

THE DISTRIBUTION, VARIATION, NATURAL HISTORY, AND RELATIONSHIPS OF *PORTHIDIUM BARBOURI* (VIPERIDAE)

Jonathan A. Campbell

Department of Biology
The University of Texas at Arlington
Arlington, Texas 76019
USA

RESUMEN

Porthidium barbouri es una víbora rara, conocida por menos de dos docenas de ejemplares. Esta especie ha sido colectada en dos regiones elevadas en la parte central del estado de Guerrero, México. Ambas regiones están situadas al oeste de Chilpancingo, Guerrero. Esta especie vive en bosques de niebla y en bosques de abetos, pinos y encinos que se encuentran de 2,400 a 3,300 msnm. Probablemente la distribución vertical que alcanza esta especie es mayor que la de los otros miembros del género.

El número de escamas ventrales y subcaudales no tiene mucha variación entre los sexos. Los machos tienen entre 130-138 ($\bar{x} = 134.2$) ventrales y 27-31 ($\bar{x} = 29.8$) subcaudales, y las hembras tienen entre 129-145 ($\bar{x} = 138.7$) ventrales y 26-31 ($\bar{x} = 28.4$) subcaudales.

La variación en el tamaño y la disposición de las placas (escamas) dorsales cefálicas es mayor que en cualquier otra especie de culebra. Algunos ejemplares tienen placas dorsales cefálicas muy agrandadas con un complemento total de once escamas, estos especímenes tienen una sola placa frontal entre los supraoculares. Por otra parte, otros ejemplares tienen escamas muy pequeñas hasta con 5 escamas intersupraoculares. *Porthidium barbouri* tiene pocas hileras de escamas dorsales comparada con otras especies de víboras del Nuevo Mundo. Por lo general, tienen 21-17-15 o 21-19-15 hileras de escamas en el cuerpo.

Análisis del contenido de los estómagos indican que el alimento más frecuente de esta culebra lo constituyen roedores y lagartijas de la familia de los ánguidos (*Barisia gadovii*). Observaciones en el campo sugieren que esta especie es diurna. Existen muy pocos datos sobre la reproducción de *P. barbouri*. En cautiverio, una hembra dio a luz 6 crías el 20 de noviembre de 1976. Las crías tenían un promedio de longitud total de 154 mm y un peso promedio de 3.70 g. Una hembra colectada el 12 de junio de 1953 tenía siete folículos ováricos agrandados, y un juvenil que tenía una longitud total de 202 mm fue colectado a fines de diciembre. Estos datos indican que el número de crías

que tiene esta especie probablemente es muy bajo y que nacen durante la época de lluvias.

Tres especies, *P. barbouri*, *P. godmani* y *P. tzotzilorum*, evidentemente tienen un parentesco semejante y se derivaron de un progenitor que estaba más extensamente distribuido.

Porthidium barbouri is a rare snake known from fewer than two dozen specimens. This species has been collected on two highland areas in central Guerrero, México, that lie to the west of Chilpancingo. It inhabits cloud forest and high fir-pine-oak forests at elevations of between 2,400 and 3,300 m; thus it may have a higher vertical distribution than any other member in the genus.

Little sexual dimorphism is present in the number of ventrals with males averaging a slightly lower number (130-138, \bar{x} = 134.2) than females (129-145, \bar{x} = 138.7). The number of subcaudals varies from 27 to 31 (\bar{x} = 29.8) in males and from 26-31 (\bar{x} = 28.4) in females.

There is considerable variation in the size and arrangement of the dorsal cephalic scales of *P. barbouri*, perhaps more so than in any other species of snake. In this species, some specimens have greatly enlarged scales with a total complement of eleven scales—in these snakes a single enlarged frontal is present between the supraoculars. At the other extreme, some specimens have small head scales with as many as five intersupraoculars. The abbreviated dorsal scale reduction formula is most often 21-17-15 or 21-19-15; *P. barbouri* has fewer dorsal scale rows than any other species of New World pitviper.

Food items recovered from the stomachs of *P. barbouri* include rodents and the anguid lizard *Barisia gadovii*. Field observations indicate it is a diurnal forager. Although little is known concerning reproduction, a captive breeding produced six young on 20 November 1976 with a mean total length of 154 mm and a mean weight of 3.70 g. A female collected 12 June 1953 had seven enlarged ovarian follicles, and a juvenile specimen that measured 202 mm in total length was collected in late December. Thus, it appears that the number of young produced is not great and that the young are born during the latter half of the rainy season or subsequently in the dry season.

Three species, *P. barbouri*, *P. godmani*, and *P. tzotzilorum*, appear to be morphologically similar and are perhaps derived from a once morewidely distributed common ancestor. Present distributions represent relictual populations that have become isolated in the highlands of southern Mexico and Central America.

INTRODUCTION

Recent checklists of New World pitvipers, inclusive of México through South America, contain about 90 species placed in

nine genera (Campbell and Lamar 1989). Pitvipers are widespread and inhabit ecologically diverse habitats. This is especially true of the genus *Porthidium*, which includes the montane and hognose pitvipers of Middle and northern South America. In the north, *Porthidium nummifer* ranges as far north-eastward as southeastern San Luis Potosí, México (Burger 1950, Taylor 1949), where it occurs in unpland moist forests of the Atlantic versant. *Porthidium hespere* inhabits the xeric Pacific foothills of Colima and is the most northwestern representative of the genus (Campbell 1976). Southern México and Central America possess the majority of species allocated to the genus *Porthidium*, but one species, *P. hyoprora*, ranges at low elevations through the equatorial forests of the Amazonian basin to Bolivia and western Brazil. Another species, *P. nasutum*, is known from the Pacific lowlands of South America as far south as Ecuador.

One species, *P. barbouri*, restricted to the highlands of Guerrero, México, is somewhat distantly isolated from its congeners. Little has been reported concerning its biology except for descriptions of individual specimens or regional checklists (Davis and Dixon 1959, Dunn 1919, Shreve 1938; Smith and Taylor 1945). *Porthidium barbouri* is uncommon in collections, and is represented by fewer than two dozen specimens, about half of which were collected during the course of this study.

It is the intent of this report to describe the habitat of *P. barbouri* in terms of physiography, climate, and vegetation; assess the intraspecific variation in external morphology; and determine portions of its natural history such as reproduction and food habits, based on field observations and museum specimens.

DISTRIBUTION

Porthidium barbouri is recorded with certainty from only two areas of the Sierra Madre del Sur in Guerrero, México (see Appendix I for listing of all known localities): the vicinity of Omilteme ("Omiltemi" to some authors) from where most specimens have been collected, including the holotype, and from the vicinity of Puerto del Gallo,

some 60 km WSW of the type locality (Fig. 1). At least one disjunction appears to be present in the distribution of *P. barbouri*, the low pass between the headwaters of the Río Papagayo and Río Yetla. Topography of the region is poorly known, but the ridge between these two rivers appears to be scarcely 1,500 m in elevation. The species undoubtedly occurs in the highlands to the northwest of Cerro Teotepec which are continuous with this mountain above the 2,000 m contour. The location of Omilteme was incorrectly stated as "3 miles NW Chilpancingo" (Smith and Taylor 1950) and "10 kilometers W Chilpancingo" (Hall 1951). Omilteme actually lies 18.5 airline km W of Chilpancingo (31.1 km by road) at 2,360 m elevation.

During the 1930's and '40's, a collection of reptiles was assembled by W. W. Brown from "the vicinity of Chilpancingo." A portion of the collection was reported by Hall (1951) who noted the unfortunate fact that most specimens bore neither exact locality nor elevation data. The presence of mesic forest species such as *Barisia gadovii* and *Storeria storerioides* in this collection leaves little doubt that some of Brown's specimens labeled "Chilpancingo" came from higher elevations than the city, which is situated in a xeric valley of approximately 1,280 m elevation. A few of Brown's specimens, including *Porthidium barbouri* (MCZ 42678, the holotype of *Agkistrodon browni*; and MZC 43282) bear data indicating that they were collected near Omilteme, and it is probable that many of his highland specimens without accurate data, including several *P. barbouri* (FMNH 38503-04), also came from this small lumber camp which was active at the time his collections were made. The locality for MCZ 42679 (a paratype of *A. browni*), is recorded as "Sierra del Burro"; Shreve (1938) stated that the specimen possessed "the same data and history as the type," which was collected at Omilteme. Also, the holotype of *Rhadinae hesperia* collected by Brown was recorded from "Omilteme, Sierra del Burro, Guerrero, México" (Bailey 1940). Myers (1974:103) was unable to pinpoint this range any more precisely than "a section of the Sierra Madre del Sur in the Chilpancingo region of central Guerrero." The Sierra del Burro is located in the immediate vicinity of Omilteme and forms, in part, the highlands to the southeast of this village. The "Parque Ecológico Estatal de Omiltemi" includes the Sierra del Burro.

