

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N. Y. 10024

NUMBER 2354

DECEMBER 18, 1968

A New Genus and Species of Dwarf Boa from Southern Mexico

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The boas of the Western Hemisphere have been assigned to 11 genera, only four of which have distributions extending into Mexico. Members of three of the genera in Mexico, *Loxocemus*, *Lichanura*, and *Boa*, appear to be largely restricted to the lowlands, although *Boa* occurs at elevations approaching 1000 meters in some areas. The fourth genus, *Ungaliophis*, is the only boa hitherto known from Mexico that occurs at elevations above 2000 meters, as shown by Conant's (1966) report of *U. continentalis* in a pine-forested area near Teopisca, Chiapas. The only other record of the species in Mexico, however, is near Tapachula, in the lowlands of the same state (Werner, 1921). In view of the meager representation of the family Boidae in Mexico, and the absence of records for members of the family in montane habitats west of the Isthmus of Tehuantepec, the discovery of a well-differentiated dwarf boa in the cloud forests in the northern portion of the state of Oaxaca was scarcely anticipated.

Relatively few reptiles occur in the cool, moist environments that prevail at elevations between 2000 and 3000 meters on the northern slopes of the Sierra de Juárez. Representatives of the ophidian genera *Thamnophis* and *Rhadinaea* occur in the area, and lizards of the genera *Sceloporus* and *Barisia* are occasionally encountered. Few of the reptiles in the cloud forests of Oaxaca, however, are restricted to such environments. Some of the species are more abundant in montane habitats

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less frequently shrouded by clouds, often at higher elevations. Others have evidently extended their distributions upward into the cloud forests from the moist lowlands of Veracruz, but few of the lowland species are known to have penetrated the mountains above the 2000-meter contour. Whether the boa found on the headwaters of the Río Valle Nacional is restricted to the cloud forests of the area remains to be ascertained. It is noteworthy, nevertheless, that the only specimens of the colubrid genus *Cryophis* Bogert and Duellman (1963) thus far reported were obtained at somewhat lower elevations in the cloud forests of the same region. One specimen of *Cryophis* was obtained scarcely 10 kilometers to the east, and the other within 50 kilometers to the southeast of the site where the boa was found. It seems probable that members of both genera will prove to be endemic.

The affinities of the boa from Oaxaca are not readily apparent, perhaps because of the adaptive modifications that have occurred since the species gained access to the cloud forest it now occupies. The nearest living relatives appear to be the dwarf boas of Central America, South America, and the West Indies, but affinities with these boas are not particularly close (Bogert, 1968). Superficially the cloud-forest species bears more resemblance to some species of *Tropidophis* in the West Indies than it does to *Ungaliophis* in Chiapas, which may merely reflect the greater diversification of the West Indian dwarf boas, for relationships with either genus are tenuous at best.

More detailed studies of the diminutive boa from Oaxaca can undoubtedly be made when members of both sexes are available. The only example of the species obtained in 1967 is a female, which may not be sexually mature. Sufficient evidence has, nevertheless, been obtained from this specimen for the species it represents, as well as the new genus to which the species is assigned, to be diagnosed and defined. In allusion to the isolated occurrence of the holotype, the generic name selected is from the Latin *exilis* (from *exigere*, to banish) and *boa*, also from the Latin, and sometimes translated as "a kind of water serpent."

EXILIBOA, NEW GENUS

TYPE SPECIES: *Exiliboa placata*, new species (described below).

DIAGNOSIS OF THE GENUS: A small, nearly unicolored, prehensile-tailed boa, characterized by its possession of a large azygous internasal in broad contact with the rostral, and flanked on each side by a single nasal. This peculiar configuration of the scales readily distinguishes *Exiliboa* from *Ungaliophis* and from *Tropidophis*, all members of which have paired internasals and divided nasal plates (fig. 1). *Exiliboa* retains

a pair of prefrontals in contrast to the azygous prefrontal of *Ungaliophis*, and the two pairs of prefrontals normally present on *Tropidophis*. The loreal is retained by *Exiliboa*, whereas it is absent from, or fused with the anterior prefrontal of, *Tropidophis*. The mental groove of *Exiliboa* is bordered by only three pairs of shields, but the groove is bordered by four scales in *Ungaliophis* and by four or five in *Tropidophis*. Furthermore, the female of *Exiliboa* differs from that of other dwarf boas in its retention of external vestiges of limbs.

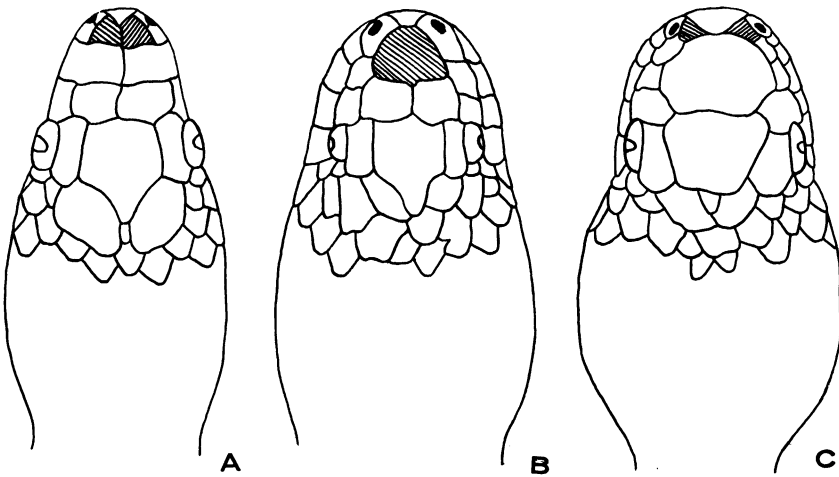


FIG. 1. Dorsal views of the heads. A. *Tropidophis semicinctus*. B. *Exiliboa placata*. C. *Ungaliophis continentalis*. Figures illustrate distinctive modifications in the cephalic plates of the three genera. Plates shaded in each are the internasals.

Trachyboa, an inhabitant of lowland forests in northern South America and Panama, is more distantly related, although it resembles *Exiliboa* in having the nostril in an undivided nasal, and it possesses comparable numbers of ventrals and subcaudals. Most of the cephalic plates have been replaced by scales on *Trachyboa*, which differs further in having from 29 to 31 rows of scales at midbody, in contrast to 21 on *Exiliboa*. Moreover, well-developed hypapophyses are present on all vertebrae of *Trachyboa*, but lacking on the precaudal vertebrae of *Exiliboa*. *Trachyboa* is an extremely rugose snake, adaptively specialized to forage on the surface (Bogert, 1968), unlike the comparatively slender, smooth-scaled dwarf boa from Oaxaca, which is evidently semifossorial.

DEFINITION OF THE GENUS: *Exiliboa* is a relatively small member of the family Boidae, with over-all dimensions that may not greatly exceed

50 cm. The trunk is less strongly compressed toward the constriction behind the head. The more strongly compressed prehensile tail, which comprises slightly more than 10 per cent of the total length, terminates in a blunt spine. Spurs, present on the female (fig. 2), are presumably more strongly developed on males. The large rostral is in broad contact posteriorly with a large undivided internasal, and on each side the rostral is followed by an undivided nasal containing the nostril. There is a

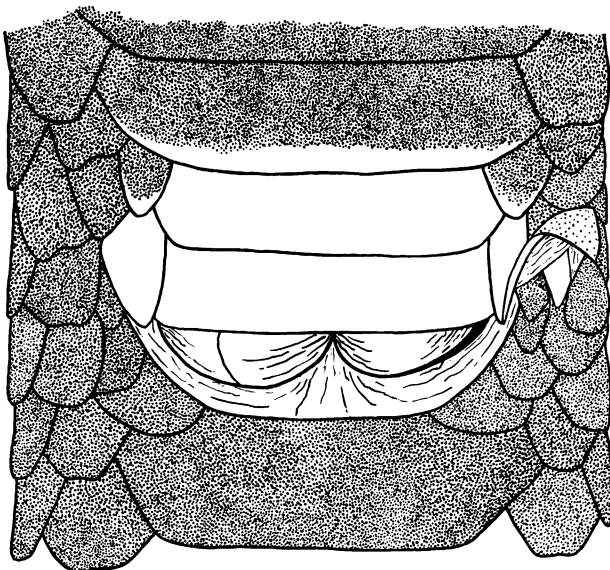


FIG. 2. Ventral view of the anal region of the female holotype of *Exiliboa placata*, A.M.N.H. No. 100000, on which the scale to the left (to the right as viewed from below) of the anal plate is lifted to expose the small, white vestige of the spur. The spur on the right remains hidden beneath the third scale to the right of the anal plate. The scales in the anal region lack black pigment, as shown in the illustration.

pair of prefrontals, and the frontal is flanked by the supraoculars and the scalelike vestiges of the parietals. In addition to the single nasal on each side of the head, there are a loreal, a preocular, two postoculars, and seven supralabials, two of which enter the orbit. On the under side of the head the first supralabials meet on a broad suture separating the large mental from a pair of small chin-shields. The mental groove is bordered by the first supralabials and two pairs of chin-shields. The dorsal scales are smooth, in 19 rows anteriorly, but increasing to 21 at midbody and diminishing to 15 at the vent. The anal plate and sub-

