of the premaxillae. The otic plate of the squamosal is well developed, and the postorbital shelf is large. Only light sculpturing of the roofing bones is present. The occipital canals are open, but are flanked laterally and medially by low ridges of bone. Frontoparietal pro-otic fusion exists. The lateral arms of the squamosals are of only moderate extent; the descending arms, of average length (Fig. 6). The braincase is of average proportions (Fig. 5). The suprapterygoid fenestrae are only slightly occluded. The medial arms of the pterygoids overlap the anteroventral portions of the parasphenoid wings for approximately one third their length. The quadratojugals are slender and extend anteriorly nearly the entire length of the pterygoid fossae. Vertebral centra are slender and the limbs are of average proportions.

B. spinulosus? (7). The skull is of average proportions (Figs. 3,7). The frontoparietals are narrow (Figs. 4,7). The irregularity of the anterior edge of the postorbital shelf tends to obscure the angular nature of the inner corner of the orbit and imparts a somewhat crescentic appearance to the entire postorbital shelf. The nasals terminate anteriorly posterior to the bases of the premaxillae and are in only reduced contact with the frontoparietals posteriorly; contact is absent in some specimens. The otic plates and lateral arms of the squamosals are reduced. No crests are present. The occipital canals are open anteriorly and either partially or totally roofed for a short distance at their posterior ends. The frontoparietals are fused with the pro-otics. The braincase is of average proportions (Fig. 5), the descending arms of the squamosals, short (Fig. 6). The suprapterygoid fenestrae are not occluded. The alate portions of the parasphenoid are overlapped anteroventrally by the medial arms of the pterygoids for less than one-third their length. The quadratojugals are moderately extensive, projecting anteriorly from one half to two thirds the length of the pterygoid fossae. The vertebral column is of average dimensions; the tibiofibulae are relatively slender; humeri and femora are of average proportions.

B. achalensis (2; not figured). The skull is of average proportions (Index = 850); the frontoparietals, narrow (Index: 1015). Crests and dermal ornamentation are lacking. The nasals contact the frontoparietals laterally, broadly exposing the underlying sphenethmoid in dorsal midline. Both postorbital shelf and otic plate of the squamosal are reduced. The frontoparietals are fused with the pro-otics. The braincase and descending arms of the squamosal are of average dimensions (Indices = 680; 643). The medial arms of the pterygoids overlap the wings of the parasphenoid for approximately one-third their length but do not occlude the suprapterygoid fenestrae. The quadratojugals are moderately extensive, projecting anteriorly for approximately three-fifths the length of the pterygoid fossae.

B. atacamensis? (2); *B. flavolineatus*? (4); *B. trifolium*? (4). None of my specimens reach the mean size reported for these species by Vellard (1959) and Cei (1962), and the following description may not, in part, accurately represent larger specimens. The skulls are of average or broader than average proportions (Figs. 3,7). The frontoparietals are narrow (Figs. 4,7). Cristation and ornamentation of roofing bones are absent. The nasals are not in sutural contact with the frontoparietals. The mid-frontoparietal suture is incompletely closed for most of its length. The postorbital shelf and otic plate of the squamosal are reduced. Although intraspecifically variable (probably ontogenetically), the terminal relationship of frontoparietal and pro-otic appears to be that of fusion. Braincases vary from average height to moderately tropibasic (Fig. 5). The descending arms of the squamosals are of average length in *B. atacamensis,* short in *B. trifolium* and *B. flavolineatus* (Fig. 6). The suprapterygoid fenestrae are slightly occluded in *B. flavolineatus,* but are open in *B. trifolium* and *B. atacamensis.* Overlap of the wings of the parasphenoid by the medial arms of the pterygoids is present to only limited extent or entirely absent. The vertebral centra are short. Humeri and tibiofibulae are of average proportions except in *B. trifolium;* its tibiofibulae are moderately slender. The femora of *B. atacamensis* and *B. flavolineatus* are short and robust; those of *B. trifolium,* of average dimensions.