The lowest elevation at which *P. barbouri* has been encountered is about 2,400 m near Omilteme (TCWC 9455); near Puerto del Gallo on the south slope of Cerro Teotepec, a specimen collected at about 3,300 m (KU 182762) is the highest recorded elevation for

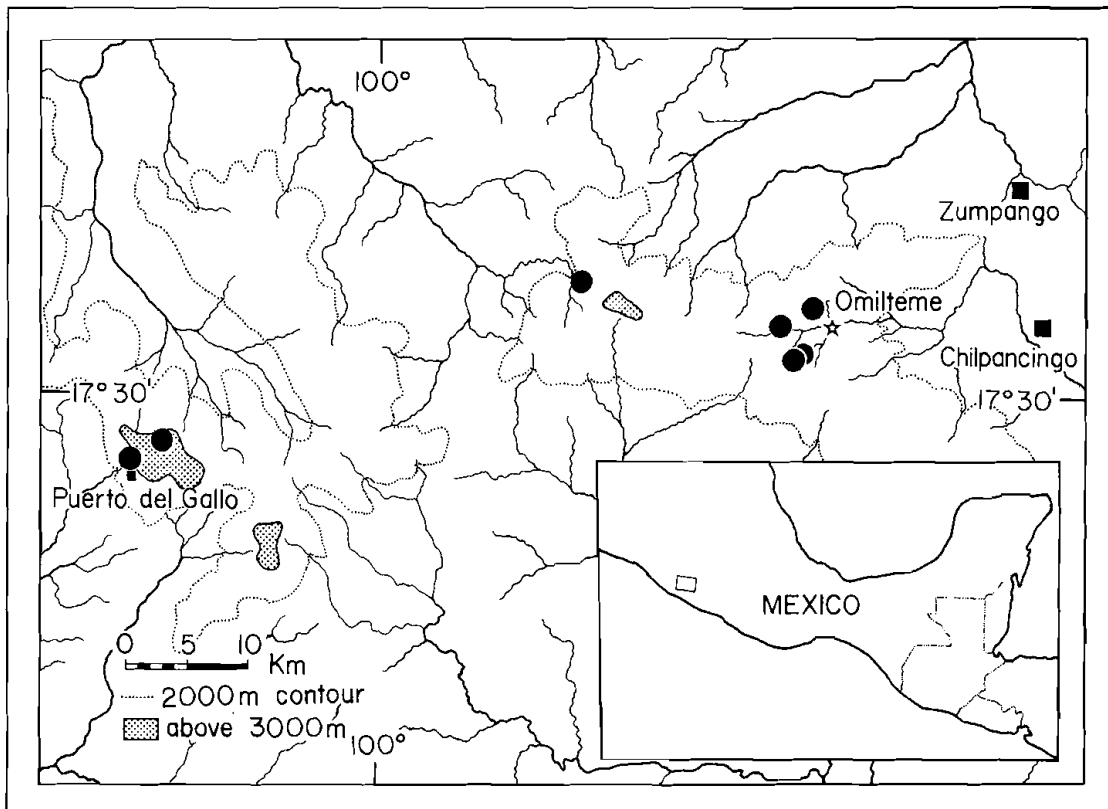


Figure 1.

Locality records (closed circles) for *Porthidium barbouri* in the Sierra Madre del Sur of Guerrero, México. Questionable localities are not included. Star, type locality at Omilteme; squares, pertinent towns.

this species, and may represent the greatest elevation achieved by the genus. Only *P. godmani* of southern Mexico and Central America is known to reach comparable elevations, with a recorded maximum of 3,200 m.

The highlands of the Sierra Madre del Sur in Guerrero are bounded to the south by the Pacific coast and are separated from the Mexican Plateau to the north by the arid Río Balsas depression. The highway from Mexcala to Acapulco roughly follows one of the low passes that separate the Guerrero highland mass from that of Oaxaca. The pass is xeric but there are pines (*Pinus oocarpa*) and fan palms on a few nearby ridges; these species apparently thrive in drier climates and were not observed at Omilteme. A number of peaks in the Sierra Madre de Sur in Guerrero reach elevations exceeding 3,000 m, Cerro Teotepec (approximately 3,550 m) being the highest.

The actual lumber camp of Omilteme is surrounded by a forest of pine-oak (*Pinus herrerae*, *P. pseudostrobus*, *Quercus* spp.). Despite intensive collecting over a period of three years (1973-1976), I did not find *P. barbouri* in this type of habitat. However, three adult specimens were found at higher elevations short distances from Omilteme in cloud forest (Fig. 2). Davis and Dixon (1959), on the basis of a specimen taken on a rocky ridge in the pine-oak forest, reported "this species apparently is not restricted to the cloud forest as previously thought" and suggested that its range was coextensive with that of *Crotalus intermedius*. Another specimen reported by these authors was taken in a humid canyon within the cloud forest.

The nature of the vegetation type on the mountains nears Omilteme is highly dependant on exposure as well as elevation. The prevailing winds in Guerrero, laden with moisture picked up from the Pacific Ocean, are from the southeast the year round (Page, 1930). As a result, the Pacific-facing slopes of the Sierra Madre del Sur tend to be considerably more humid than the northern slopes that drain into the Balsas Depression and possess a denser vegetation. At the higher elevations, cloud forest occurs on the windward side of the mountains while on the leeward side at a corresponding altitude pine-oak forest prevails. Limestone outcroppings often line the crests of these mountains.

From the information at hand, it is apparent that *P. barbouri* is usually an inhabitant of the thicker, more mesic cloud forest (the Humid Upper Tropical Subzone of Goldman 1951), but owing to the

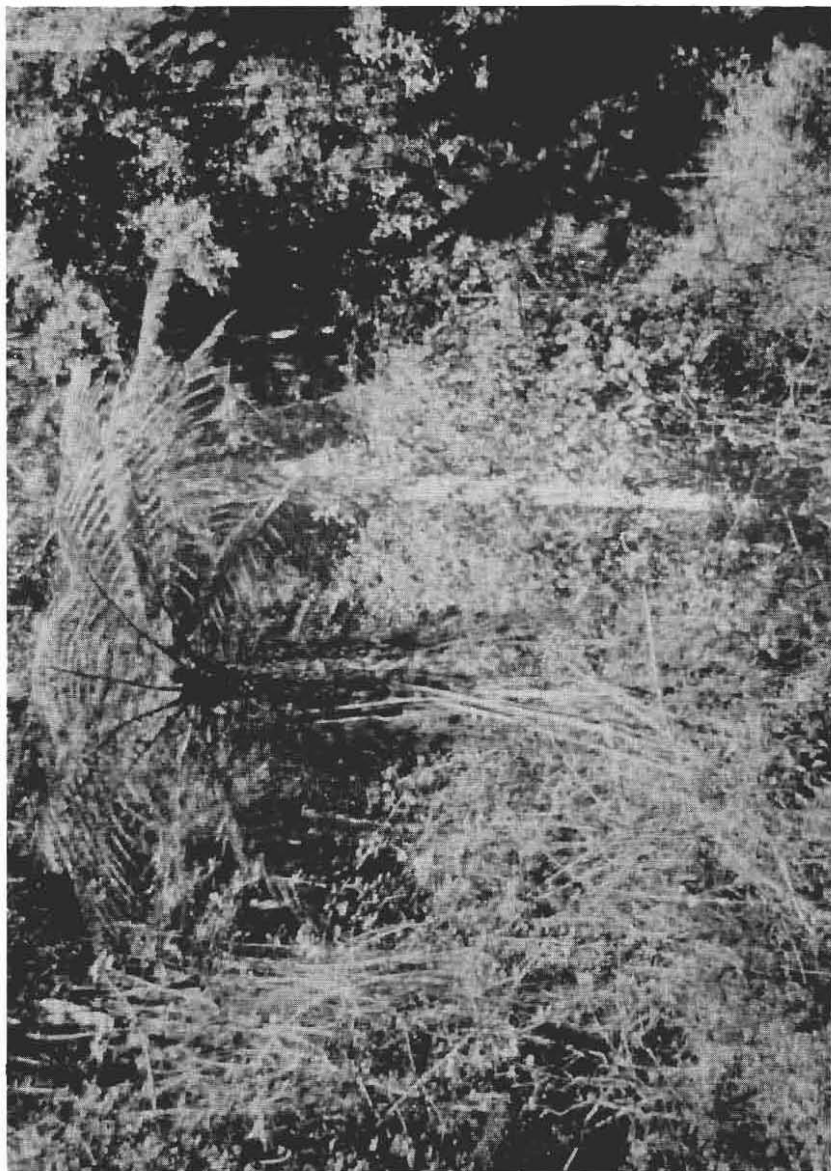


Figure 2.