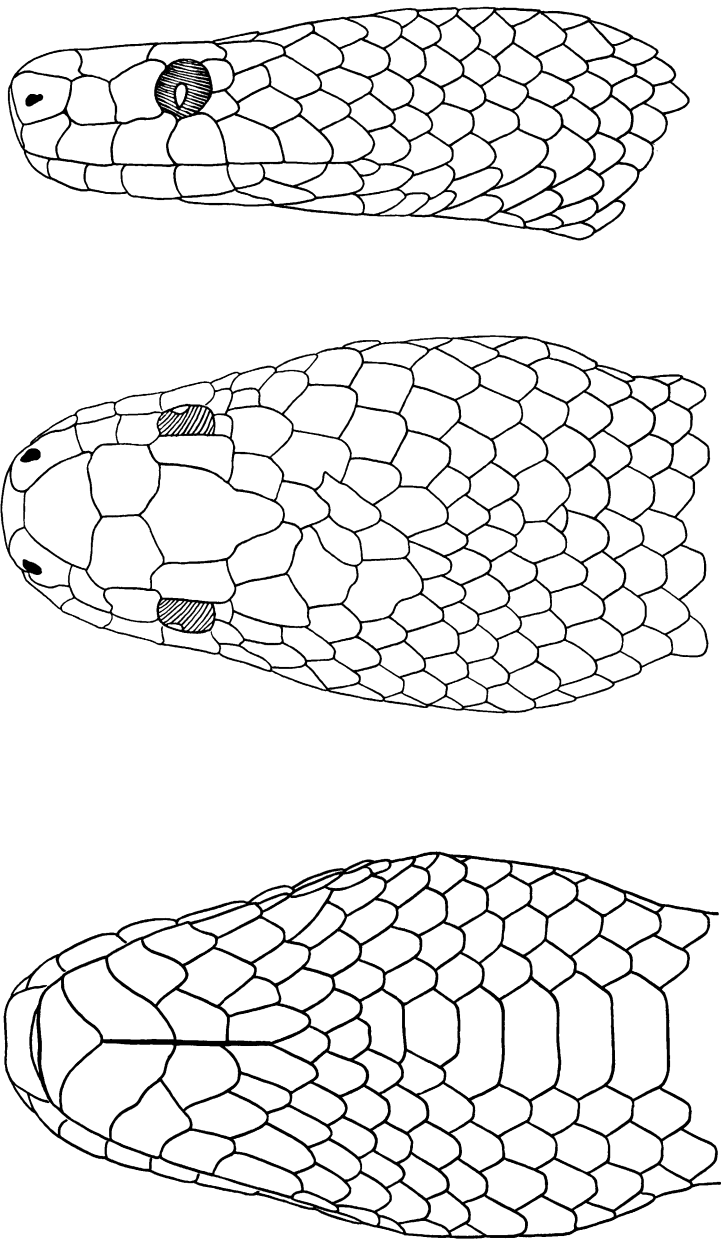


FIG. 3. Lateral, dorsal, and ventral views of the holotype of *Exiliboa placata*, A.M.N.H. No. 100000.

caudals are undivided. The iris is black, and the vertical pupil is semi-elliptic, as shown in figure 3. The tongue is black and relatively short.

From 17 to 19 teeth are present on the maxilla, 19 on the dentary; the teeth are relatively long and slender anteriorly, but progressively smaller toward the rear. Hypapophyses are restricted to a few vertebrae at the anterior end of the trunk. The tracheal lung is followed by the right lung, without any demarcation between them. There is no vestige of the left lung. The kidneys are lobulated, and situated well toward the rear of the body cavity.

DESCRIPTION OF THE TYPE SPECIES

When discovered, the dwarf boa described below was apparently active and probably foraging beneath the large rock that sheltered it. The snake made no effort to escape when it was suddenly exposed, and, when seized, it drew its trunk into a compact coil as though it were attempting to hide its head. The name selected for the species is an adjective derived from the Latin verb *placare*, to calm.

Exiliboa placata, new species

HOLOTYPE: A.M.N.H. No. 100000, a female, obtained near latitude 17° 37' N. and longitude 96° 25' W., at an elevation of approximately 2300 meters on the headwaters of the Río Valle Nacional on the northern slopes of the Sierra de Juárez, in the state of Oaxaca, Mexico. There are few human habitations in this portion of the Sierra Madre del Sur. The village most readily found on maps, Valle Nacional, lies in the foothills approximately 25 kilometers northeast of the type locality. The holotype was discovered in a clearing in the cloud forest by J. Stuart Rowley and C. M. Bogert on the afternoon of August 10, 1967.

DIAGNOSIS: As noted in the discussion of generic characters, the boas of the genera *Ungaliophis* and *Tropidophis* appear to be the nearest living relatives of the dwarf boa discovered in Oaxaca. The peculiarities of *Exiliboa* that serve to distinguish it from these other genera, therefore, are also diagnostic of *E. placata*. The species differs from all other boas in Mexico in having the scales arranged in 21 rows at midbody, and in having a large azygous internasal that extends across the snout to an undivided nasal and the anterior portion of the loreal on each side. The number of midbody scale rows varies from 19 to 25 in *Ungaliophis*, but Mexican representatives of the genus have 25; many more scale rows are present on *Loxocemus*, *Lichanura*, and *Boa*, the only other genera of the family Boidae known to occur in Mexico.

DESCRIPTION OF THE HOLOTYPE: A female, possibly immature, with an over-all length of 412 mm., and a tail 45 mm. in length that comprises 10.9 per cent of the total length. The head is 14.5 mm. in length and 8.0 mm. in width, and the diameter of the trunk behind the head is 5.0 mm. The trunk is increasingly more compressed toward the base of the tail, where it is appreciably higher than wide. The short, laterally flattened tail tapers rapidly to a blunt scale at the end. The dorsal scales, all smooth, are disposed in 21 rows immediately behind the head, in 19 rows on the anterior portion of the trunk, increase in number to 21 at midbody, and diminish to 15 at the base of the tail. In the following dorsal scale formula the figures in parentheses are the lateral rows indicated by number, and the paravertebral rows by P, followed by the ventral count where the change occurs:

$$21 \frac{(-4) 7}{(-4) 6} \quad 19 \frac{(+5) 49}{(+5) 49} \quad 21 \frac{(-5) 87}{(-5) 90} \quad 19 \frac{(-4) 144}{(-4+P) 142} \quad 16 \frac{(-P) 149}{15} = 166$$

There are 166 ventrals, followed by an undivided anal and 24 undivided subcaudals, not counting the blunt scale on the end of the tail.

The rostral is appreciably wider than high (2.9 mm. in width, 1.7 mm. in height) and visible from above, where the median portion of it reaches a broad, undivided internasal, the largest scale on the head. Behind the internasal there are two large prefrontals in broad contact with the frontal, and the anterior end of the supraocular. The frontal, with a blunt apex behind the suture of the paired prefrontals, is flanked laterally by supraoculars, followed by vestiges of the parietals. The scalelike parietals extend to a median scale behind the tapered end of the frontal (fig. 3).

On each side of the head the rostral is in broad contact with the first supralabial and the nasal on each side. The nostril is near the middle of an undivided nasal situated above the first supralabial and bordered posteriorly by the loreal, which lies below the suture between the internasal and the prefrontal. The preocular is approximately the size and shape of the rectangular loreal in front of it, but slightly smaller than the nasal. The distance between the eye and the border of the mouth is less than the diameter of the eye. The pupil is vertical and semi-elliptical, rounded above but pointed below. Two postoculars are followed by two scales between the supralabials and the vestiges of the parietal. There are seven supralabials, the first and second of which reach the loreal on the left, but on the right, a small portion of the third supralabial reaches the loreal. The third and fourth supralabials reach the eye; the third supralabial is largest.

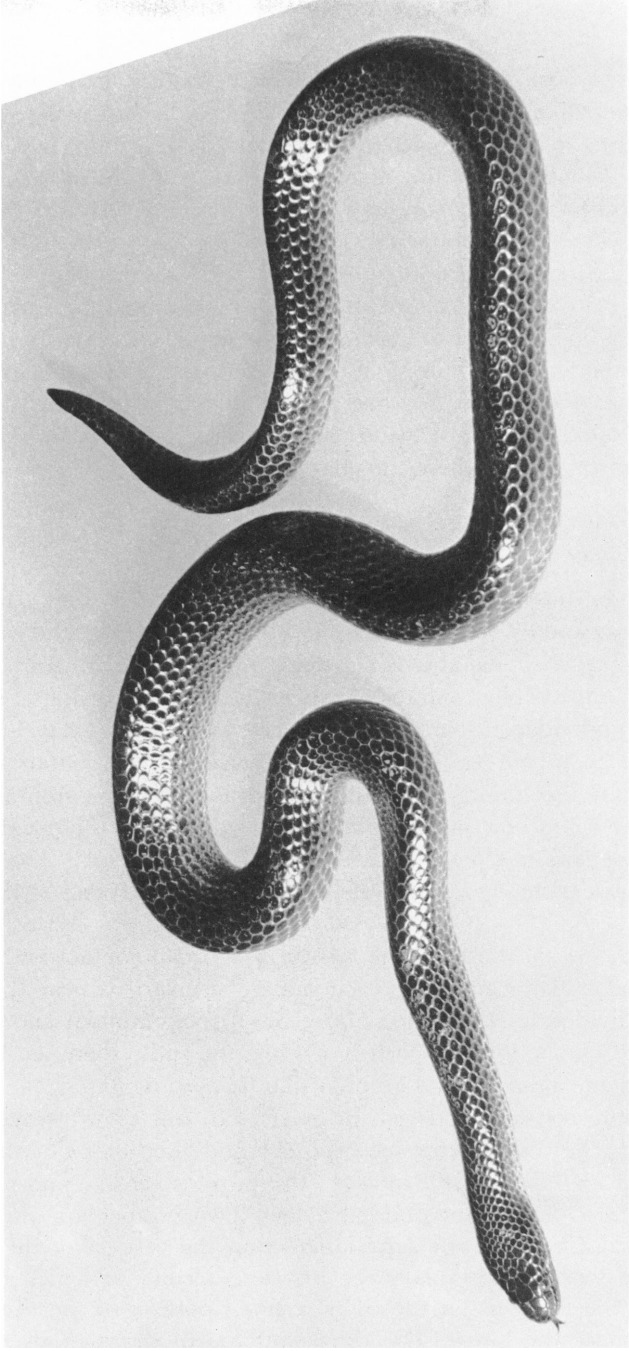


FIG. 4. Dorsolateral view of *Exiliboa placata*, the holotype, in life. Note faint light stripe extending along the posterior margin of the upper lip.



FIG. 5. Holotype of *Exiliboa placata*. A. Coiled with the under side of the tail exposed to show the position of the white spot on the anal region. B. Dorso-lateral view of the head of the same individual, enlarged to show the arrangement of the plates.

The lower margin of the mouth is bordered by seven infralabials on each side. The anteriormost infralabials, which are much larger than the others, meet on a broad suture behind the blunt apex of a large mental, thus separating it from a pair of short chin-shields. These are followed by a second pair of much more slender chin-shields, which meet on the mental groove; these are longer but indistinguishable in other respects from the first of four gular scales that separate the mental groove from the first ventral. The scales in contact with the outer edges of the second pair of chin-shields are in the same row as those bordering the ventral scales posteriorly. Small pustules, present on all cephalic plates, are more numerous on the sides of the head, particularly on the lips.

The dorsum is almost uniformly black, although the scales on the trunk are more heavily pigmented near the middle than at their margins. The gular scales are margined with gray, which is to some extent true of the ventrals. The only conspicuous marking, however, is an immaculate white area that covers the anal scute, the contiguous scales, as well as the margin of the penultimate ventral. Faint traces of a narrow light stripe extend through the upper portions of the supralabials from the angle of the mouth (figs. 4 and 5).

