

Intraspecific Variation in the Feeding Ecology of the Crotaline Snake *Calloselasma rhodostoma* in Southeast Asia

JENNIFER C. DALTRY,¹ WOLFGANG WÜSTER,² AND ROGER S. THORPE²

¹Madras Crocodile Bank, Postbag 4, Mamallapuram, Tamil Nadu 603 104, India, and

²School of Biological Sciences, University of North Wales, Brambell Building, Bangor, Gwynedd LL57 2UW, United Kingdom

ABSTRACT.—Two hundred twenty five prey items were identified from the stomach contents and faeces of museum specimens, roadkills, and live *Calloselasma rhodostoma* collected throughout Southeast Asia. Overall, this snake was found to eat a broad range of vertebrate and invertebrate prey, but exhibited strong intraspecific variation in its diet. Ontogenetic variation was evident in all regions, typically expressed as a transition from predominantly ectothermic prey (arthropods, amphibians, and/or reptiles) to endothermic prey (mammals and birds), although the opposite trend occurred in parts of Thailand. Among snakes of similar size, significant geographic variation emerged in the proportions of different prey taxonomic classes constituting diet. Sexual variation in prey type was also detected and feeding behavior changed according to reproductive status: gravid female pitvipers ceased feeding, and adult males appeared to fast during the mating season. Possible reasons for intraspecific variation in feeding ecology are discussed.

Diet has often been found to vary within snake species, with substantial differences in prey size or taxon reported between different populations (Arnold, 1977; Campbell and Solorzano, 1992), age groups (Fitch, 1960; Klauber, 1972; King, 1993), and genders (Pernetta, 1977; Houston and Shine, 1993). Diet may also vary seasonally and annually (Garcia and Drummond, 1988; Kephart and Arnold, 1982; King, 1993). This phenomenon has a crucial bearing on our ability to understand variation in many other aspects of ophidian biology, such as dentition (Savitsky, 1983), body shape (Voris and Voris, 1983), and niche separation (Toft, 1985).

Regrettably, relatively few species have been adequately studied to determine whether they exhibit patterns of geographic, ontogenetic, or sexual variation in diet. The reason usually given is that the vast majority of specimens in museum collections or encountered in the field have empty stomachs (e.g., Macartney, 1989; King, 1993). However, it is more commonly feasible to obtain faeces from these reptiles, and past meals can be identified from their undigested remains (e.g., Wallace and Diller, 1990; Luiselli and Agrimi, 1991).

We report on the combined use of stomach contents and feces to investigate intraspecific patterns of variation in the diet of the Malayan pitviper, *Calloselasma rhodostoma*. This small (<1 meter) ground-dwelling viperid occurs in lowland forests, plantations, and gardens in Java, northern Peninsular Malaysia, Thailand, Cambodia, Laos, and southern Vietnam, where it has the dubious distinction of being the leading cause of venomous snakebite (Warrell, 1986). Although abundant in many parts of Southeast

Asia and well represented in museum collections throughout the world, our past understanding of the feeding ecology of *C. rhodostoma* was chiefly limited to anecdotal observations of captive specimens, which reportedly accepted amphibians, rodents, fish, lizards, and/or birds.

Our objectives were to quantitatively determine whether *C. rhodostoma* exhibits ontogenetic, sexual and geographic variation in diet, and to discern whether the feeding ecology of this snake changes with reproductive status. This study was principally conducted to enable us to subsequently explore evolutionary relationships between diet and intraspecific variation in morphology, behavior, and venom. Further to this, however, we felt that a better understanding of the feeding habits of this medically important species could prove useful for identifying ways of controlling snake numbers in areas where they pose a major hazard to humans.