Cloud forest habitat of *Porthidium barbouri*, 2.0 kilometers northwest of Omilteme, Guerrero, México, 2,560 meters elevation. Tree ferns are characteristic of this forest. Photo taken in May 1973.

tight interdigitation of pine-oak and cloud forests in some areas, it may occasionally invade pine-oak forests. Also, it may be present in sheltered humid canyons surrounded by pine-oak forests that contain flora typical of southeastern slopes.

On the highest peaks, the cloud forest begins to thin out at approximately 2,600 m, giving way to a forest principally of firs (*Abies religiosa*), pines, and oaks (Goldman 1951). One specimen of *P. barbouri* was secured basking near a large log in fir-pine-oak forest near Puerto del Gallo (UTA R-4450), and another was taken in bunchgrass on the sparsely wooded southern slope of Cerro Teotepec (KU 182762). These records indicate that the species, although hardly wide-spread, at least inhabits several recognizable vegetation associations.

In the mountains of Guerrero over 90% of the yearly precipitation falls between May and October, and the mean annual rainfall was recorded as being between 1,500 and 2,000 mm (Page 1930). These figures are for the pine-oak zone and the amount of precipitation received in cloud forest is presumed to be somewhat higher.

Co-occurrence of *P. barbouri* with other crocodyline snakes is rare. *Sistrurus ravus exiguus*, *Crotalus intermedius omiltemanus*, and *Ophryacus undulatus* inhabit in the mountainous regions of Guerrero, but are most frequently encountered in pine-oak forests at elevations of 1,950-2,300 m. *Sistrurus* appears to be restricted in the region to relatively flat, bushy valley bottoms (Campbell and Armstrong 1979). *Crotalus* and *Ophryacus* prefer the open, rocky hillsides which abound in the pine-oak zone, but individuals of both species occasionally disperse into cloud forest or reach higher elevations in areas of open forest. *Crotalus intermedius* has been observed on a rocky mountain crest near Cerro Teotepec at over 3,000 m.

Much of the forest covering the Guerrero highlands was destroyed by an extensive fire in 1982-1983. Although the effect this burning had on populations of *P. barbouri* is not known, the outlook for the continued survival of this species over most of its range does not appear to be good.

VARIATION

Twenty specimens of *P. barbouri* were available for study, 14 of which have data indicating that they or their parents came from the environs of Omilteme. The others were labeled "Chilpancingo," but as previously observed, were probably collected near Omilteme. No obvious differences were noted for the three specimens from near Puerto del Gallo, and they were included with the others in the analysis of variation for this species (see Appendix II). I have not examined the holotype of *P. barbouri* nor have I included data given in the original description (Dunn 1919). Most characters given for the holotype fall within the range of variation presented below. However, the sex was not stated and it was purported to have 154 ventrals and 32 subcaudals, higher numbers than I have observed in the species. These counts require verification; it is possible that they include preventrals and the paranals.

Sex Related Variation. - Differences in lepidosis and proportion were noted between the sexes. Sex was determined for all specimens of *P. barbouri*, either by eversion of the hemipenes during preservation or by making small incisions on the tail of preserved specimens. There were eleven males and nine females. The number of ventrals differed slightly between sexes: males had 130-138 ($\bar{x} = 134.2$) and females possessed 129-145 ($\bar{x} = 138.7$). Unlike most snakes, little sexual dimorphism is apparent in the number of subcaudals. Males have from 27 to 31 ($\bar{x} = 29.8$) and females range from 26-30 ($\bar{x} = 28.4$). However, males have proportionally longer tails than females. A scatter diagram of tail versus body length is given in Fig. 3; the fit for both linear and exponential models (Fig. 3) is good ($P < 0.0001$). The tail comprises from 11.3 to 12.9% ($\bar{x} = 12.1\%$) and from 10.1 to 11.4% ($\bar{x} = 10.9\%$) of the total length in adult males and females, respectively. The hemipenes of two specimens were inverted to the levels of subcaudals 8 and 12, with hemipenial bifurcation occurring at the levels of the fourth and fifth subcaudals, and the *m. retractor penis magnus* bifurcating at the level of subcaudals 10 and 14, respectively. Anal glands in two females extend to subcaudal 6.

Ontogenic Variation. - In juvenile *P. barbouri*, the posterior edges of the dorsal body scales are more rounded posteriorly and the dorsal scales are less strongly keeled than in adult specimens. Not only do the dorsal scales become more acute as the snake matures, but the tail spine becomes more pointed and longer. At birth, the tail spine

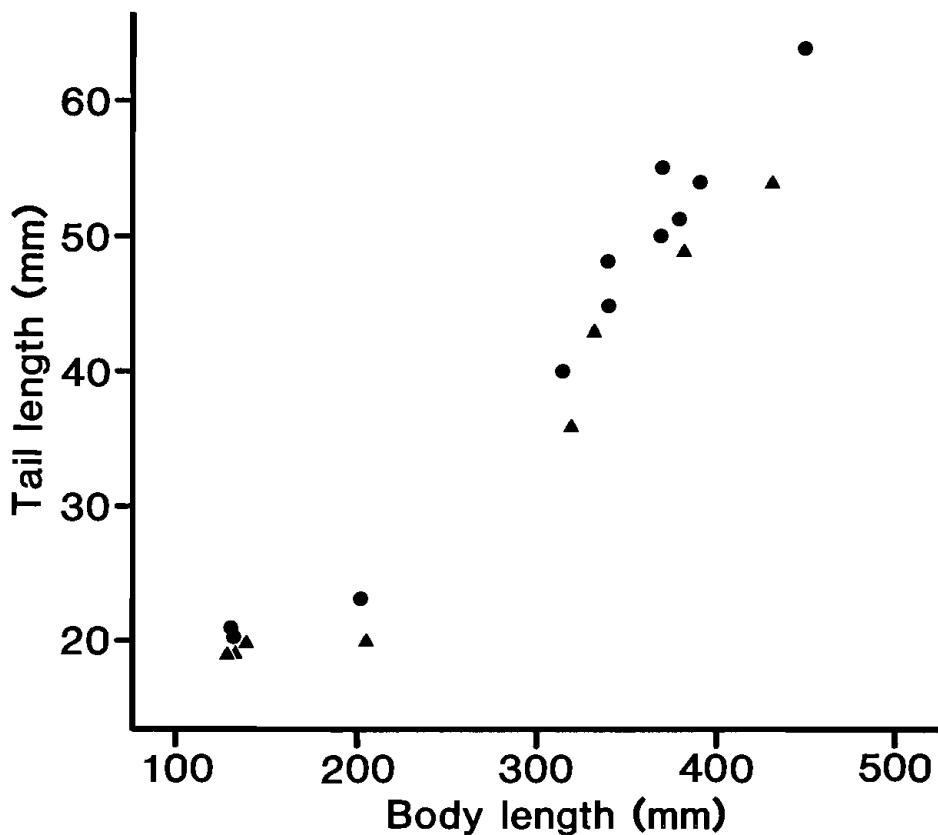


Figure 3.

Scatter diagram of tail length versus body length in male and female *Porthidium barboursi*. Body lengths in millimeters are indicated on the horizontal axis. The vertical axis is the tail length in millimetres. Males are represented by open circles, females by open triangles.

averages between 2 and 2½ subcaudals in length and increases to a length of between 3 and 4 subcaudals in most large specimens.