INTERNAL CHARACTERS: An exhaustive study of the internal anatomy of *Exiliboa* must await the acquisition of additional specimens. The skull of the holotype was not removed, but the viscera were examined *in situ*, and three vertebrae were removed. Information concerning several osteological characters was obtained from roentgenograms of the holotype prepared by Mr. Robert E. Logan. The teeth, including those on the pterygoid, were readily counted with the skull *in situ*, after the investing tissue and replacement teeth had been removed.

The counts that follow include vacant sockets as well as teeth, and those on the right are listed first: maxilla, 16-19; palatine, 5-7; pterygoid, 11-10; dentary, 19-19. All teeth are moderately stout, recurved, and unspecialized. The maxillary teeth are subequal anteriorly but progressively smaller toward the posterior extremity of the bone. The left maxilla probably contains the normal complement of teeth; the third tooth on the right maxilla is appreciably stouter than the others, as though two teeth might have fused in one socket. The presence of fewer teeth on this maxilla is probably to be construed as an abnormality. The teeth on the dentary, palatines, and pterygoids are nearly the same size and shape as those on the maxilla, and those on the dentary diminish in size posteriorly in much the same fashion as those on the maxilla.

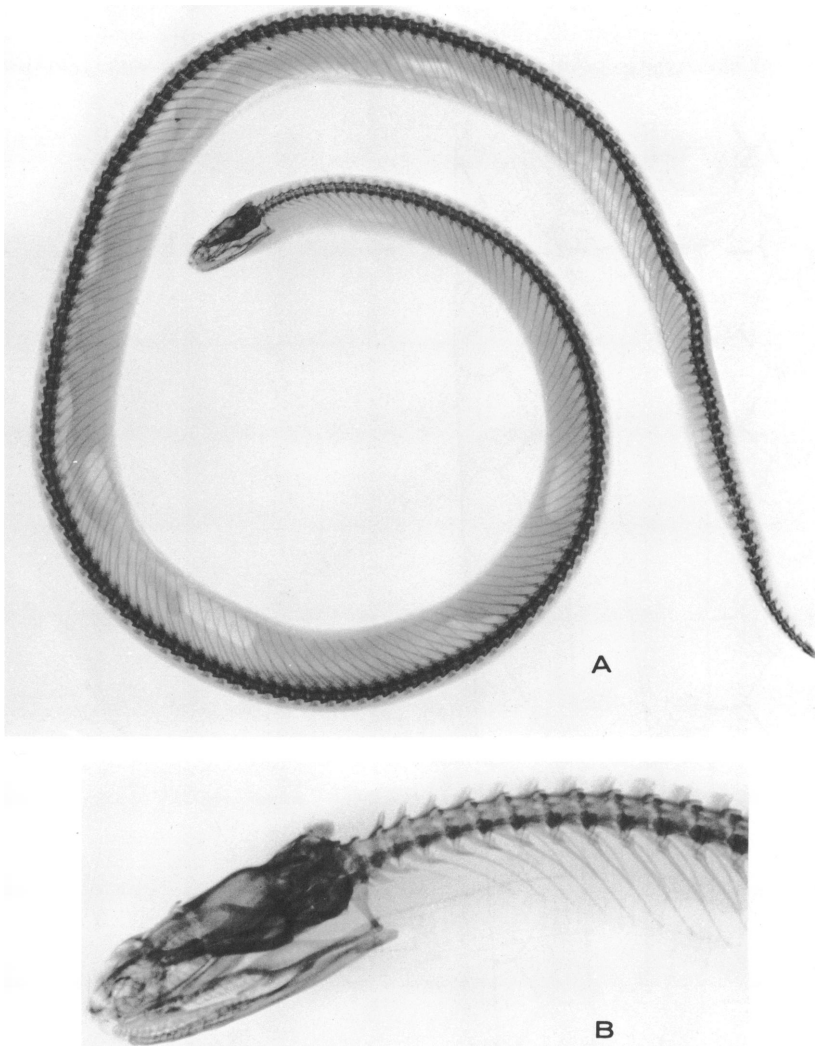


FIG. 6. A. Radiograph of the holotype of *Exiliboa placata*, showing osteological characters. B. Head of holotype, enlarged. Note the posterior portion of the hypobranchium terminating near the fifth rib.

The anterior portion of the hypobranchium is obscured by the mandibles in roentgenograms (fig. 6), but it is apparent that the hypohyal arms are convergent below the level of the pro-otic, but they may or

may not meet slightly farther forward. Each hypohyal element terminates near the end of the fifth rib. The neural spine on the first vertebra behind the axis is pointed, but the spines become progressively longer

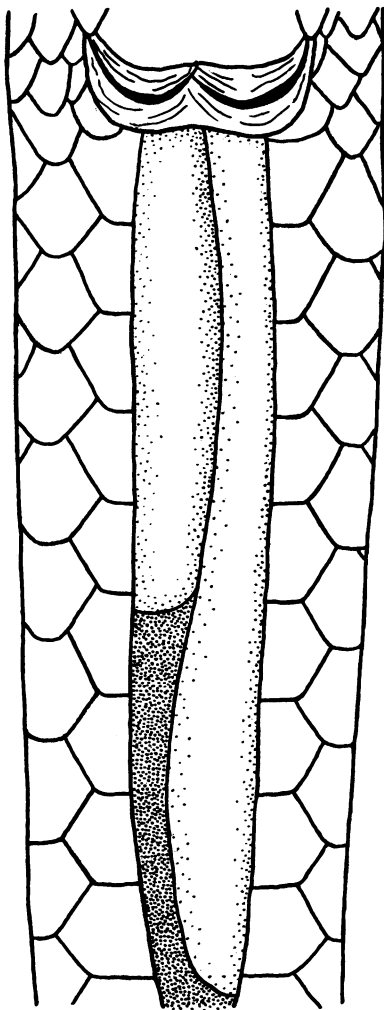


FIG. 7. Ventral view of the tail of *Exiliboa placata*, showing the staggered arrangement of the anal glands.

on successive vertebrae behind it, and there is an overhang at the rear of the crest of the spine on the vertebrae posterior to the seventh. The hypapophysis on the axis is longer and less strongly recurved than the hypapophyses on the vertebrae behind it. The pointed hypapophyses on the vertebrae behind the head are progressively smaller posteriorly,

where the transition from hypapophyses to haemal keels occurs somewhere beyond the twentieth vertebra. There are 166 vertebrae bearing ribs, in addition to three above the anal plate, and 28 in the tail, the last four or five of which are partially fused. The vertebra depicted in figure 8 is the 122nd.

As may be seen in figure 8, there are no hypapophyses on the pre-caudal vertebrae of *Exiliboa*, although a low haemal keel is present on each vertebra between the well-defined subcentral ridges of the tapering centrum. The neural arch is flattened, with emarginations between the prezygapophyses and parazygapophyses. The crest of the moderately high neural spine extends three-fourths of the length of the neural arch, slightly overhanging the posterior margin. The zygosphenes are convex and slightly wider than the cotyles. The neural canal is relatively large, nearly as high as it is wide, with a distinct subneural process. The prezygapophyses extend posteriorly almost to the base of the zygosphenes. The zygantrum is wide and low, the cotyle slightly oval. The paradiapophyses are auriculiform, and the condyle is slightly oblique, with a distinct neck.

The transition from the tracheal lung to the right lung occurs near the heart, which is approximately 11 to 12 cm. behind the head. No vestige of the left lung was detected. The liver barely overlaps the tip of the heart. The lobulated kidneys are situated relatively close to the vent; the one on the right extends from the 127th ventral to the 134th and that on the left from the 134th ventral to the 142nd. (When measured from the tip of the snout the anterior end of the right kidney is 231 mm. from the snout; that of the left, 235 mm.) The right kidney is slightly shorter than the left, which has a length of 5.5 mm. The arrangement of the anal (scent) glands is the reverse, the right gland being situated posterior to the left. Each of the two ducts leading from the anal opening increases in diameter before it merges with the gland. Consequently precise measurements of the glands cannot be obtained, but the left gland extends from approximately the first subcaudal to the fifth, whereas the gland on the right extends from the third subcaudal to the ninth (fig. 7).

HABITAT AND HABITS

As noted in the Introduction, the holotype of *Exiliboa placata* was discovered in a clearing in the cloud forest that flanks the northern escarpment of the Sierra de Juárez. The "clearing" is essentially a shelf, where earth and rocks have been excavated from the steep slope of the mountain. The terrain on the shelf had been leveled at least 10 years

earlier. The type locality is roughly 700 meters below the higher portions of the crest of the escarpment, which rises to elevations slightly exceeding 3000 meters. On the summits of the highest peaks and ridges the forest is largely *Pinus hartwegi*, but on the steep slopes below the summits there are a few firs, *Abies religiosa*, and pines of several species, including *Pinus ayacahuite*. Much of the forest around the summits is pine-oak woodland, but at lower elevations, beginning at approximately the 2500-meter contour, such trees as *Liquidambar styraciflua* are encountered. Below this level oaks become progressively less abundant, and the forest near the type locality of the boa is comprised largely of other hardwoods. Tree ferns occur sporadically, but they are more abundant near the 2000-meter contour.

The hardwood forest in the area bordering the clearing where the boa was found supports a vast number of epiphytes, and there is a dense understory of smaller trees, shrubs, vines, and herbs. Rocks and logs had been left in the clearing, where a few shrubs were growing, but most of the terrain was hidden beneath a dense ground cover. Moisture-laden currents sweeping in from the Gulf across the wet lowlands are forced upward as they reach the escarpment. As a result the area is shrouded in clouds throughout much of the summer. Rivulets of water flowed across the clearing, and the soil was wet beneath the rock where the boa was found.

When the rock was overturned the snake was motionless, but it evidently had been crawling through a passageway in the rocky soil. Presumably it had been seeking its prey, which may consist largely of small frogs. Several individuals of *Eleutherodactylus mexicanus* were obtained in the same area. Both adult frogs and juveniles were abroad, but many more were hidden under rocks or logs. Another frog, *Eleutherodactylus decoratus*, was less frequently encountered on the afternoon of August 10 when the boa was found. Several days later, on August 27, when the area was searched intensively in an effort to find another boa, *E. decoratus* proved to be somewhat more abundant. Adults, juveniles, and eggs of the species were found under rocks in the area. Under captive conditions the boa devoured juveniles of both species of *Eleutherodactylus*, although the snake would not eat when exposed to light. It could be induced to feed during the day, but only when light was excluded from the container in which it was kept. It was also active at night, but it is uncertain whether it forages during the hours of darkness in its native habitat.