MATERIALS AND METHODS

Prey samples from *C. rhodostoma* were collected by the following means: (a) feces from newly-caught live snakes (if the pitviper did not defecate voluntarily, we palpated feces from it under light methoxyflurane anaesthesia [Metofane[®]: C-Vet Ltd, Bury St. Edmunds, UK]); (b) spontaneous regurgitation of stomach contents by newly-caught live snakes; (c) feces and stomach-derived food items of snakes found dead on roads; (d) feces and stomach-derived food items of museum specimens (returned to the body after identification). Methods "a," "b," and "c" were conducted during fieldwork in Vietnam, Thailand, Malaysia, and Indonesia between 1991 and 1994, with visits to each country timed

to coincide with the start of the rainy season. Snakes were captured by hand during the day and by driving along roads at night.

Note that although seasonal or annual variation in diet could potentially influence the findings from self-caught pitvipers, data from method "d" reflects the species' diet throughout its distribution range year-round over many decades, and thus should help counter any temporal bias.

All snakes were sexed and measured, and females were examined for signs of eggs. No snakes were intentionally sacrificed for this study, and all live snakes were returned to their capture sites shortly after examination.

Identification to species level was usually feasible for prey items found whole in the stomach, and intact prey were weighed and measured. Material from the lower intestine was examined under a binocular microscope for undigested fragments. Our primary aim was to establish the taxonomic class of the prey, although, where possible, identification was continued to family, genus, and species. Because keratin is highly resistant to digestion, fur, feathers, scales, and claws pass down the gastro-intestinal tract largely unaffected (lizard feet and squamatan tails, being encased in keratinous scales, often remained intact and identifiable throughout the system). Arthropod exoskeletons also resist digestion, but often break apart at the joints due to the mechanical effect of the stomach. Teeth usually remain intact, especially enamelled mammalian teeth. Bones are broken down with greater efficiency, but fragments are sometimes evident in snake scats. Soft body tissues are even more readily digested, but fragments of tough amphibian skin can sometimes be recovered from the lower intestine. Seed husks and other plant materials were occasionally encountered in the feces of the pitvipers, but we attributed these to accidental or secondary ingestion.

Recognition of arthropod and amphibian prey from the feces posed special problems. Arthropods could be primarily or secondarily ingested (Neill and Allen, 1956), and therefore were recorded only if the arthropod was found alone and intact in the stomach or would clearly have been too big relative to the size of the snake to have been ingested via an even larger prey animal. Amphibians are efficiently digested by the snakes and ingestion of these could only be confirmed if: (1) an amphibian was found whole in the stomach, or (2) if there were fine bone fragments, small arthropod fragments from the amphibian's gut and no remnants from any other vertebrate prey in the stomach or feces.

Prey items in the feces were ignored if there was doubt as to their taxonomic class and

whether they had been primarily ingested. The inevitable underestimation of amphibian and arthropod prey as a result of this rule, together with the variability in the rate at which different types and sizes of prey are digested (Skoczylas, 1978; Schoener, 1989), prohibits extrapolation of the contribution of different types of prey to the snakes' diets in terms of total number or biomass. Because the criteria for identifying prey items were kept constant throughout this investigation, however, the diets of snakes from different geographic regions or of different age-groups, gender or reproductive status could justifiably be compared. The chi-squared goodness-of-fit test was used to statistically compare the diets of different groups of pitvipers (Siegel and Castellan, 1988).

RESULTS

Calloselasma rhodostoma typically ingests one, relatively large animal at a time; for example, a male of 689 mm snout-vent length (SVL) contained a 307 mm total length *Enhydryis jagori* (Colubridae: Serpentes); and a 680 mm SVL female was observed in the field ingesting an adult male rat, *Niviventer cremoriventer* (Muridae: Rodenta) weighing 75 g (30% snake's body mass). The only evidence of multiple meals came from a 611 mm SVL female (AMNH 90639) which had consumed three young *N. cremoriventer* in quick succession.

Fewer than 80% of dissected snakes contained any material in the stomach, but most had identifiable fecal matter in the lower intestine. Similarly, few of the live snakes had perceptibly full stomachs, but feces were extruded from more than 90% of non-gravid specimens. We identified a total of 225 prey items to taxonomic class level or further, of which 216 were obtained from 214 snakes of known geographic origin. One hundred seventy-seven of the latter were identified from the faeces of live, roadkilled, and preserved specimens; the remaining 39 prey items were from the stomach. The overall diet of the species was found to be remarkably broad, encompassing at least two arthropod and five vertebrate classes (Table 1), but dietary findings varied widely among different groups of pitvipers (Table 2). Note that only prey identified from feces are shown in Table 2, and only one prey taxonomic class was recorded per snake.