Klauber (1938) demonstrated that head to body length comparisons in rattlesnakes were best represented as a simple linear equation, $H = aL + b$, where H = head length, L = body length, a = slope, and b = y -intercept. In the same study, colubrid head proportions were found to vary from the rattlesnake mode in some instances where an exponential equation best suited the head-body length relationship. *Porthidium barbouri* is similar to rattlesnakes in these proportions. The ratio of head to body length is not constant. Juveniles have larger heads; the head length comprises an average of 8.78% of the body length for six newborn snakes, whereas in adult specimens only 5.0-6.5% of the body length is represented by the head. The proportionally larger heads of the small snakes are no doubt of benefit in swallowing prey. The regression line for *P. barbouri* is represented by the equation $H = 0.0425L + 6.2007$.

Individual Variation.- The following variation, neither sex nor age related, was noted in *P. barbouri*. There are invariably 1/1 loreals in all specimens examined. The loreal is relatively large, and contacts the postnasal and canthal anteriorly, the upper preocular and supraocular posteriorly (a unique character, insofar as I know, for New World pitvipers), the prefrontal (which is sometimes divided) above, and the supralacunal, prelacunal, and prefoveal below (Fig. 4). A supra-, pre-, and sublacunal are present. The supralacunal does not extend to the orbit. There are 0-7 prefoveals (with most commonly 2 to 4), 0-2 subfoveals (most frequently none), and 0-1 postfoveals (usually none). The middle preocular is small and azygous with the supralacunal. The middle preocular is usually completely excluded from the orbit so that only 2/2 preoculars (the upper and lower) form the anterior edge of the orbit (Fig. 4). In contrast, *P. godmani* has a supralacunal and middle preocular that are separated by a vertical suture, and the sublacunal and anterior subocular are in contact. The subocular scales do not show as strong a tendency toward fusion as in *P. godmani*, 2 to 5 being recorded in *P. barbouri* at the following frequencies: 2 (30%), 3 (14%), and 5 (15%). From 1 to 4 postocular scales may be present, with the following frequencies for all specimens examined: 1 (2.5%), 2 (55%), 3 (42%), and 4 (12.5%). There are from 7 to 10 supralabials in the following frequencies: 7 (7.5%), 8 (50%), 9 (40%), and 10 (2.5%); and from 8-11 infralabials occur in the following frequencies: 8 (2.5%), 9 (50%), 10 (40%), and 11 (2.5%). The

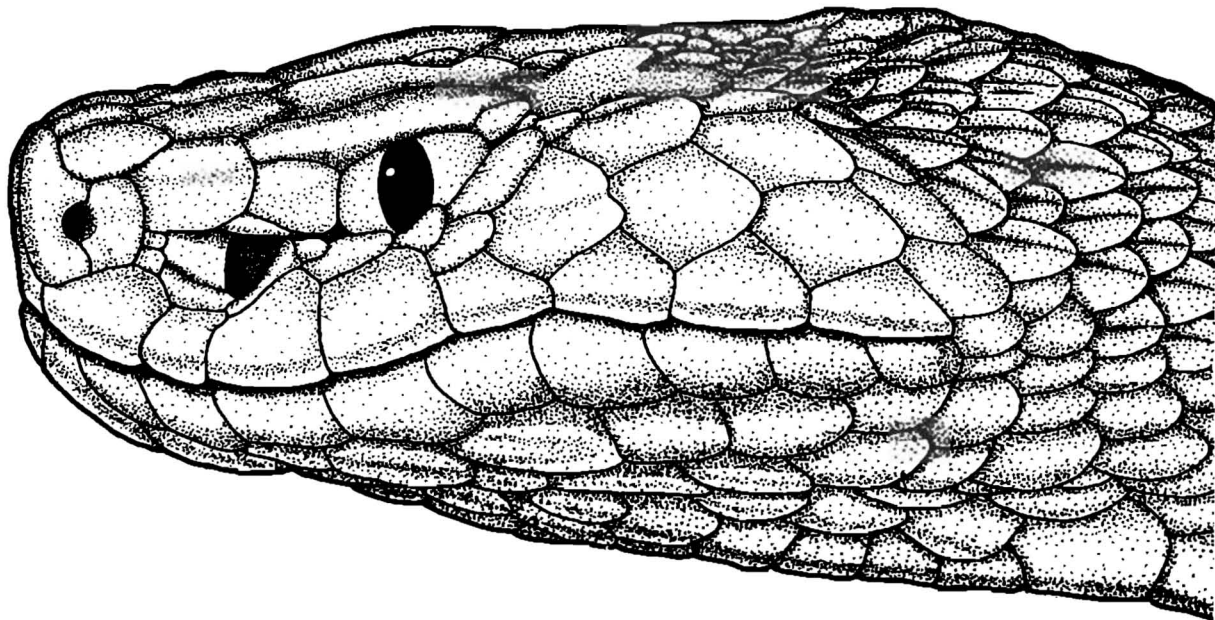


Figure 4.

Lateral aspect of head of *Porthidium barboursi*, adult male, UTA R-4450, collected 0.8 kilometers north of Puerto del Gallo, Guerrero, México, 2,896 meters elevation.

oculabial series is incomplete, with usually two supralabials in contact with the suboculars.

To my knowledge, the number and arrangement of the scales on the top of the head of *P. barbouri* are more variable than those reported for any other snake. At one extreme, a distinctly colubrid-like arrangement is present with a total complement of 11 scale including paired internasals, prefrontals, supraoculars, parietals, and canthals and a single frontal (Fig. 5a). This condition differs from the primitive 9 head shield condition found in crotalines such as *Agkistrodon* and *Sistrurus* in that an extra pair of scales, the canthals, is present and the parietals are separated from one another by small scales. Conversely, some specimens have extremely fragmented head scales with no well defined, large prefrontals, frontal, or parietals (Fig. 5d). In these specimens the internasals, canthals, and supraoculars are present, but are smaller than in specimens with undivided head plates. In contrast to scales from colubrid-like specimens, many of the scales in the prefrontal, frontal, and parietal areas have from one to three keels. Intermediate conditions also exist, with partial fragmentation of the prefrontals, frontal, or parietals (Figs. 5b and c). Nine of 20 specimens had large frontals that were in contact on either side with the supraoculars; these specimens all had large prefrontals and parietals, although in some the scales were slightly fragmented. There were fewer scales on top of the head in the postparietal region in these specimens.

One male specimen (UTA R-15558) was maintained alive in the laboratory for over ten years and reached a total length of 512 mm. Several snakes, males and females, were preserved immediately after capture and measured between 420 and 484 mm in overall length. If any sexual size dimorphism exists in this species, it is not apparent with existing data.

Dorsal Scale Reductions.- The abbreviated dorsal scale reduction formulae for this species are 21(20)-19-15(14) (7 specimens), 21-17-15 (8 specimens), and 19-17-15 (4 specimens). One snake has dorsal scales disposed in 23-21-15 longitudinal rows. The complete scale reduction formula for UTA R-4450 is:

$$21 \frac{4+5(11)}{4+5(11)} \quad 19 \frac{4+5(90)}{4+5(92)} \quad 17 \frac{3+4(114)}{4+5(128)} \quad 15(140)$$