Although the boa seems to have been foraging during the day, it is questionable whether members of the species often venture to the sur-

face. As noted in the description, the pupil of *Exiliboa* differs from that of the larger boas in having the upper edge rounded rather than pointed. Even when the eye was exposed to bright light while the head was being examined under a binocular microscope, the aperture of the iris retained the shape of an inverted pear, and the shape changed little even when the pupil expanded in dim light.

The floor of the cage that housed the snake in the laboratory was covered with sphagnum moss. During the day the snake invariably remained hidden beneath the moss, but when placed on the surface it crawled slowly, directing its head downward whenever it encountered any depression. Although branches were added to its cage, the boa never displayed the slightest tendency to climb. When placed on a shrub or branch the snake invariably descended, even though it experienced no difficulty in moving, and might easily have directed its movements upward. On the ground it most often employed lateral, undulatory movements, but, like other boas, it could shift to rectilinear locomotion.

The boa ignored small treefrogs, *Hyla andersoni*, and newborn mice when these were offered to it in the laboratory. In its native habitat the boa may depend heavily on hatchling *Eleutherodactylus*, but it seems improbable that its diet is restricted to frogs of the genus. At least one tree frog, *Hyla chaneque*, inhabits the area around the type locality of the boa, which is large enough to prey on juveniles of the species. Salamanders, although not encountered at the elevation where the boa was found, are likely to occur within its range, and they, too, are probably part of its normal diet.

The only other snake found in the immediate vicinity of the type locality belongs to the *Rhadinaea decorata* group. Another member of the genus, *R. fulvivitta* (or *vittata* to persons who suppress secondary homonyms), occurs at higher elevations at the headwaters of the Río Papaloápan, but it seems to be replaced by the other species at lower elevations in the cloud forest. A small anguid lizard, *Barisia viridiflava*, was taken 200 meters above the level where the boa was found; this may be near the lower limit for this species, which is more abundant at elevations nearer the summit. Unless arbitrary criteria are employed, it is perhaps impossible to define the upper limits of the cloud forest in the area.

Clouds are frequently encountered at the crest of the escarpment, where the terrain is likely to be as moist as it is where the boa was found. Environments are appreciably warmer near the 2000-meter level than they are near the summits. The temperature of the soil beneath the rock that sheltered the holotype of *Exiliboa* was approximately 18° C.

This was on the afternoon of an unusually clear day, although it rained later in the afternoon. Nearer the summit of the escarpment, slightly below 3000 meters, where clouds descend on the pine-oak woodland, the temperature of the air, the water, and the substratum closely approximates 10° C. Fluctuations above or below this level proved to be less than 1° C. when temperatures were recorded on successive years near a stream on the north side of Cerro Pelón. Until additional specimens of *Exiliboa placata* are obtained, the vertical distribution of the species must remain in doubt, but it is questionable whether this boa will be encountered at elevations exceeding the 2500-meter level. It may be expected at somewhat lower elevations in the cloud forest, however, although it is highly improbable that its distribution extends into the lowlands. It appears to be adaptively specialized as a subfossorial inhabitant of cool, moist environments in the cloud forest.

AFFINITIES

DISTRIBUTIONAL IMPLICATIONS: The living members of the family Boidae were grouped in 58 species and 23 genera by Stull (1935), who resurrected three of the genera that Boulenger (1893) had synonymized. In addition to her recognition of *Acrantophis*, *Morelia*, and *Sanzinia*, Stull proposed a number of minor changes. Her arrangement of the genera, however, was essentially that of Boulenger. Some of the species that Stull overlooked or synonymized have since been revived, and a few other names have been proposed for species or subspecies. Names other than those used by Stull have since been employed for five of the genera she recognized, *Corallus* for *Boa*, *Boa* for *Constrictor*, *Candoia* for *Enygrus*, *Bothrocheilus* for *Nardoana*, and *Ungaliophis* for *Peropodum*. The only generic name that has been proposed for any boa discovered since the turn of the century, however, is *Xenoboa*, the name applied by Hoge (1953) to a moderately large species, *Xenoboa cropani*, found in Brazil. *Xenoboa* is evidently related to *Epicrates*, which might be redefined to include *cropani*.

With the addition of *Exiliboa*, the living members of the family Boidae are currently assigned to 25 genera, 12 of which are restricted to the New World. Approximately 50 per cent of the genera contain only one species, although in some instances partially differentiated populations (notably those of *Boa constrictor* in the Americas) have been recognized, or even regarded as species. The only genera containing six or more species are *Eryx*, *Python*, and possibly *Liasis* in the Old World, and *Epicrates* and *Tropidophis* in the Americas. If the views expounded by Schwartz and Marsh (1960) prove to be acceptable, the genus *Tropidophis* contains at least 14 species, two of which are restricted to South America and

the others to the West Indies. According to Schwartz and Marsh, eight or nine of these species occur on Cuba.

The boas of the genus *Lichanura* occupy arid and semi-arid regions in the southwestern portion of the United States and the contiguous portions of Mexico. The distribution of *Charina* is disjunct, but it extends from the mountains of southern California northward to British Columbia (Logier and Toner, 1961) and eastward to the mountains of Utah and Montana. The other boas in the Americas are restricted largely to the tropics, although the range of the polytypic species *Boa constrictor* extends northward well beyond the Tropic of Cancer into semi-arid portions of southern Sonora, and southward into the temperate portion of Argentina. Some of the pythons, notably the larger species of Africa and Asia, also occupy extensive ranges. The species outside the tropics do not attain dimensions comparable to those restricted to the warm lowlands near the equator, but a few small boas are virtually as tolerant of cool environments or short growing seasons as other snakes in temperate climates. The range of *Eryx* in Eurasia extends well north of the Caspian Sea (Terentev and Chernov, 1949), to approximately the latitude reached by *Charina* in Canada (Logier and Toner, 1961).

The majority of the genera are largely tropical in distribution, but the family Boidae differs little from the larger families of snakes in this respect. Comparisons of ophidian faunas at various latitudes suggest that boas, as a group, are only slightly less adaptable than other snakes to environments outside the tropics. Of the species with distributions that extend into the United States, approximately 1.7 per cent are boas, and the percentage is only slightly higher in Europe (Mertens and Wermuth, 1960). Taylor (1951) recognized 125 species of snakes in Costa Rica, of which 2.4 per cent are boas. One additional boa, *Ungaliophis panamensis*, undoubtedly occurs in Costa Rica (Bogert, 1968), which would raise the percentage to 3.2. The most recent account of the snakes in any relatively large area in the American tropics is that of Roze (1966), who reported 117 species of snakes in Venezuela, of which only 3.4 per cent are members of the family Boidae.

It is conjectural whether a larger percentage of the extinct species inhabited the tropics, but no doubt exists that boas once occupied extensive areas where the family is no longer represented (Auffenberg, 1963). The fossil record fairly well substantiates the belief that the dispersal of boids, at least in the New World, antedates that of other families of snakes, some of which are probably much more diversified at present than the boas were in the past. Thus far paleontologists have not assembled sufficient evidence to show conclusively that species in the family

Boidae were more numerous at any one time in their history than they are today. It seems probable, nevertheless, that the family is well beyond its peak of abundance and diversification. Climatic changes may well have affected the boas adversely, but perhaps changes in the biotic environment were of even greater importance. Although satisfactory evidence is lacking, it may be inferred that the expansion and evolution of more "progressive" snakes now assigned to other groups accelerated the decline of the boas. Peculiarities in the distribution of boas in the Americas seem to support this assumption.

As noted above, less than 4 per cent of the snakes occupying areas on the mainland are boas. On several of the islands in the West Indies, however, boas comprise much larger percentages of the ophidian faunas. Four of the 18 species, or somewhat over 22 per cent of the snakes listed by Cochran (1941) for the island of Hispaniola, are boas. The proportion is higher on Jamaica, where three of the seven snakes reported by Lynn and Grant (1940) are members of the family Boidae. If Schwartz and Marsh (1960) are correct in their belief that "eight or nine" species of *Tropidophis* occur on Cuba, in addition to species of *Epicrates*, boas outnumber all other snakes on the island, at least in terms of species.

The disparity in the representation of boas on Cuba as compared with that on the mainland suggests that the mainland boas have been largely supplanted by the more advanced species. It is uncertain whether the diversification of *Tropidophis* on Cuba antedated the dispersal of colubrids in the Americas, but improbable that boas would have expanded their distribution on the island had many colubrids reached it. It might be argued that the snakes of the genus *Tropidophis* are atypical boas, more like colubrids than many other members of their family, and hence more adaptable. This assumption is belied, however, by the presence of two species of *Tropidophis* with restricted distributions in South America, where they survive as relicts.

Boas occur on many of the islands in the Indo-Australian Archipelago (Rooij, 1917), where the family is comparatively well represented, particularly on the larger islands. Somewhat more than 6 per cent of the snakes (not counting the sea snakes) that de Rooij listed for New Guinea are members of the family Boidae, whereas boids comprise scarcely more than 1 per cent of the 360 species (exclusive of the hydrophiids) of snakes listed by Malcolm Smith (1943) for India and Ceylon.

Existing distributions are, of course, the result of extremely complex interactions between animals and their environments, and the sequence in the events that have affected the dispersals of species. The genus

Tropidophis has perhaps become diversified in the West Indies because of some peculiarly favorable combination of events in the history of the group. Insular environments *per se* may have advantages for some groups of animals (Cowles and Bogert, 1944), and few doubts exist that islands have also served as havens for species that have disappeared on mainlands. Despite the wide occurrence of boas, the peculiar distribution of the species suggests that the family has been decimated. A few species thrive, but the family is represented by not many more than 70 species, nearly 50 per cent of which are in the Americas. As a group, the family contains a rather large percentage of relicts, some of which are restricted to islands or to limited portions of the mainland, whereas the distribution of others, such as *Charina* (Klauber, 1943) or *Ungaliophis* (Bogert, 1968), is disjunct, leaving no doubt that such forms were once more widely distributed. Some species, of course, have fared much better than others; the distribution of *Boa constrictor* is scarcely that of a relict. The species may nevertheless have occupied an even more extensive range in the past than it does today.

In the absence of pit vipers, and with few colubrids occupying Cuba, the degree of speciation in the genus *Tropidophis* exceeds that of other boas, but approximates that of many of the more adaptable colubrid genera. The adaptive radiation of the Boidae on the mainland, which took place much earlier, was far more extensive, as indicated by the survival of boas that are primarily aquatic (*Eunectes*), largely arboreal (*Corallus*), terrestrial (*Trachyboa*, *Lichanura*, and most species of *Tropidophis*), or more nearly fossorial (*Loxocemus*, *Exiliboa*, and some species of *Tropidophis*). The occurrence of *Ungaliophis* in banana shipments would suggest that at least one species, *U. panamensis*, is both secretive and arboreal. *Boa constrictor* and some, if not all, species of *Epicrates*, which appear to be less specialized, apparently forage either on the ground or in trees. There appear to be no records of *Tropidophis* in trees, but *Charina*, which is more commonly found under trash or debris on the ground, has been captured 12 feet above the ground in a chipmunk's nest (Ross, 1931). Boas in the New World occupy rain forests, cloud forests, arid and semi-arid lowlands, and pine-oak woodland. Moreover, the range in the dimensions attained by adults is far greater among the Boidae than it is in any other family of snakes.