Variegatus group.—*B. variegatus* (4). The specimens examined are below average body size for the species (Cei, 1962) and the reduced nature of the dermal bones may be in part ontogenetic. The skull is of average proportions (Figs. 3,7). The frontoparietals are narrow (Figs. 4,7) and do not contact the nasals anteriorly. The nasals are reduced and terminate far posteriorly to the bases of the premaxillae. The frontoparietals diverge broadly anteriorly; posterior to the sphenethmoid, a conspicuous fontanelle is present. Posteriorly, midline contact of these bones is only approximated in my sample. Dorsolaterally, they do not extend beyond the occipital canal. The occipital canals are open. The otic plate of the squamosal is reduced to a narrow bar of bone applied only laterally to the pro-otic. Partial frontoparietal-pro-otic fusion is present in one of the specimens I have examined. The braincase is slightly elevated (Fig. 5) and the descending arms of the squamosal are of average length (Fig. 6). The suprapterygoid fenestrae are not occluded. The medial arms of the pterygoids abut the pro-otics, but do not contact the parasphenoid. The quadratojugal is very short and does not reach the maxilla. No columellae auris are present. The vertebral centra are narrow. Humeri and femora are of average dimensions; the tibiofibulae short. Although treated separately, *B. variegatus* is similar to the members of the *spinulosus* group possessing narrow frontoparietals and is probably closely related to them.

DISCUSSION

The most obvious osteological division, and possibly that which represents an early major evolutionary dichotomy in *Bufo,* is the separation of species possessing narrow frontoparietal bones from those whose frontoparietals are broad. Intermediate conditions exist, primarily in Central America (R. F. Martin, in press), but these are not as common as either extreme. This character reflects favorably the extensiveness of dermal bone in the roofing bones of the cranium, and correlates well with other characters (development of cristation, degree of closure of occipital canals, size of otic plate of squamosal) which are also dependent upon extensiveness of dermal bone. A general trend in the evolution of the Amphibia has been progressive reduction of dermal bone in elements of the cranium; presumably, protection lost has been selectively offset by reduction in weight and increased mobility. Theoretically, loss of dermal bone is considered progressive, and Tihen (1960, 1962a) has hypothesized that well-ossified skulls were characteristic of primitive *Bufo.* Both frontoparietal types are represented on all continents inhabited by *Bufo.* Their respective topographic distributions may reflect weight-oriented major adaptive trends. Broad frontoparietals generally occur in lowland groups; narrow, in groups inhabiting upland environments. Although some difficulties of interpretation exist in the fossil history of the genus, representatives of both frontoparietal types appear to be present by the Miocene in South America (*see* discussion of *B. edentatus;* Tihen, 1962b; in press). This, in addition to the apparently broad distribution of the genus at that time, suggests a considerable history for the genus earlier in the Tertiary. Both lines have undergone parallel reduction of bone in the dermal elements, and it is possible that dermal bone has been added secondarily at least once in the narrow line.

The distribution of *Bufo* is nearly cosmopolitan; only Australia shows no evidence of occupation. Darlington (1957) believed its origins lay in Africa. More recently, accumulating biological data have provided stimulus for reanalysis of the zoogeography of *Bufo*. Overland routes connecting South, Central and North America with Asia have been investigated and found chronologically acceptable as avenues of dispersal by Tihen (1962a), Blair (1963) and Savage (1971). Low (1967) has reviewed the problems of waif transport in application to anurans, and concluded that the hypothesis of rafting from South America to Africa is tenable. Savage (1971) has attempted to relate patterns of amphibian distribution to continental drift. Low (1967), Bogart (1967), W. F. Martin (1967) and Blair (in press) have considered in detail possible sites of origin of the genus and favor South America.

BROAD FRONTOPARIETAL LINE

Guttatus group.—These forest dwelling forms are characterized by cryptic dead leaf coloration, smooth-textured skins and, at least in *B. blombergi* and *B. haematiticus,* by enormous folded testes which appear to produce an inhibitory secretion occurring in the seminal fluid (Blair, in press). Low (1967) noted a high biochemical affinity between the parotoid secretions of *B. haematiticus* and *B. blombergi.* Although their osteology is not strikingly similar, both species possess broad, acristate frontoparietals which fuse with the pro-otics relatively late in development. Coupled with this, the pair exhibits a striking and, in the New World, unique vertebral modification.