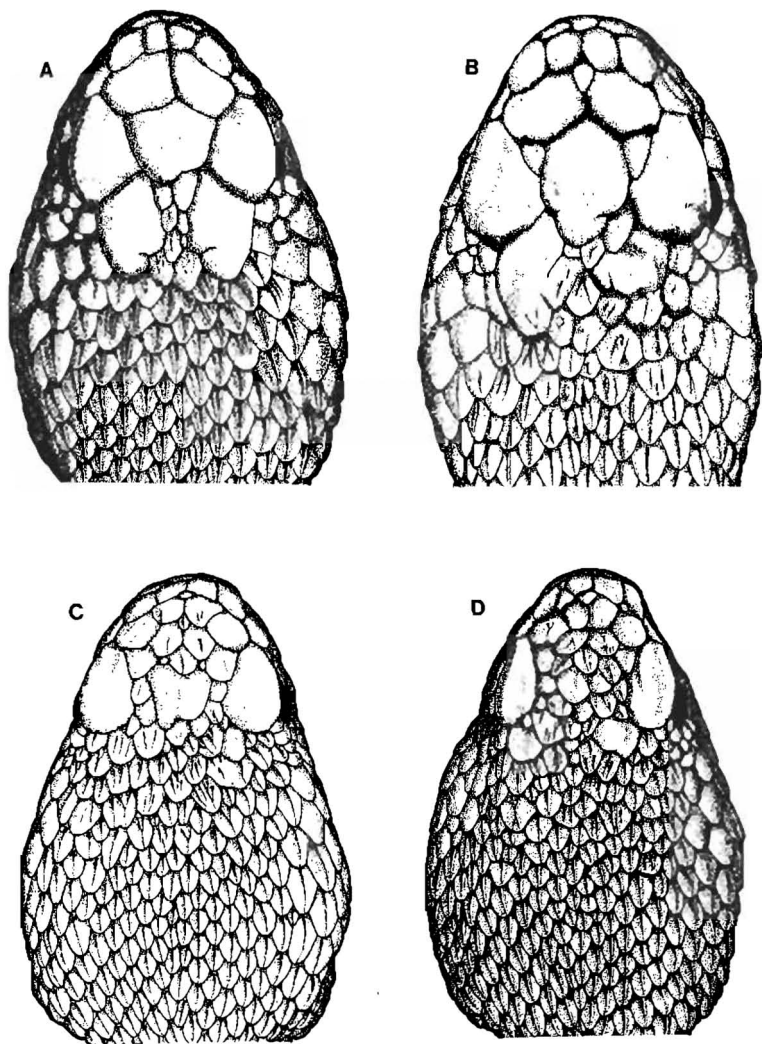


Figure 5.

Variation of dorsal head scales in *Porthidium barbouri*; all from Guerrero, México. A. MVZ 45253, adult male, "near Chilpancingo". B. UTA R-4450, adult male, 0.8 km N Puerto del Gallo. C. MCZ 43283, adult male, Omilteme. D. TCWC 9455, adult female, 3.2 km W Omilteme.

Tooth Numbers.- Three specimens of *P. barbouri* each have 3 palatine and 10 dentary teeth; pterygoid teeth vary from 10 to 12.

Color and Pattern.- The pattern and color of *P. barbouri* were reported from alcoholic specimens by Dunn (1919) and Shreve (1938). The type of *P. barbouri* was described as dull olive with no mention of a dorsal pattern (Dunn 1919). Shreve (1938) described *Agkistrodon browni* (= *P. barbouri*) as having a brownish ground color with a dorsal pattern of pale-edged chevrons. The only report of live specimens is that of Davis and Dixon (1959) where two adult specimens were described as "deep brown with darker brown crossbands." Although variations occur in the pattern of *P. barbouri*, a re-examination of the type and paratype of *A. browni*, as well as the Davis and Dixon specimens does not verify the descriptions given by previous authors. Because life colors disappear quickly in preservative and the brief descriptions of pattern provided heretofore are inaccurate, notes on individuals of this rare snake, taken from life, are provided below. References to particular colors are those taken from the color plates of Maerz and Paul (1950).

An adult male (UTA R-15558; Fig. 6) collected 2.5 km SW Omilteme: ground color pewter (pl. 48, L-3); dark brown, ill-defined dorsal zig-zag stripe narrowly bordered with black; 27/26 dark brown lateral body blotches, rounded above and extending to ventrals; first lateral body blotch extending posteriorly from back of head for 10 scale lengths along the side of body; 3/2 pale, staggered, vertical bars on tail extending to dorsal midline; venter mahogany with black stippling becoming more intense posteriorly; dark brown postocular stripe; area below postocular stripe, including supralabials, pinkish with fine brown stippling; small brown subocular spot; infralabials dark brown with 4/5 vertical pale markings in centers of infralabials.

An adult female (UTA R-6231), collected 2.0 km NW Omilteme: similar to the male described above in pattern and coloration except for the following: 28/28 dark brown lateral body blotches, first extending 12/17 scale lengths posteriorly; venter pink with 4/4 pale, staggered, vertical bars extending to dorsal midline; supralabials pinkish beige; 6/6 pale vertical markings on infralabials; iris brownish yellow with fine black stippling.

An adult male (UTA R-4450), collected 0.8 km N Puerto del Gallo: ground color copper brown (pl. 6, 11-C); dark Indian red

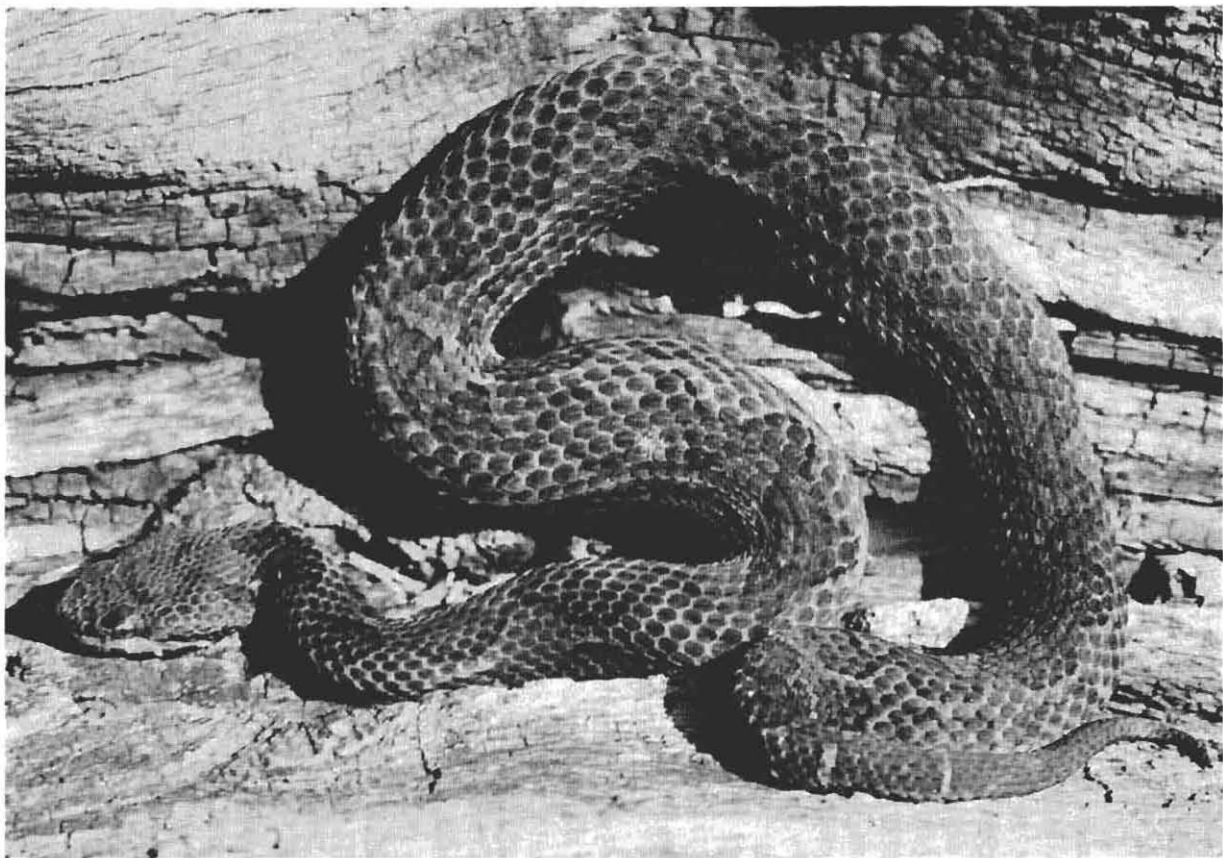


Figure 6.

Adult male *Porthidium barboursi*, 512 mm total length (UTA R-15558), collected 2.5 kilometers southwest of Omilteme, Guerrero, México, 2,490 m.

(pl. 6, 12-L) dorsal blotches, sometimes fused to form a zig-zag pattern, narrowly edged with black; anterior lateral body blotches, and postocular stripe same color as dorsal blotches; posteriorly, lateral blotches becoming almost indistinguishable from ground color; medial, elongate nape blotch with blotches on either side, extending from parietal region to back of head; venter bright pinkish salmon, progressively more darkly stippled with black posteriorly; 6/5 pale tail bars; 5/5 pale infralabial markings.