To control for any discrepancies in the findings from stomach and fecal analyses (see Schoener, 1989), only prey items identified from feces (Table 2) were used in statistical comparisons. The snakes were divided into four groups according to capture locality: Java (West Java Province), Malaysia and South Thailand (Peninsular Malaysia and Thai provinces south of

TABLE 1. Taxonomic distribution of the prey of wild Malayan pit vipers (*Calloselasma rhodostoma*). 225 prey taxa were identified from the faeces and stomach contents of snakes throughout Southeast Asia.

Class	Family	Genus/species
Chilopoda	Scolopendridae	<i>Scolopendra</i> sp.
Neuroptera	Myrmeleonidae	
Coleoptera	Scarabaeidae	
Pisces	(unidentified)	
Amphibia	Ranidae	<i>Rana</i> spp.
Reptilia	Agamidae	<i>Calotes versicolor</i>
	Scincidae	<i>Mabuya multifasciata</i> <i>Mabuya rugifera</i> <i>Tropidophorus</i> sp.
	Gekkonidae	<i>Hemidactylus</i> sp.
	Colubridae	<i>Aplopeltura boa</i> <i>Enhydryis jagori</i> <i>Liopeltis baliodeira</i> <i>Lycodon aulicus</i>
Aves	(unidentified)	
Mammalia	Muridae	<i>Mus musculus</i>
		<i>Mus shorridgei</i>
		<i>Niviventer</i> <i>cremoriventer</i>
		<i>Rattus rattus</i>
		<i>Rattus surifer</i>

Chumphon), North and West Thailand (all provinces north of Chumphon and west of long. 101°E), and East Thailand and Indochina (Thailand east of long. 101°E, Laos, Cambodia, and Vietnam).

To compare the diets of snake size classes, the pitvipers were simply classified as large (>400 mm SVL) or small (<400 mm SVL). Between these two size classes, three of the regional

groups (A, B, and C) exhibited a significant ontogenetic shift from ectothermic prey (reptiles, amphibians, and/or arthropods) to endothermic prey (mammals and birds). This trend was particularly strong in snakes from Java ($\chi^2 = 30.86$; $df = 1$; $P = < 0.0001$). Surprisingly, in the North and West Thailand group, the ontogenetic shift was predominantly from endothermic prey (small mice and possibly shrews) to ectothermic prey (mostly reptiles) ($\chi^2 = 4.57$; $df = 1$; $P = < 0.05$). These findings were supported by the analysis of stomach contents.

As well as ontogenetic variation, strong geographic variation was evident in the classes of prey eaten. In Java, for example, the principal prey of large pitvipers were mammals, whereas lizards and snakes were the main prey of large *C. rhodostoma* in North and West Thailand. Among the large snakes of the four regional groups, the variation in emphasis on endothermic versus ectothermic prey was statistically significant ($\chi^2 = 11.60$; $df = 3$; $P < 0.01$) and cannot be attributed to variation in snake SVL in the groups concerned (ANOVA, $F = 1.89$; $P > 0.1$). The findings from stomach contents again supported the results of the fecal analysis, but the sample sizes of the former were too small to be statistically tested.

The relative importance of ectothermic and endothermic prey also showed significant geographic variation among the small snakes in the four groups ($\chi^2 = 18.36$; $df = 3$; $P = < 0.001$). However, the patterns of geographic variation in small and large snakes were not congruent: small snakes of groups A, B, and C chiefly preyed upon ectotherms (mainly amphibians in

TABLE 2. Percentage contribution of different prey taxonomic groups to the diet of *Calloselasma rhodostoma* (177 prey items identified from the faeces of 177 snakes).