Admittedly these characteristics are not those of most other relictual groups, or families, which are usually comprised of a few species that are restricted largely to one sort of environment or to one mode of existence. Despite evidence of their adaptability, the Boidae are absent from so many areas or so poorly represented in others that manifestly

they cannot be considered a flourishing group. Rather it would seem that the species now extant are remnants of a family well beyond its peak of abundance. A few species appear to have been sufficiently well adapted, or adaptable, to cope successfully with changes in the biotic environment, whereas others survive (or even thrive) only in isolated havens where conditions have been relatively stable. The remains of gigantic boas (*Madisoia*) from Eocene deposits in Patagonia (Simpson, 1933), and the occurrence of bones of much smaller species in formations of similar age in Wyoming (Hecht, 1959) leave no doubt that members of the family were widely distributed at this relatively early stage in the evolution of snakes. This wide distribution would suggest that the adaptive radiation of the Boidae was well advanced even before the Tertiary. If colubrids were becoming diversified in the Americas during the Miocene, as suggested by the fossil record, the decline of the Boidae may have been initiated before the close of the Eocene.

When the fossil record and present-day distributions of boas are taken into account, the existence of well-differentiated species at the periphery of the range of the family becomes more comprehensible. With the decline of the Boidae, few annectant forms remained. The larger boas, *Eunectes*, *Boa*, *Corallus*, *Epicrates*, and *Xenoboa*, form a reasonably compact group, perhaps with a comparatively recent center of dispersal in the region of the Amazon Basin. The distributions of some of the smaller boas are largely but not entirely peripheral to this region. The genera *Tropidophis*, *Ungaliophis*, and perhaps *Trachyboa* as well, appear to be represented in South America by a few disjunct populations, essentially relicts. The ranges of the genera *Loxocemus*, *Exiliboa*, *Lichanura*, and *Charina* are more remote geographically, although *Charina* is the only genus with a distribution wholly outside the tropics.

Loxocemus is not readily grouped with any other member of the Boidae. The boas in western North America, *Charina* and *Lichanura*, were considered by Hoffstetter (1962) to be related to *Eryx*. There are, of course, differences as well as similarities in the snakes of these three genera, but the peculiarities they share are not readily attributable to convergence. *Charina* and *Lichanura* are perhaps remnants of an Asiatic dispersal that extended to North America when more favorable climatic conditions prevailed. However divergent these three genera may be, they would appear to be more closely related to one another than to any of the boas that may have evolved as elements of an adaptive radiation in the American tropics.

Brongersma (1951) has shown that *Trachyboa* and *Tropidophis* share peculiarities indicative of affinities, despite rather profound differences

in their external morphology. The inclusion of *Ungaliophis* in this group appears to be justified, even though Butner's (1963) description of the internal anatomy of *U. panamensis* was inaccurate, as previously noted (Bogert, 1968). The vertebrae of *Ungaliophis* and *Tropidophis*, which neither Brongersma nor Butner examined, prove to be far more variable than Underwood (1967) assumed in his account. The specializations of the three genera of dwarf boas perhaps account for the differences between them, and their divergence can scarcely have been initiated recently. There is no evidence to suggest that any of these dwarfs was independently derived from any of the large boas now extant, but they may have arisen from an early branch of the family in South America.

Should *Exiliboa* prove to be related to *Ungaliophis*, which might be expected on zoogeographical grounds, the degree of divergence does not preclude the possibility that the boa in Oaxaca survives as a derivative of a parental population that has long been isolated in the cloud forest west of the lowlands at the Isthmus of Tehuantepec. If so, the divergence of *Exiliboa* may have been initiated at least as early as the Pliocene, or it could be a relict of an earlier radiation of the dwarf boas. The only characters suggestive of any link between *Exiliboa* and the larger boas are mainly those used to group the species in the same family.

The tribe Tropidophini has not been adequately defined, but, if it warrants retention, the group, which now includes *Tropidophis* and *Trachyboa*, should be expanded and redefined to include *Exiliboa*, as well as *Ungaliophis*. The comparisons that follow are premised on this assumption. There are less convincing arguments for placing *Exiliboa* and *Ungaliophis* in a separate tribe, and any further partition of the American boas may prove to be misleading or unwarranted when more detailed investigations have been completed.

COMPARISONS WITH OTHER DWARF BOAS: To facilitate discussion of the characters that have been investigated in an effort to ascertain the affinities of *Exiliboa*, the data assembled have been partly summarized in table 1. Differences as well as similarities are readily apparent in the scutellation, which has been modified along different lines in each of the four genera (see fig. 1). The number of midbody scale rows sheds no light on the affinities of the dwarf boas, and scale-row reductions are subject to so much variation in some species of *Tropidophis* that it is hopeless to attempt to use scale-reduction formulas in comparisons of genera.

The plates on the head of the dwarf boas readily distinguish the four genera, each of which has evolved its own peculiarities. Except for the absence or near absence of parietals, the number and the arrangement

TABLE 1
CHARACTERS OF THE GENERA TENTATIVELY PLACED IN THE TROPIDOPHINI

Character	<i>Exiliboa</i>	<i>Ungaliophis</i>	<i>Tropidophis</i>	<i>Trachyboa</i>
Internasals	Azygous, enlarged	Paired, in contact or separated	Paired, in contact	Paired, in contact
Prefrontals	One pair	Azygous, enlarged	Two pairs (rarely one pair)	Scalelike or in two or three pairs
Nasal	Single, nostril near middle of shield	Paired, nostril in anterior shield	Paired, nostril on suture between shields	Single, nostril near middle of shield
Loreal	Single	Single	Absent (fused with prefrontal)	Indistinguishable
Supralabials	7	8-10	8-12	9-11
Pairs of shields on mental groove	3	4	4 or 5	4 or 5
Midbody scale rows	21	19-25	21-29	29-33
Ventrals	166	204-258	140-225	132-152
Subcaudals	24	39-47	22-45	25-33
Maxillary teeth	17-19	12-15	12-23	19-20
Spurs	Present on δ δ and ♀ ♀	Restricted to δ δ	Restricted to δ δ	Restricted to δ δ
Hypapophyses	Restricted to anterior vertebrae	Restricted to anterior vertebrae	Present on posterior vertebrae, but vestigial on some species	Well developed on vertebrae through-out trunk
Hypohyal extends to	Rib 5	Rib 7	Rib 7, 8, 9, or 10	Rib 9 or 10
Kidneys	Lobulated	Lobulated	Not lobulated	Not lobulated
Anal glands	Posterior to anal opening	Posterior to anal opening	Contiguous to anal opening	Contiguous to anal opening
Tracheal lung and right lung	Present (no left lung)	Present (with vestige of left lung)	Present (no left lung)	Present (no left lung)

of the plates on the head of *Tropidophis*, *Ungaliophis*, and *Exiliboa* more nearly resemble those of colubrids than those of the larger boas. The significance of this superficial resemblance to members of the family Colubridae is obscure. Plainly trends toward a reduction in size did not invariably entail a reduction in the number of cephalic scutes. This is shown by *Trachyboa*, on which the fragmentation of the shields on the head exceeds that of many of the large boas. As may be noted in table 1, the trend is reversed in *Exiliboa*, on which there are fewer shields on some portions of the head than on the other boas, although some shields have fused on *Tropidophis* and *Ungaliophis*. On *Tropidophis* there are normally two pairs of prefrontals, members of one pair being fused with the loreals, and the prefrontals of *Ungaliophis* have become coalesced and expanded over much of the snout. In contrast, *Exiliboa* retains the prefrontals, but it is the only dwarf boa on which the internasals (which are invariably paired and even separated on one species of *Ungaliophis*) have become fused at the midline so that a single, relatively large, somewhat triangular shield separates the undivided nasals (fig. 3).

The adaptive significance of the fused internasals in *Exiliboa placata* is not readily apparent. It is nevertheless noteworthy that single internasals characterize several colubrid genera, *Atridium* in Asia, *Limnophis* in Africa, *Helicops* in South America, and *Liodytes* in North America. The snakes of these genera are restricted to extremely moist environments, principally swamps, where all of them prey on frogs to some extent. Their superficial resemblance to *Exiliboa* may or may not be attributable to adaptive convergence, but this possibility cannot be ruled out in view of the similarity of their habits and environments. A few of the colubrids with fused internasals prey on fishes as well as frogs. Such snakes evidently forage in the water to some extent, whereas *Exiliboa* must normally seek its prey in moist, terrestrial habitats.

Adaptive modifications in the scutellation of the dwarf boas have perhaps obscured many of the characters they shared before the distribution of the ancestral population became fragmented. Some characters of *Exiliboa*, including the numbers of midbody scale rows, ventrals, and subcaudals, fall within the range of variation reported for *Tropidophis*. The extensive variation in these characters of *Tropidophis* is largely the result of the divergence that accompanied the adaptive radiation of the genus in the West Indies, where the paucity of colubrids has permitted the dwarf boas to exploit a moderately wide range of terrestrial habitats. As far as can be ascertained, the species of *Tropidophis* that have approximately the same number of scale rows, ventrals, and subcaudals as *Exiliboa* are the secretive, subfossorial members of the

group that most closely resemble the cloud-forest boa in their mode of existence. Manifestly it would be gratuitous to assume that *Exiliboa* is closer to the ancestry of any one species of *Tropidophis* than it is to another.

The number of midbody scale rows is presumably the result of selection, as suggested by a cline or geographical trend in *Ungaliophis panamensis* (Bogert, 1968). The number of scale rows varies from 19 in Colombia, to 21 in Panama, and rises to 23 in southern Nicaragua. Specimens of unknown origin that may represent populations in northern Nicaragua or portions of Honduras have 25 scale rows. The species is replaced by *U. continentalis* from central Honduras northeastward through Guatemala to eastern Chiapas. The few specimens of *U. continentalis* thus far discovered, however, are all characterized by their possession of 25 midbody scale rows. In this respect *Exiliboa* closely resembles the Panamanian population, but it differs from Chiapan representatives of *Ungaliophis* in having fewer scale rows.