This group seems of particular interest when intercontinental comparisons are made with other *Bufo.* Members of the African *regularis* group (*B. regularis, rangeri, garmani, brauni, latifrons*) display broad, crestless frontoparietals which are independent from the pro-otics and possess (Bogart, 1968) a chromosome number of only 20 (2N=22 for all non-African *Bufo*). They show one-way metamorphosis with some New World species but little genetic compatibility (Blair, in press) or biochemical similarity (Low, 1967) with Palearctic species. This evidence has led to the hypotheses of raft dispersal from South America and the search for a likely ancestral group there. An alternative hypothesis exists: Tertiary dispersal through Central America, North America and Eurasia to Africa followed by extinction of similar forms in the former continents. The *guttatus* group seems a possible candidate for the ancestral position. Low (1967) has found very high chromatographic affinities between the *guttatus* group and the *regularis* group and its African allies. Speculative consideration of allied species discloses other facts: *Bufo mauritanicus* of northern Africa is very similar to the *regularis* group in osteology (R. F. Martin, in press; Tihen, 1962a) but shows the greater degree of dorsal concavity of the frontoparietals characteristic of the *guttatus* group. Importantly, it possesses 22 chromosomes (Bogart, 1968) and shares with *B. blombergi* of the *guttatus* group the ability to produce two basic types of vocalizations (W. F. Martin, 1967). The large African *B. superciliaris* shows osteological similarity (broad acristate unfused frontoparietals, light dorsal bone sculpturing, closed occipital canal) and biochemical similarity (Low, 1967) to the *regularis* group. In addition, it displays the cryptic leaf coloration of the *guttatus* group and possesses large folded testes (Noble, 1923) shown elsewhere only in *Bufo haematiticus* and *B. blombergi.* Recently, the chromosome number of *superciliaris* was determined to be 2N=20 (Bogart, pers. comm.). With this information, it is possible to speculate that *B. mauritanicus* and *B. superciliaris* are intermediate forms in an evolutionary transition between a 22-chromosome Neotropical stock similar to the *guttatus* group and the African 20-chromosome *regularis* group.

A third possible hypothesis follows from Savage's (1971) interpretation of frog distributions in relation to continental separation and shift. Savage hypothesized that bufonid (and other anuran) stocks were split upon the separation of South America and Africa in the Cretaceous and that the Neotropical stock subsequently colonized North America, then Eurasia, while the African remnant radiated intracontinentally. Applying this model, the *regularis* group would represent the Old World tropical stock, possibly evolved from *mauritanicus* and *superciliaris.* Alternatively, the former species could be a relative newcomer. Unfortunately, Savage's estimate of the date of fragmentation of the Southern Continent (Cretaceous) considerably antedates the fossil record of *Bufo.*

B. asper is possibly an Asian branch of this postulated evolutionary line. It possesses broad unfused frontoparietals and appears quite similar to *B. haematiticus* in many osteological characters. Both have long narrow skulls (Figs. 3,7), closed occipital canals, projecting nasals, elongate vertical squamosal shafts, greatly flattened neural spines and long vertebral transverse processes and centra. As in the *regularis* group, the frontoparietals are not fused with the pro-otics. Since other lines of evidence are incomplete or do not support this proposed affinity, osteological similarity may only indicate convergence rather than phyletic proximity.