Juvenile *P. barbouri* color and pattern differ from those of the adults and are described here for the first time. Six young (UTA R-6181-6183 and 6237-6239) born in captivity to a female from near Omilteme (UTA R-6231) permit the following observations of juvenile color and pattern (Fig. 7): pattern much more distinct than that of adult; dorsal ground color brownish green (Pl. 15, 9-L); dorsal pattern consisting of dark brown blotches, almost all of which are fused to form a zig zag pattern; postocular stripe and lateral body blotches dark brownish gray, almost black; lateral body blotches separated from each other by pinkish yellow, separated from ventrals by pinkish edging on ventrals (not present posteriorly in several specimens); postocular stripe narrowly pale-bordered below; top of head and paired nape blotches dark brown; infralabials and gular region dark gray except for 4-6 prominent pink vertical markings centrally located on posteriormost infralabials; venter dark gray except for pinkish edging on most ventrals (more evident anteriorly); proximal portion of tail with 3-6 pinkish yellow vertical bars extending to dorsal midline; distal half of tail chartreuse; iris color of bronze.

FOOD AND FEEDING BEHAVIOR

Food records were obtained for six adult specimens of *P. barbouri* (body lengths from 315 to 448 mm). Four these specimens were collected in May or June, one was collected in late September, and no date is available for one specimen. Three of these specimens, all from the vicinity of Omilteme (MCZ 426578, 43283; TCWC 9455), contained rodent hair, and another (UTA R-15558) disgorged an adult *Barisia gadovii* (UTA R-2843) upon capture. The lizard had been swallowed



Figure 7. Juvenile *Porthidium barbouri*, 154 mm total length (UTA R-6238), captive progeny of parents collected near Omilteme, Guerrero, México.

head first. The scat of a specimen captured near Puerto del Gallo (UTA R-4450) contained scales clearly belonging to *B. gadovii*. The stomach of a specimen from Asoleadero, about 20 km WNW of Omilteme, contained a small unidentified mouse that had been swallowed head first.

Field observations indicate *P. barbouri* is diurnal. Two specimens, of *P. barbouri* from near Omilteme were found coiled in leaf litter during the late morning hours in areas where small patches of sunlight penetrated the dense cloud forest. *Barisia* were often seen basking in these same situations. Owing to their great abundance and availability, *Barisia gadovii* probably constitute an important portion of the diet of *P. barbouri*. The Puerto del Gallo specimen (UTA R-4450) was taken coiled in the sun at 1600 hrs next to a large log, underneath of which two *Barisia* were found. In May 1975, a specimen was seen near Omilteme at about 10:30 a.m. The snake was basking about a meter from the ground on an old pine stump. Another *P. barbouri* was observed 21 June 1976 at 11:00 a.m. at a locality 6.5 km W Omilteme for over five minutes. The snake was actively foraging in leaf litter around the edge of an open, marshy area where water seeped from the side of a hill. The snake was observed to move slowly around the edge, venturing several times out of the leaf litter into the short grass. Twice the snake closely approached an adult *Barisia*, five or six of which were basking in the leaves, but in each instance the lizard escaped. Each time a lizard scurried away, the snake raised its head slightly from the ground with its neck flexed in a sigmoid curve and became motionless except for rapid tongue flicks. After 15-20 seconds, the snake resumed its search.

Nothing is known concerning the feeding habits of young *P. barbouri*; they may also prey heavily on *Barisia*, particularly juveniles. The population density of this lizard reaches its maximum peak in the Sierra Madre del Sur of Guerrero during mid to late May, coincident with the first heavy rains in the area. In a series of 24 females taken from 15 to 27 May in 1974 and 1975, six still retained two to nine ($\bar{x} = 6$ almost) fully developed young. Eleven females taken during this period measured 30 to 37 mm ($\bar{x} = 33.4$ mm). Davis and Dixon (1961) reported five females from Guerrero collected in June, none of which had ova larger than one millimeter in diameter. Their data are consistent with that from specimens I have taken in June and July at Omilteme. *Norops liogaster* and *N. omiltemanus* are frequently encountered in the cloud forest near or on the ground and are likely to be common prey for young *P. barbouri*.

A litter of six *P. barbouri* born in the laboratory were never induced to feed although they were offered a variety of food items, including crickets and lizards of the genus *Norops*.

REPRODUCTION

Data for a captive breeding of a pair of *P. barbouri* that I collected near Omilteme was presented by Murphy and Mitchell (1984). The female gave birth to 6 young (UTA R-6181-83, 6237-39) on 20 November 1976 after a gestation period of at least six months. These young ranged from 132-138 mm (\bar{x} = 134.3 mm) in body length, from 152-158 mm (\bar{x} = 154.0 mm) in total length, from 19-21 mm (\bar{x} = 19.6 mm) in tail length, and from 3.50-4.05 g (\bar{x} = 3.70 g) in weight. The tail comprised from 12.3 to 13.7% (\bar{x} = 12.8%) of the total length.

A female *P. barbouri* (TCWC 9455) collected 3.2 km W Omilteme in June 1953 had a body length of 430 mm and contained enlarged, maturing ovarian follicles. The ova appeared to be of three distinct size classes: three measuring from 10.3 to 11.5 mm in length (\bar{x} = 10.9 mm) and 6.0 to 6.3 mm in diameter (\bar{x} = 6.2 mm); four measuring from 4.6 to 8.5 mm in length (\bar{x} = 6.8 mm) and 3.2 to 4.1 mm in diameter (\bar{x} = 3.8 mm); and about six small ova less than 2.0 mm in length. The larger size class may have represented maturing follicles for the proximate reproductive cycle. Juvenile specimens collected on 6 August (KU 182762) and 29 December 1971 (CAS 134466) were 225 and 202 mm in total length, respectively. The umbilical scar is clearly evident and these snakes almost certainly are not more than a few months of age. These fragmentary data suggest that *P. barbouri* gives birth during the middle to late rainy season, after the reproductive season of such reptile species as *Barisisa gadovii*.

RELATIONSHIPS OF *Porthidium barbouri*

Composition and distribution of Porthidium godmani group. - The terrestrial genus *Porthidium* is composed of 14 species (Campbell and Lamar 1989) and includes several distinct lineages, (a) the

lowland hog-nosed pitviper group (7 spp.), (b) the stout-bodied jumping pitviper, *P. nummifer*, and its allies (3 spp.), (c) *P. melanurum*, and (d) the montane pitvipers. *Porthidium barbouri* is a member of the montane pitviper group, which consists of two other species of Middle American pitvipers (*P. godmani* and *P. tzotzilorum*). *Porthidium barbouri* is the northernmost representative of this group (hereafter referred to as the *P. godmani* group).

Each of the first three of these lineages is characterized by several derived characters that establish the monophyly of these groups. However, many of the features shared by members of the *P. godmani* group may be primitive and therefore are of no use in identifying these species as a monophyletic evolutionary lineage. Several of the features suggested to unite the *P. godmani* group are the presence of small paired apical scale pits (reportedly absent in hog-nosed pitvipers), the hyoid skeleton with relatively long branchials (second ceratobranchials according to some authors), and the basal portion of the pterygoid as long or longer than the ectopterygoid (Burger, 1971). Of these features, the first two are possibly plesiomorphic, but the latter is probably derived. I currently am inclined to recognize the *P. godmani* group as a monophyletic lineage, albeit somewhat tenuously.

The most widespread species within the *P. godmani* group is *P. godmani* whose distribution extends across the Nuclear Central American highlands from southeastern Oaxaca to northern Nicaragua. A major hiatus in its range occurs in the Nicaraguan lowlands, but the species is present in Isthmian Central America from the western portion of the Cordillera Central in northcentral Costa Rica to the southwestern portion of the Cordillera de Talamanca in northwestern Chiriquí Province in Panamá. This species inhabits pine-oak and cloud forest at elevations of 1,420-3,200 m.

A third species, *P. tzotzilorum*, occurs on the Mesa Central of Chiapas and may be sympatric there with *P. godmani* (Campbell 1985). This species is known from the San Cristóbal de Las Casas region across the Mesa to a little east of Teopisca. It has been collected in humid pine-oak forest and almost pure stands of pine at elevations of 2,200-2,750 m.

Outgroup comparisons.- For outgroup comparison I have examined members of the predominantly Central American "hog-nosed" pitviper group that contains *P. nasutum*, members of the

group that contains *Bothrops asper*, and members of the arboreal genus *Bothriechis*.