All specimens of *Ungaliophis* examined have at least 38 more ventrals, and 15 more subcaudals, than the holotype of *Exiliboa*, and it is questionable whether additional specimens of the Oaxacan boa will reveal an overlap in the number of scales in either series. Adaptive modifications in the ventrals, subcaudals, and scale rows have undoubtedly occurred in both genera, and the differences do not preclude the possibility that both genera were derived from the same ancestor.

The maxillary teeth are somewhat more specialized in *Ungaliophis* than they are in *Exiliboa* or the other dwarf boas, but the number of teeth varies extensively in *Tropidophis*, with differences between species that exceed the differences between any two other genera. Dentitional characters are of some value in defining the species and genera, but they shed no light on the affinities of the individual genera. They merely point to the possibility that the dentition of the dwarf boas has become modified in the populations derived from a common ancestor.

The vestigial spurs on the female of *Exiliboa* can scarcely have any functional significance. Spurs have been lost by the females of the other genera of dwarf boas, and despite Underwood's (1967) definition of the Tropidophini ("pelvic spurs in male") Stull (1928) has reported their absence from both sexes of *Tropidophis semicinctus*. Presumably external remnants of limbs were present on both sexes of the boa ancestral to *Exiliboa*, females of which retain them as a primitive character, although the vestiges of the pectoral girdle, which are retained along with spurs by the males of dwarf boas, are lacking on the holotype of *Exiliboa*, as revealed by roentgenograms. *Exiliboa* need not be regarded as being

more primitive than the other dwarf boas merely because the females of the genus retain vestiges of spurs. Their presence has phylogenetic implications, for it is evident that *Exiliboa* has retained some peculiar combination of genes that the female dwarf boas of other genera lack. Several possible explanations might be offered, but it will suffice to note that the retention of spurs, presumably by both sexes of *Exiliboa*, affords no clues to the affinities of the genus.

Because the vertebrae are more often found as fossils than other portions of the skeleton, paleontologists have devoted considerable attention to vertebral characters. Auffenberg (1963), Hoffstetter (1960), and Underwood (1967) have discussed vertebrae and some of the problems that arise when they are used in systematic investigations. It has become evident that intracolumnar and intraspecific as well as interspecific variations must be taken into account, along with ontogenetic changes, and in some instances sexual dimorphism (Bogert, 1964). Auffenberg, one of the few authors who has made a serious effort to define the terms used in descriptions of vertebrae, observed that such structures as the hypapophyses are not satisfactorily described merely as being present or absent. Variations noted in the dwarf boas range from the strongly developed hypapophyses of *Trachyboa* to the moderately well-developed structures of *Tropidophis melanurus*, and the feebly developed haemal keel on the precaudal vertebrae of *Tropidophis feicki* (the keel is even less strongly developed on *Tropidophis semicinctus*). Vestiges of the keel are discernible on large specimens (600 mm. in over-all length) of *Ungaliophis panamensis*, but there is scarcely a trace of the haemal keel on smaller specimens, and it is virtually lacking on the precaudal vertebrae of an adult specimen of *Ungaliophis continentalis* from Chiapas.

Auffenberg apparently considers hypapophyses to be present whenever the merest trace of a median keel, even a bulbous structure, is present. Thus he refers to the "haemal keel of variable shape on the middle and posterior vertebrae" of typhlopids and aniliids, whereas Underwood states explicitly that members of the families Typhlopidae and Aniliidae lack hypapophyses. Similarly, the presence of hypapophyses on the posterior trunk vertebrae of *Sanzinia* has been questioned by Dowling (1959), whose illustration would suggest that a haemal keel is retained. Virtually every degree of development of the hypapophyses is revealed by an examination of the vertebrae of the smaller members of the family Boidae. In view of the variations in the shape and the degree of development of the hypapophyses, it seems futile to expect investigators to be wholly objective in their choice of terms. In lieu of descriptions, therefore, the vertebrae of several of the smaller American boas, including

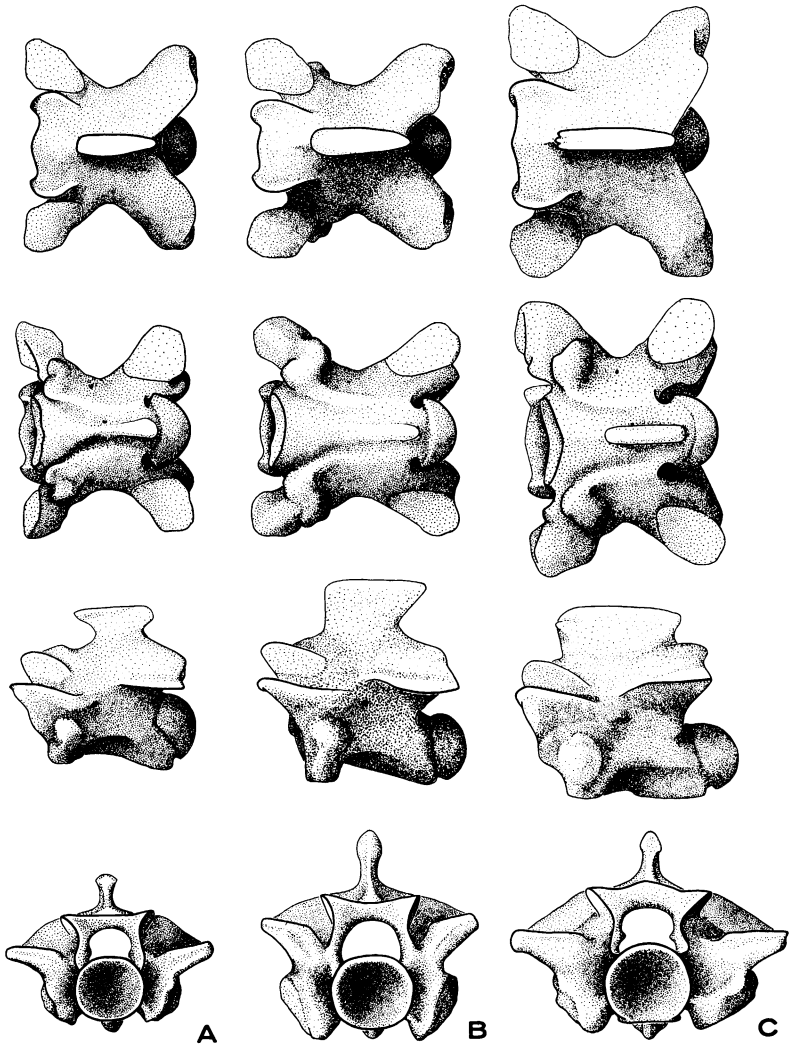


FIG. 8. Dorsal, ventral, lateral, and anterior views of precaudal vertebrae. A. *Ungaliophis panamensis*, A.M.N.H. No. 76305. B. *Exiliboa placata*, holotype. C. *Tropidophis feicki*, A.M.N.H. No. 81128.

Exiliboa, are depicted in figures 8 to 10. In this account vestiges of the haemal keel are not considered to be hypapophyses, and vertebrae with faint traces of the keel are described as lacking hypapophyses.

Illustrations of the vertebrae of *Trachyboa*, *Ungaliophis*, and *Tropidophis*

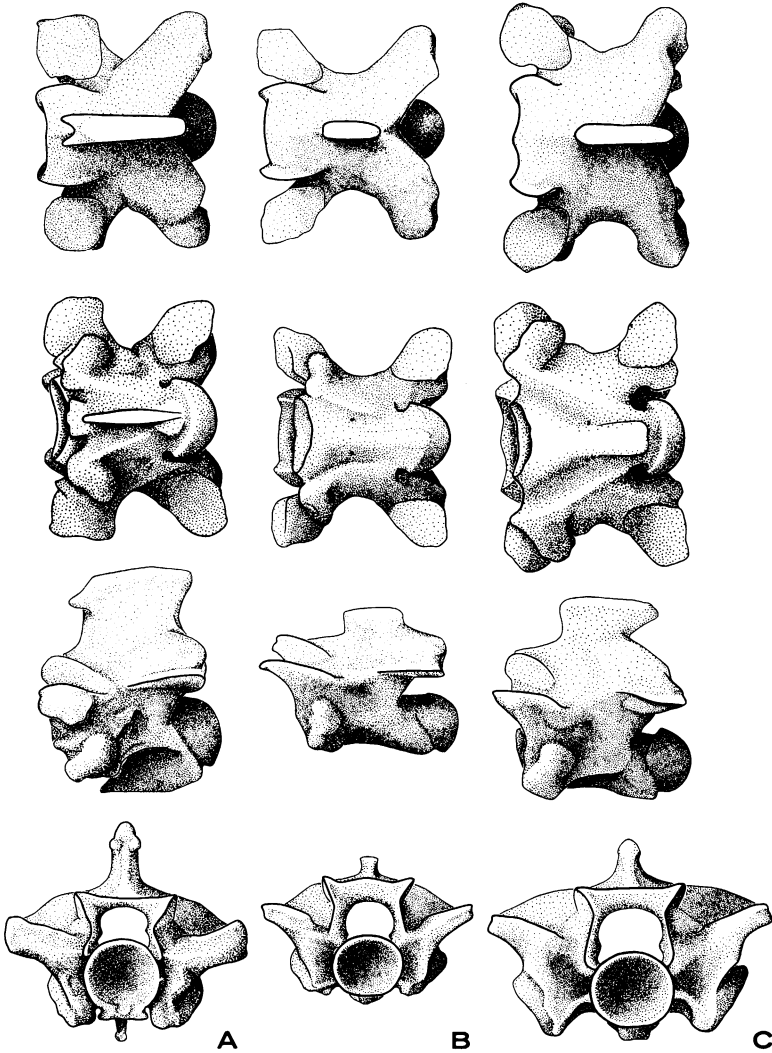


FIG. 9. Dorsal, ventral, lateral, and anterior views of precaudal vertebrae. A. *Tropidophis melanurus*, A.M.N.H. No. 93002. B. *Ungaliophis continentalis*, A.M.-N.H. No. 93813. C. *Loxocemus bicolor*, A.M.N.H. No. 44902.

cana have already been published (Bogert, 1968). All vertebrae illustrated in figures 8 to 10, with the exception of the fossil *Dunnophis*, were removed from the middle precaudal portion of the column. Although no evidence of sexual dimorphism in the precaudal vertebrae of boas