Granulosus group.—The frontoparietals vary from broad to medium in the South American *granulosus* group. The frontoparietals are fused to the pro-otics and the pterygoid flanges are extensive. The extreme degree of dermal ossification, particularly at the snout and squamosal, is possibly not primitive but secondarily evolved. Panamanian specimens display very reduced parietal crests; in others the crests are conspicuous. Specimens of *major* and *fernandezae,* collected sympatrically in Resistancia, Argentina, display great disparity in limb proportions, and Cei and Erspamer (1966) demonstrated that these populations also show considerable differentiation in the concentration of 6-indolealkylamine in their integument. Although this differentiation is present, all forms share the unique "closed orbit" and heavy ornamentation. Previously, Gallardo (1965), in his morphological study, treated these forms as subspecies. J. M. Cei (unpubl. data) has stressed that *major* and *fernandezae* maintain their identity in sympatry, and W. F. Blair (pers. comm.) regards the complex as a superspecies. Although samples are small, considerable osteological differentiation is present between populations. Obviously, considering the information above, *fernandezae* and *major* represent species; possibly *humboldti* and *d'orbignyi* do as well. Tihen (1962a) has placed *B. granulosus* in the Caribbean section of his *valliceps* group. Reciprocal metamorphosis occurs with *B. arenarum* of the *marinus* group (Blair, in press); osteological data also indicate proximity with this group.

Marinus group.—The broad frontoparietals of the *marinus* group possess cristation patterns similar to the *granulosus* group; as in the latter, heavy ornamentation is present and pterygoid and squamosal are well developed. A closely allied fossil form exists from the Miocene of Colombia (Estes and Wassersug, 1963). Members of the Mexican and Central American *valliceps* group (Porter, 1964; R. F. Martin, in press) are also similar in cristation pattern to the *marinus* group, but the thickness of dermal ornamentation is generally more reduced and flanges of the pterygoid and squamosal are also less extensively developed. Crosses between members of this group and *B. arenarum* of the *marinus* group have yielded high reciprocal metamorphosis (Blair, 1966; in press). Considering Tihen's hypothesis (1960, 1962a) that primitive *Bufo* possessed densely ossified skulls, the probable origin of *Bufo* in South America, and the relative distribution of *marinus* and *valliceps* groups, it appears likely that the latter are more osteologically advanced members of a common stock. Blair (in press) does not consider *B. crucifer* a member of his *marinus* group; it shows only low, if any genetic compatibility with that group or any other with which it has been tested. Tihen (1962a) has lumped *B. arenarum, B. crucifer, B. marinus, B. ictericus* and *B. paracnemis* with *B. blombergi* and *B. chilensis.* His view of assemblages is broader than that employed in this research, which indicates that the latter two species should be placed elsewhere.

NARROW FRONTOPARIETAL LINE

Spinulosus group.—Considerable disparity exists between *B. chilensis* and other members of this Andean group in extensiveness of dermal ossification (Fig. 7). Tihen (1962a), in fact, included *B. chilensis* in the South American section of his *valliceps* group and *B. spinulosus* and *B. trifolium* in his *spinulosus* group; at that time, considering only available osteological evidence and no other Andean forms, this was quite justified. Actually, a continuum in dermal bone extensiveness, ranging from *B. flavolineatus, trifolium* and *atacamensis,* through *B. achalensis, spinulosus* and *limensis,* to *chilensis* exists. Interestingly, Blair (in press) has recorded control-level metamorphosis in reciprocal artificial hybridizations between the osteologically disparate *B. spinulosus* and *B. chilensis.* Vellard (1959) and Cei (1962) discussed the ecology and morphology of members of this group and treated most members as subspecies of *B. spinulosus.* Geographical differences in skin amines of several members of this group were noted by Cei and Erspamer (1966). Guttman (1967) described differences in transferrins characteristic of populations in Peru, Chile and Argentina. Cei (pers. comm.) and Blair (in press) presently regard the group as a superspecies; considering the degree of osteological differences, this is also the view of the author. Several major interpretations of above data may be considered; none preclude the possibility that several species groups are actually present. First: branches from both hypothetical (broad and narrow) major lines may be represented. Second, more conservatively, the group may be an offshoot from the broad line along which progressive reduction in dermal elements has occurred. The third, and presently followed alternative, places the group in the narrow line with secondary elaboration of dermal bone in *B. chilensis.* Metamorphosis occurs in reciprocal artificial hybridizations between the *spinulosus* group and other groups possessing both broad (*valliceps, marinus* groups) and intermediate (*marmoreus* group) width frontoparietals.

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