Character analysis.- The number and arrangement of the scales covering the top of the head is extremely variable among New World pitvipers. Most specimens of *P. barbouri* have distinctly enlarged, flattened scales arranged in a pattern resembling the typical colubrid conditions. However, the condition found in *P. barbouri* differs from that of most colubrids, *Agkistrodon*, and *Sistrurus* in having an extra pair of scales, the canthals, and in that the parietals, if enlarged, are usually separated from each other by small scales (Fig. 5). *Porthidium godmani* and *P. tzotzilorum* usually have enlarged scales in the frontal and parietal regions, but these enlarged scales tend to be bordered by small keeled scales and the scales of the crown are more fragmented overall than in *P. barbouri*.

There are most frequently eight supralabials in *P. barbouri* whereas there are nine in *P. godmani* and *P. tzotzilorum*. Because a low number of supralabials characterizes snakes of the genus *Agkistrodon* and most members of the *Bothrops asper* group, I consider the higher number derived. The number of scale rows at midbody is generally 21 in *P. godmani* and *P. tzotzilorum* and 17 in *P. barbouri*. Whereas a number of Neotropical pitvipers have 21 midbody scale rows, 17 as a modal number is apparently unique to *P. barbouri* and seems to be derived. All species in the *P. godmani* group have relatively few ventrals and subcaudals. Only a few other stout-bodied species of *Porthidium* possess a comparable number of ventrals and subcaudals including some members of the *P. nasutum* and *P. nummifer* groups (the latter appears to be closely related to the *P. godmani* group). Several interesting trends relating to the number of ventrals and subcaudals in males and females of the various species in the *P. godmani* group are apparent. Most species of snakes are sexually dimorphic with regard to the number of ventrals and subcaudals, with females possessing more ventrals and fewer subcaudals than males. However, no such sexual dimorphism is present in *P. godmani* with respect to the number of ventrals, or in *P. barbouri* and *P. tzotzilorum* with regard to the number of subcaudals; I regard the absence of sexual dimorphism as derived and possibly related to the somewhat dwarfed condition of this highland-adapted group of snakes. The mean number of ventrals is significantly less in *P. tzotzilorum* than in the other two species, and is lower than any species of Neotropical pitviper except

for *P. nummifer* and *P. olmec*. The number of teeth borne by the palatine, pterygoid, and dentary in members of the *P. godmani* group is comparable to *P. nummifer*, members of the *P. nasutum* group, and some species of *Bothriechis*; *Porthidium melanurum* and *Ophryacus undulatus* tend to have fewer, and the large terrestrial species of *Bothrops* tend to have more. The relatively low number of teeth in *P. barbouri* and *P. tzotzilorum* seems to be plesiomorphic.

Regression equations that express the relationships between the head and body lengths of members in the *P. godmani* group are presented in Table 1. *Porthidium tzotzilorum* possesses a relatively long head and that of *P. barbouri* is short. Differences of the head to body length relationship among these three species are highly significant. Plotting values for individual specimens of other species reveals that the heads of *P. godmani* and *P. tzotzilorum* are relatively large for Neotropical pitvipers; I consider this a derived character.

Relationships.- The *P. godmani* group represents an endemic Middle American element. The closest relationships of the group are probably to be found in other Central American pitvipers such as the *P. nasutum* group. The monophyletic lineage considered herein as *Bothriechis* may be the sister-group to *Porthidium*. Within the *P. godmani* group there is ample evidence that the Mexican isolate *P. barbouri* is the sister-species to the widespread *P. godmani* and *P. tzotzilorum*, which is isolated on the Chiapan Plateau. The latter two species share a greater number of head plates, supralabials, and teeth; further, they both have relatively long heads. A hypothesis of the relationships of the *P. godmani* group is presented in Fig. 8.

DISCUSSION

Based on their similar morphology, *Porthidium barbouri*, *P. godmani*, and *P. tzotzilorum* appear to be close allies, although their monophyly is yet to be clearly demonstrated (Campbell 1985, Campbell and Lamar, 1989), and perhaps were derived from a common ancestor that was once more widely distributed in the lowlands of Middle America. Assuming they comprise a distinct lineage, their ancestor may have already begun to invade the uplands when populations ancestral to the three species became isolated from each other by physical or ecologi-

Table 1

Comparison of certain features in species for the *Porthidium godmani* group. See text for details. The range of means for *P. godmani* is based on eleven samples taken from populations throughout its range. *indicates mode.

Characters	<i>P. barbouri</i>	<i>P. godmani</i>	<i>P. tzotzilorum</i>
1. Head scales between supraoculars	1-4(1*)	3-7(5*)	3-5(3*)
2. Supralabials	7-10(8-9*)	7-13(9*)	9-11(9*)
3. Dorsal scale rows	21-17-15*	23-21-17*	23-21-17*
4. Ventrals (males)	130-138(134.2)	130-148(136-144)	120-135(126.9)
(females)	129-145(138.7)	130-148(136-146)	125-134(129.2)
5. Sexual dimorphism (females with significantly greater number of ventrals)	Present	Absent	Present
6. Subcaudals (males)	27-31(29.8)	26-36(28-35)	27-31(29.2)
(females)	26-30(28.4)	23-34(25-32)	26-32(28.3)
7. Sexual dimorphism (males with significantly greater number of subcaudals)	Absent	Present	Absent
8. Teeth (palatine)	3	4-5	4
(pterygoid)	9-12	14-18	11-13
(dentary)	8-10	13-16	13-14
9. Relationship between head (H) and body length (L)	$H = 0.0425L + 6.2007$	$H = 0.0498L + 5.9648$	$H = 0.0444L + 8.7576$

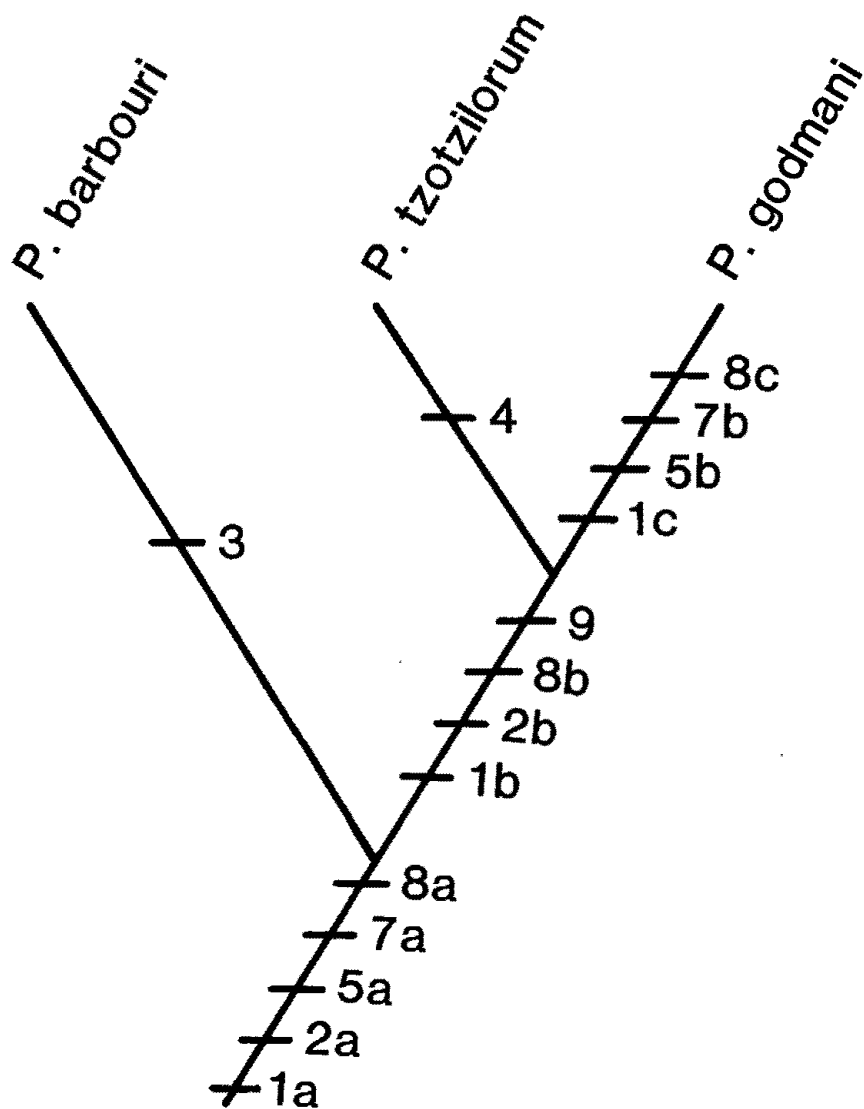


Figure 8.