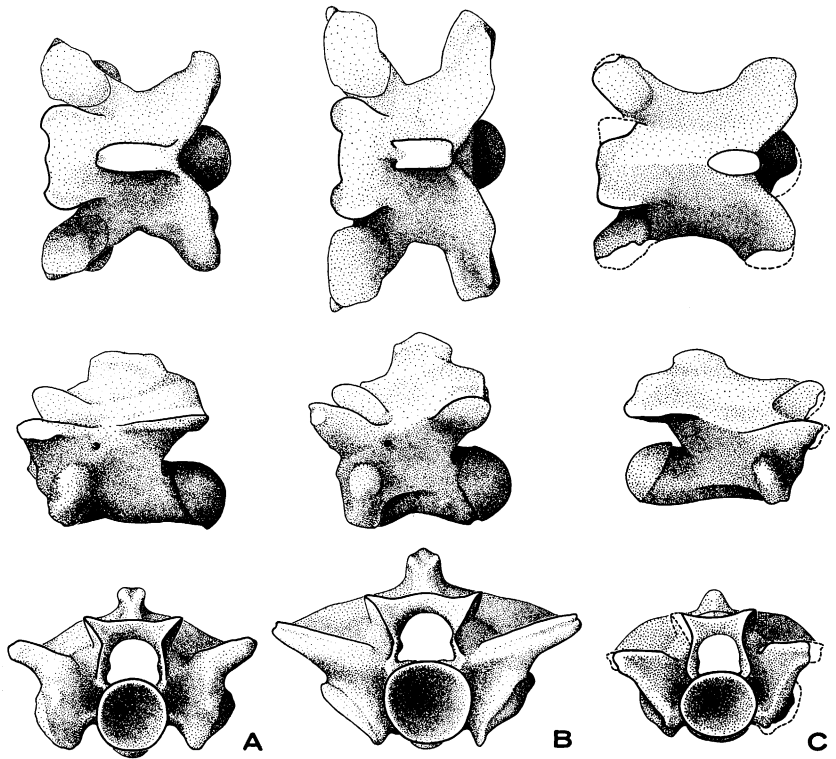


FIG. 10. Dorsal, lateral, and posterior views of precaudal vertebrae. A. *Charina bottae*, A.M.N.H. No. 64945. B. *Lichanura roseofusca*, A.M.N.H. No. 73360. C. *Dunnophis microechinis*, holotype, A.M.N.H. No. 3830 in the Department of Vertebrate Paleontology.

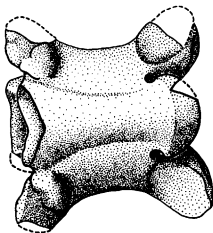


FIG. 11. Ventral aspect of the vertebra (holotype) of *Dunnophis microechinis*, showing the absence of any trace of the haemal keel or other vestiges of the hypapophysis.

has been reported, whenever possible vertebrae taken from females have been selected for illustration. An examination of vertebrae from three females of *Ungaliophis* reveals differences in the degree of development of the hypapophyses (as noted above) and the neural spine. Because

the two specimens of *U. panamensis* (one of which is appreciably larger than the other) that were examined lack locality data, it is uncertain whether the differences noted are attributable to ontogenetic changes or to individual variation. The vertebrae of a moderately large individual of the other species, *U. continentalis*, more closely resemble those of the smaller specimen of *U. panamensis*. Whether the differences noted in the vertebrae are genetic or ontogenetic cannot be ascertained at present.

Comparisons of the vertebrae of *Exiliboa* with those of other small boas in the New World do not show conclusively that the species discovered in Oaxaca is necessarily more closely related to *Ungaliophis* than it is to *Tropidophis*. The faint traces of the haemal keel discernible on the vertebra of *Exiliboa* more closely resemble those on the larger specimen of *Ungaliophis* than those of any species of *Tropidophis* examined. The size and shape of the neural spine and the hypapophyses vary from species to species. There is relatively little variation in the proportions of the precaudal vertebrae of *Tropidophis*, which are discernibly broader than those of *Ungaliophis*. The precaudal vertebrae of *Exiliboa*, however, are proportionately longer than those of other genera of dwarf boas, including *Trachyboa*, which has extraordinarily broad vertebrae, and much more strongly developed neural spines and hypapophyses (Bogert, 1968).

The neural spine is subject to as much variation as the hypapophyses, in size as well as in shape. On *Tropidophis* the crest of the neural spine may overhang toward the front or the back end of the vertebrae, or at both ends, as it does on *T. melanurus*. As viewed in profile, the neural spine of an adult female *Ungaliophis panamensis* has the crest projecting above the base at both ends, whereas on an adult female of *U. continentalis* there is no overhang, and the neural spine is even more reduced in a smaller specimen of *U. panamensis* illustrated (Bogert, 1968) in an account of the boas of the genus.¹ As compared with the neural spines of

¹ Dr. Max K. Hecht has called my attention to the vertebra from the Bridger Formation that he described (1959) and illustrated as *Dunnophis microechinis*. The neural spine on *Dunnophis* (present paper, fig. 10) is somewhat more reduced, and farther to the rear than that on *Ungaliophis*, and other differences are readily apparent. It seems probable that *Dunnophis* can be assigned to the Boidae, although Hecht, who was unaware of the greatly reduced neural spine on some specimens of *Ungaliophis*, had suggested that *Dunnophis* might represent a new family. The vertebra designated as the holotype by Hecht lacks any trace of the haemal keel (present paper, fig. 11), and in this respect as well as in the shape of the neural arch, it resembles the precaudal vertebrae of *Charina* (present paper, fig. 10). The proportions of the vertebra of *Dunnophis* resemble those of *Exiliboa* more closely than those of *Charina*, on which the vertebrae are relatively broad. The occurrence of *Dunnophis* in the Bridger Formation suggests that small, fossorial or subfossorial boas had evolved in the Americas as early as the Eocene.

Tropidophis and *Ungaliophis*, the neural spine on the vertebra of *Exiliboa* is proportionately higher, although the height of the spine is closely approached on the vertebrae of *Tropidophis melanurus*, one of the largest members of the genus. In having the neural spine notched below the crest, which overhangs the base of the condyle, the vertebra of *Exiliboa* most closely approaches that of *Tropidophis canus*.

The extent of the variation in the vertebral characters of *Exiliboa* remains to be ascertained, but on the whole the differences between the vertebrae of this genus and those of *Tropidophis* and *Ungaliophis* are less profound than the differences in external characters. It may be added that, as viewed from the side, the precaudal vertebrae of *Exiliboa* resemble those of *Loxocemus*, which are, however, much broader and flatter in proportion to their length. In this respect, as well as in having a relatively low neural spine, the vertebrae of *Loxocemus* are more like those of *Lichanura* and *Charina*. Contrary to inferences drawn by Johnson (1955), it seems probable that vertebrae have been subject to adaptive modification, despite their retention of ancestral peculiarities. Similarities in structure of the neural spine of *Loxocemus* and *Exiliboa* strongly suggest convergence, for there is no evidence of close affinity in other respects.

Roentgenograms of *Exiliboa* fail to reveal any significant differences between the caudal vertebrae of this genus and those of *Tropidophis* and *Ungaliophis*. The neural spines on the caudal vertebrae of all three genera differ little from those on the precaudal vertebrae. As might be inferred from the external appearance of the tail, the dwarf boas of the American tropics lack the elaborate modifications on the vertebrae near the end of the tail of *Eryx* and *Charina* (fig. 12). As compared with the caudal vertebrae of these genera, those toward the end of the tail of *Lichanura* are relatively simple, although the neural spine becomes progressively broader, with a median groove on the crest of each spine on the terminal 12 vertebrae. The similarity in the structures on the caudal vertebrae of *Eryx johni* and *Charina bottae* may well be construed as evidence of affinity. The caudal vertebrae of *Lichanura* are so little modified, however, that it is problematical whether the genus shares close ancestry with the boas placed in the tribe Erycini. Underwood (1967), who has most recently discussed the relationships of *Lichanura*, evidently entertained doubts concerning its affinities. Plainly the relationships of *Lichanura* are closer to *Charina* and *Eryx* than to any of the dwarf boas of the American tropics, although, judged by caudal vertebrae, *Charina* is closer to *Eryx* than either of these genera is to *Lichanura*.

Roentgenograms of *Exiliboa*, *Ungaliophis*, *Trachyboa*, and several species of *Tropidophis* reveal the length of the hyoid (fig. 6), which proves to be

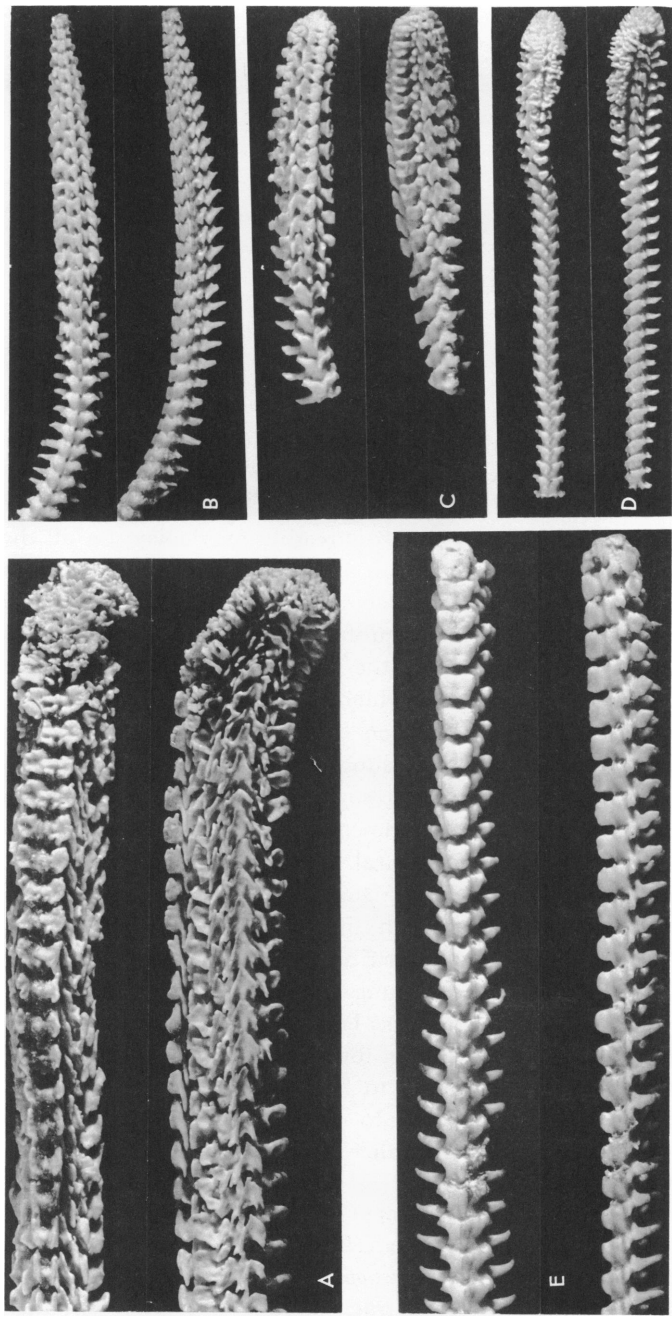


FIG. 12. Caudal vertebrae of boas, dorsal and lateral views, respectively. A. *Eryx johni*. B. *Eryx colubrinus*. C. *Eryx jaculus*. D. *Charina bottae*. E. *Lichanura rosefusca*.