	Snake snout-vent length	Mammals and birds	Reptiles	Amphibians	Arthropods
A. Java	<400 mm N = 32	6.25	28.13	62.50	3.13
	>400 mm N = 34	73.53	23.53	2.94	0.00
B. Malaysia & South Thailand	<400 mm N = 17	29.41	35.29	29.41	5.88
	>400 mm N = 44	45.45	43.18	11.36	0.00
C. North & West Thailand	<400 mm N = 10	70.00	30.00	0.00	0.00
	>400 mm N = 15	26.67	66.67	6.67	0.00
D. East Thailand & Indochina	<400 mm N = 16	18.75	50.00	25.00	6.25
	>400 mm N = 9	66.67	22.22	11.11	0.00

Java; reptiles in groups B and C), whereas endotherms formed a more dominant part of the diet of small snakes in North and West Thailand. These patterns were repeated among the stomach-derived samples.

Sexual differences in diet were also investigated. Among the large snakes from group A (N = 34) there was a significant difference in the diet of males and females in the number of ectothermic and endothermic prey recorded ($\chi^2 = 3.91$; $df = 1$; $P = < 0.05$); that is, Javan males showed a stronger tendency than Javan females for eating ectotherms. However, there was also a significant difference in the SVL of the two genders within this group, with females tending to be larger (ANOVA, $F = 22.29$; $P = < 0.005$). When snakes exceeding 570 mm SVL (the length of the largest Javan male) were excluded from the analysis, the gender-related discrepancy in prey taxonomic class was still perceptible, but no longer statistically significant ($\chi^2 = 0.61$; $df = 1$; $P = > 0.7$). The large snakes from the Malaysia and South Thailand group (N = 44) did not exhibit significant gender-related variation in predation upon ectotherms versus endotherms ($\chi^2 = 0.017$; $df = 1$; $P = > 0.9$), but nor did the two genders in this group significantly differ in body length (ANOVA, $F = 1.35$; $P = > 0.2$).

Dissections of museum specimens and road-kills revealed that the two genders vary in feeding ecology according to their reproductive status. Of more than 50 dissected gravid female *C. rhodostoma* collected throughout Southeast Asia, not one had food in the stomach and this organ appeared severely shrunken and displaced anteriorly. The liver of dissected gravid females was also much reduced in size and greatly folded upon itself: the normal position of the posterior lobe in a non-gravid female was above the 94-97th ventral, but during early vitellogenesis it had migrated to about the 85th ventral, and was typically anterior of the 80th ventral in specimens with fully developed eggs. The kidneys also appeared abnormally thin in gravid females. These findings support Koch's (1991) observations that captive *C. rhodostoma* cease to feed whilst gravid.

Adult male *C. rhodostoma* appeared to fast earlier in the year, during the mating season. In Malaysia, for example, none of the 25 road-killed adult males collected during late February/March (the peak mating season for this region) contained any evidence of food throughout the gastro-intestinal tract. Pitvipers found on roads typically had empty stomachs (perhaps partly because snakes generally become more sedentary after feeding), but the lack of remains even in the lower intestine is indicative of prolonged aphagia.

DISCUSSION

Analysis of stomach contents is generally preferable to fecal studies because newly-ingested prey can more easily be identified to species level, but very few of the *Calloselasma rhodostoma* examined had food in the stomach. This absence presumably reflects (1) a naturally low rate of feeding, (2) the tendency of snakes to become less active after a meal (and hence less likely to be seen and collected), and (3) the remarkable speed with which even large prey items are digested. The venom of *C. rhodostoma* contains powerful digestive enzymes (Daltry et al., 1996a) and the bulge in the stomach of a post-prandial pitviper was normally perceptible for only a couple of days after ingestion.

Fortunately, feces provided a valuable alternative source of dietary information in this study, with approximately 4.5 times more prey items identified from scats than from stomach contents. Although fecal analysis incurs several drawbacks, such as a greater risk of underestimating the importance of invertebrate and amphibian prey, we generally found it much easier to palpate feces from the pitvipers than their stomach contents. Moreover, this approach was probably less detrimental to the live snakes.