A hypothesis of the relationships of the *Porthidium godmani* group. Numbers refer to characters given in Table 1. See text for discussion.

cal barriers in the Isthmus of Tehuantepec region during the Miocene or early Pliocene. *Porthidium godmani* probably evolved in the Nuclear Central American highlands (Savage 1966) as ancestral populations, uplifted by orogenic events in the late Miocene-early Pliocene (Stuart 1950, 1951), gradually adapted to the prevailing cool environments of the higher elevations. It seems unlikely that *P. godmani* or *P. tzotzilorum* could have evolved in the warm and only moderately elevated uplands present prior to that time. The Pliocene orogeny provided the requisite environmental conditions for differentiation of a highland species from a lowland ancestor (Stuart 1951). The presence of Miocene sediments found at 2,286 m elevation on the Meseta Central de Chiapas give some indication of the amount of uplift starting in Pliocene time (Schuchert 1935).

Porthidium barbouri probably evolved in the Sierra Madre del Sur west of the Isthmus. Depression of temperatures during glacial maxima allowed the development of wide-spread coniferous forests and distributions of many highlands species were maximized at this time. A gradual increase in temperatures and the development of more mesic conditions in recent times, particularly along the Pacific coast, has eliminated these forests over much of their former areas. *Porthidium barbouri*, *p. godmani*, and *P. tzotzilorum* occur only in cloud forests or pine-oak forests and, even though the range of *P. godmani* is rather extensive, they are best considered isolated relicts.

The employment of the low ridge that forms the Continental Divide across the Isthmus of Tehuantepec as a dispersal route by montane species of amphibians during the Pleistocene has been suggested by Duellman (1960). No continuous corridor of montane forest (pine, pine-oak, cloud, or fir) at present connects the two highland masses on either side of the Isthmus. A few species show little or no differentiation on either side of the Isthmus, while other species having affinities with one another such as *P. barbouri*, *P. tzotzilorum*, and *P. godmani* strongly suggest a longer isolation as inferred from their level of divergence. Stuart (1954) suggested that populations of the genera *Hyla* and *Cnemidophorus* were isolated by barriers in the Isthmus region in the Pliocene and have since differentiated into distinct species. Conversely, the similarity of the populations of *P. godmani* in the two widely separated Central American highland blocks suggests a comparatively recent isolation.

Certainly, for the most part, the herpetological assemblages of the highlands of Nuclear and Isthmian Central America

are distinctive from one another. The similarity of these highland faunas is slight apparently owing to the unique geological history of each of the areas of because of the absence of dispersal routes adequate for most species. The few species of snakes common to both highlands tend to show considerable vagility. Scott (1969) recorded only three snakes, *P. godmani*, *Bothriechis nigroviridis*, and *Rhadinaea godmani*, as being common to the herpetofauna of both highland areas. Highland populations of *Bothriechis* from Nuclear Central America previously considered to be *B. nigroviridis* were subsequently shown to be specifically distinctive from that species (Campbell and Lamar 1989).

To what levels various vegetational zones were lowered by Pleistocene climatic events remains obscure. Disparate speculations have been set forth concerning temperature depression during the Pleistocene, but probably a maximum temperature reduction from mean annual temperature of no more than 6°C (Savage 1966) to 8°C (Flint 1947) occurred in Central America. The spread of highland species onto the southern highland block may have occurred in early Pleistocene prior to the development of xeric conditions that characterize the Pacific coast of much of México and Central América to northwestern Costa Rica. Moisture would appear to be a limiting factor, particularly in the oviparous *Rhadinaea godmani* in which the eggs would be susceptible to desiccation. That *P. godmani* reaches its lowest vertical distribution in the most mesic portions of its range and that *P. barbouri* appears to be wholly restricted to the most mesic forests of Guerrero, strongly suggests that these species reached their most extensive distributions when mesic conditions prevailed. Nevertheless, the manner in which *P. godmani* reached Costa Rica has been termed one of the mysteries of that country's herpetogeography (Scott 1969).

The present-day restrictions of *P. barbouri* to a small portion of the Sierra Madre del Sur in Guerrero is not readily explainable, although the area has a high degree of endemism and harbors its distinctive group of organism owing to its unique paleohistorical events and/or ecological conditions. On the other hand, the distribution of most Mexican species of reptiles and amphibians is so imperfectly known that it would not be astonishing to discover *P. barbouri* in the highlands of Oaxaca. It is perhaps notable that every species of crotaline found in the highlands of Guerrero (*Ophryacus undulatus*, *Crotalus intermedius*, and *Sistrurus ravus*), exclusive of *P. barbouri*, also occurs in Oaxaca, indicat-

ing that ancestral populations were contiguous. It is possible that subtle differences in habitat have eliminated *P. barbouri* from areas of its former range to the east. Still, it is reasonable to speculate, especially in view of the recent discovery of such montane, moisture-loving species as *Geophis omiltemanus* near San Andrés Chicahuaxtla, Oaxaca (C. M. Bogert, pers. comm.), that local populations of *P. barbouri* may eventually be found on some of the high peaks in Oaxaca.

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APPENDIX I

Specimens of *Porthidium barbouri* examined in this study are listed below. Museum acronyms follow Leviton *et al.* (1985). Where appropriate, locality data have been converted to metric equivalent.

MEXICO: *Guerrero*: Asoleadero, road to Cerro Teotepec from Milpillas (CAS 134466, 135274); "Chilpancingo", (FMNH 38503-04); "near Chilpancingo", (MVZ 45253); 2.5 km SW Omilteme, 2,490 m (UTA R-15558); Omilteme (MCZ 42678-holotype of *Agkistrodon browni*, MCZ 43283); 3.2 km W Omilteme, 2,377 m (TCWC 9455); 4.0 km SW Omilteme, 2,591 m (TCWC 10803); 2.0 km NW Omilteme, 2,500 m (UTA R-6231); 9.4 km NE Puerto del Gallo, 3,296 m (KU 182762); 0.8 km N Puerto del Gallo, 2,896 m (UTA R-4450); Sierra del Burro (MCZ 42679-

paratype of *Agkistrodon browni*); offspring of mating between UTA R-6231 and 15558 (UTA R-6181-83, 6237-39).

APPENDIX II

Selected features for specimens of *Porthidium barbouri*.

Diagonal slashes separate right/left sides, respectively. Numbers in column under Frontal represent the least number of scales between supraoculars.

Mus. No.	Sex	Prelovels	Labials		Frontal	Ventrals	Subcaudals	Dorsals	Length	
			Supra-	Infra-					Body	Total
CAS 134466	M	2/1	8/8	9/9	1	137	30	21-19-15	179	202
CAS 135274	M	2/2	8/8	8/8	1	138	29	19-17-15	315	355
FMNH38503	M	0/0	8/8	9/9	1	130	30	21-19-15	370	425
FMNH38504	M	0/0	7/7	9/9	1	133	27	21-19-15	339	384
MCZ42678	M	0/0	8/8	9/9	1	130	31	21-17-15	390	444
MCZ43283	M	4/4	8/9	8/9	3	138	31	21-17-15	340	388
MVZ45253	M	0/0	7/8	9/9	1	134	29	21-17-15	370	420
UTAR-4450	M	2/2	8/8	10/10	1	138	30	20-19-15	380	431
UTAR-6182	M	3/2	9/10	10/11	5	132	30	21-19-15	132	153
UTAR-6183	M	3/2	9/9	9/10	5	130	30	23-21-15	133	153
UTAR-15558	M	4/2	8/8	10/9	3	136	31	19-17-15	448	512
KU 182762	F	3/3	9/8	10/9	1	129	26	21-19-15	205	225
MCZ42679	F	0/0	8/8	9/9	1	139	26	21-17-15	320	356
TCWC9455	F	7/5	9/8	10/9	4	145	29	21-17-15	430	484
TCWC10803	F	3/2	9/9	10/10	5	142	30	21-17-15	351	394
UTAR-6231	F	4/4	9/8	9/10	4	141	29	19-17-15	381	430
UTAR-6181	F	1/1	9/9	9/9	3	143	30	21-17-15	133	152
UTAR-6237	F	2/1	9/9	10/10	2	137	30	19-17-15	138	158
UTAR-6238	F	1/2	9/9	10/10	2	137	29	21-17-15	135	154
UTAR-6239	F	2/1	8/9	10/10	4	135	27	21-19-14	135	154

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