shorter in *Exiliboa* than it is in the other three genera. The significance of the difference is obscure, and the account of Langebartel (1968) suggests that information concerning the hyoid sheds little light on affinities. The specimen of *Ungaliophis* examined by Langebartel proves to be *U. panamensis* rather than *U. continentalis* to which he assigned it, and it is evident from roentgenograms that the hypohyal (or cornua) on both species of *Ungaliophis* extends farther posteriorly than he has indicated. Langebartel would apparently group *Trachyboa* and *Tropidophis* with *Casarea* and *Bolyeria*, but if he derived any information from his examination of *Ungaliophis* he failed to mention it in his discussion of the phylogenetic implications of his investigation. Langebartel has also repeated the statement that *Tropidophis* lacks the coronoid, as first reported by Dowling (1959). Dr. Herndon G. Dowling has informed me, however, that his statement was based on an examination of freshly prepared skulls, on which the presence of the coronoid could not be detected, but it became apparent later when the mandibles had become more thoroughly desiccated. The coronoid is readily overlooked on all dwarf boas, but it appears to be present on all specimens critically examined.

Brongersma (1951) advocated placing members of the genera *Tropidophis* and *Trachyboa* in a separate subfamily, the Tropidophinae. Brongersma characterized members of the subfamily as having a tracheal lung, a right lung, and kidneys, which lacked lobes, that are situated farther posteriorly than they are on other boas. Butner (1963), who reported a tracheal lung, a right lung, vestiges of the left lung, and kidneys without lobes in *Ungaliophis*, suggested that the genus be placed with the Tropidophinae. Butner's description was based on a specimen in the American Museum of Natural History (A.M.N.H. No. 76305), which does have vestiges of the left lung, as well as the tracheal lung, but, contrary to Butner's illustration, the right lung is essentially a continuation of the tracheal lung, as described by Brongersma for *Tropidophis*. Moreover, the vestige of the left lung is situated farther forward than Butner indicated in his illustration. The kidneys are situated well beyond the terminus of the right lung, toward the rear of the body cavity; the right kidney extends from 45 to 54 ventrals anterior to the vent, and the one on the left from 37 to 47 ventrals from the vent. The kidneys are roughly the same distance from the vent in several species of *Tropidophis*.

Butner's statement that the kidneys of *Ungaliophis* lack lobes proves to be erroneous, as previously noted (Bogert, 1968). Lobulated kidneys were found in both species of *Ungaliophis*, as well as in *Exiliboa*, which also possesses a right lung and a tracheal lung. No vestige of the left

lung could be found in *Exiliboa*, in which the right lung and the tracheal lung conform closely to Brongersma's description of those of *Tropidophis*. The retention of the vestigial lung by *Ungaliophis panamensis* is not of great significance, however, for Cope (1894) reported that the left lung had been lost by species congeneric with some that retained vestiges.

In view of the general absence of the tracheal lung among the Boidae, the presence of such lungs in *Trachyboa*, *Tropidophis*, *Ungaliophis*, and *Exiliboa* is perhaps the most nearly conclusive evidence of their relationship. Furthermore, most other boas retain a relatively large left lung, most notably *Loxocemus*, the left lung of which is only 20 per cent shorter than that on the right (Underwood, 1967). Some importance can also be attached to the position of the kidneys, which were reported by Brongersma (1951) to be much closer to the vent in *Trachyboa* and *Tropidophis* (as they also prove to be in *Ungaliophis* and *Exiliboa*) than in other members of the family. In having lobulated kidneys, *Exiliboa* and *Ungaliophis* differ from *Trachyboa* and *Tropidophis*, the kidneys of which lack the characteristic lobes seen on other boas. The staggered arrangement of the anal glands of *Exiliboa* (fig. 7) conforms closely to the condition illustrated for *Ungaliophis* (Bogert, 1968), whereas the anal glands of both *Trachyboa* and *Tropidophis* lie close to the vent. Although the anal gland on the right may be slightly shorter than the one on the left of *Trachyboa* and *Tropidophis*, the strongly staggered arrangement of the glands is not known to occur in these genera.

An examination of the anal glands of the small boas of other genera reveals considerable variation. On 11 of 17 specimens of *Eryx*, including representatives of seven species, the right gland was slightly longer than the left, but on two the left was longer, and on four the glands were of approximately the same length. On most individuals the glands extend to the fourth or fifth subcaudal, or scarcely beyond the second subcaudal on some juveniles, but as far as the sixth on large examples of *E. johni*. On three adults of *Lichanura* the left gland extends from two to four subcaudals beyond the one on the right, and both glands are exceptionally large on these boas; the smallest gland noted extended to the twentieth subcaudal. On 10 specimens of *Charina* the glands ranged in length from the fifth to the seventeenth subcaudal, and those of juveniles were appreciably longer than those of adults. Moreover, the right gland was the longer of the two on the juveniles, whereas on adults the left was longer, although on one adult male the two glands were approximately equal in length.

Much larger series will be required for the nature of the changes that

occur during the growth of *Charina* to be ascertained, but these meager data suggest that the glands become progressively shorter with age, and the glands of adult males tend to be somewhat shorter than those of females. The right gland of juveniles may extend from three to seven subcaudals beyond that on the left. In this respect the staggered arrangement of the glands of juvenile *Charina* more nearly approaches that observed in *Exiliboa*. The variations noted in the size and shape of the anal glands of *Charina* detract from their usefulness in studies of relationships. Nevertheless, the lobulated kidneys and the staggered arrangement of the scent glands in *Exiliboa* and *Ungaliophis* distinguish the boas of these genera from those in *Trachyboa* and *Tropidophis*. If these four genera are to be grouped in the Tropidophini, two of them are largely Middle American in distribution, and two are largely West Indian and South American. There is, however, some interdigitation in the distributions of the two groups in northern South America and Panama.

It is evident from the information reviewed above that each of the four genera tentatively grouped in the Tropidophini has evolved its own array of peculiarities. Consequently, the differences between the genera in the characters thus far studied outnumber the similarities. The most distinctive character that appears to be shared by all the dwarf boas is the tracheal lung, although these boas differ from most if not all other members of the family in having lost all or nearly all of the left lung. Otherwise it is impossible at present to find diagnostic characters that are peculiar to all members of the tribe. Virtually all other structures noted on these boas are either variable or not particularly distinctive. Thus three of the four characters listed by Underwood in the summary of his "classification" are not invariably characteristic. As noted in the preceding discussion, it is questionable whether the coronoid is lacking from any of the species; the posterior hypapophyses are vestigial in some species of *Tropidophis*, and all but lacking on some specimens of *Ungaliophis*. Furthermore, the spurs have been lost by both sexes of at least one species of *Tropidophis*, even though vestiges of spurs are retained by the female of *Exiliboa*.

Plainly the four genera are well differentiated, but perhaps derived from an ancestor in which the tracheal lung evolved at an early stage in the adaptive radiation of the boas in South America. The only dwarf boa that seems to be partly arboreal is *Ungaliophis*. The short-tailed, rugose species assigned to *Trachyboa* is not adapted for climbing, and it seems probable that it forages on the surface. The various species of *Tropidophis* are either terrestrial or partly fossorial, and, although *Exiliboa* may not burrow, it appears to avoid exposing itself to predators on

the surface by seeking its prey under rocks or logs. The feeding habits of *Trachyboa* are unknown, but *Tropidophis* apparently preys almost exclusively on lizards, including geckos and *Anolis*, whereas the diet of *Exiliboa* is largely restricted to frogs. *Exiliboa* could not be induced to eat newly born rodents, but Oliver (1956) reported that a captive *Ungaliophis panamensis* accepted small mice. Nothing has been learned about the feeding habits of either species of *Ungaliophis* under natural conditions.

ACKNOWLEDGMENTS

The herpetological explorations in the mountains of Oaxaca that led to the discovery of *Exiliboa* in 1967 were carried out with the cooperation of Dr. Rodolfo Hernández Corzo, Director General of the Departamento de Conservación y Propagación de la Fauna Silvestre, Secretaría de Agricultura y Ganadería, who most obligingly issued a permit. I am deeply grateful to Dr. Hernández for all he has done to further our investigations in Oaxaca.

Among the persons who assisted in the field, I am particularly indebted to the late Mr. J. Stuart Rowley, Mrs. Roy Jones, and my wife, Mrs. Martha R. Bogert. Laboratory investigations were carried out with the competent assistance of Mrs. Ellen Bowler, who was immensely helpful in assembling the information derived from other members of the family Boidae in an effort to ascertain the affinities of *Exiliboa*. Mrs. Bowler also cheerfully undertook the task of preparing all the drawings that accompany this report, and my thanks for her efforts on my behalf are gratefully acknowledged. I am also grateful to Mr. Robert E. Logan of the Division of Photography of the American Museum whose skillful use of radiographic techniques greatly facilitated comparisons of the internal structures of boas. Mr. George Foley also assisted in the preparation of specimens for study, and Mrs. Margaret Shaw patiently endured revisions of the manuscript and typed the final copy. My thanks go to these individuals, as well as to Dr. Samuel B. McDowell, Dr. Max K. Hecht, and Dr. Herndon G. Dowling, who have discussed with me some aspects of the evolution of the Boidae. They have also called my attention to references that might otherwise have been overlooked.

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ADDENDUM

On September 24, 1968, after the galley proofs of the preceding account had been corrected, a male example of *Exiliboa placata* was obtained. The specimen was taken 6 kilometers southwest of the type locality, at an elevation of approximately 2425 meters. The male, which is slightly larger than the holotype, closely resembles the female in having a white blotch on the anal region, but a larger white blotch is also present on the right side of the base of the tail. The spurs on the male are white, as they are on the female, but they are appreciably larger and readily discernible.

The male, discovered by J. W. Wright, was coiled beneath a small log in an area where trees had been felled in 1967. The terrain on the slope where the boa was found was littered with tree trunks surrounded by low, dense vegetation growing in the clearing. The temperature of the substratum at the site where the boa was found ranged from 19° to 21° C. The male will be described in greater detail after it has been preserved and catalogued in the collection of the American Museum of Natural History.