Our fecal analysis showed that although the overall diet of the pitviper *C. rhodostoma* is remarkably broad, these snakes specialize upon a rather narrow range of prey according to their area of origin, age (size) and, to a lesser extent, gender.

Geographic variation in diet has previously been discerned in other snakes including *Notechis ater* (Schwaner, 1985), *Crotalus viridis* (Maccartney, 1989), and *Pseudechis australis* (Shine, 1991a). Shine (1991b) suggested that "in species with very broad dietary habits, the types of prey encountered will have a strong effect on the types of prey eaten." In support of this hypothesis, Kephart (1982) reported that the "generalist" colubrids *Thamnophis sirtalis* and *T. elegans* displayed congruent patterns of local specialization at 22 sites in California, with the prey taken at each site closely correlating with the local relative abundance of fish, amphibians, and other taxa. The abundance of different classes of small vertebrates shows geographic variation throughout the distribution range of *C. rhodostoma*, apparently in association with climatic variation (Fisher, 1968). Relatively arid regions such as northern Thailand, for example, support relatively more terrestrial lizards and fewer frogs than humid regions such as Malaysia (Inger and Colwell, 1977; Inger, 1980). However, there was no obvious correlation between the diet of *C. rhodostoma* and regional variation in rainfall. Moreover, the pattern of geographic

variation in the diet of small snakes often opposed the adults' pattern (Table 2).

Alternatively, it is possible that different populations of *C. rhodostoma* are genetically predisposed to select particular prey, as has been convincingly demonstrated in the colubrid snake *Thamnophis elegans* by Arnold (1981a, b). Perhaps differing selection pressures, such as evolved anti-snake defenses in local prey populations (Poran et al., 1987) or competition from sympatric snakes (Shine, 1977; Toft, 1985) could cause pitvipers to specialize upon different classes of prey in different regions.

Ontogenetic variation in diet has previously been recorded in a variety of snake species. Large and small snakes differ in their ability to catch, subdue, and ingest prey of different sizes, so it is hardly surprising that an ontogenetic increase in the size of prey is commonly observed (reviewed by Arnold, 1993). Because prey species vary in mean size, adult snakes usually eat larger taxa than juveniles; for example, young *Crotalus viridis* in Idaho feed almost exclusively upon shrews, whereas adults can manage larger mammals such as rabbits (Wallace and Diller, 1990).

The shift in prey species is often more dramatic than this, however, with a growth-related transition from predominantly ectothermic to endothermic prey. This is a particularly common phenomenon among the Viperidae (Greene, 1992), but cannot easily be explained. In the case of *Calloselasma rhodostoma*, for instance, it seems unlikely that the ontogenetic shift can be attributed to changing nutritional requirements because populations in different geographical regions showed major discrepancies in the nature of the ontogenetic change. Perhaps the change in diet simply reflects age (size) related differences in habitat use or activity cycles, causing adults and juveniles to encounter a different spectrum of potential prey (see Garcia and Drummond, 1988; Houston and Shine, 1993; Greene et al., 1994).

Alternatively, the type of prey taken may be a consequence of different selection pressures acting upon the various age groups, leading to congenital changes in prey selection according to the snake's size. After all, snakes of dissimilar size differ in susceptibility to local predators and probably also with regard to interactions with local competitors (which may also vary in abundance, and hence influence, between different geographic regions). Divergence of feeding habits among different age-groups might even be an adaptive mechanism for avoiding intra-specific competition. Evidence that the ontogenetic dietary changes in *Calloselasma rhodostoma* are congenital comes from Koch (1991), who observed that his captive group readily ate frogs,

but refused mice of comparable size until six months of age. Juvenile *Nerodia erythrogaster* similarly show an ontogenetic switch from fish to a batrachian diet, regardless of previous feeding experience (Mushinsky et al., 1982).

Whether a passive reflection of locally accessible prey or the result of intrinsic selection processes, when diet becomes specialized there is scope for morphological, physiological, and behavioral adaptations to improve feeding efficiency on the selected prey (Gans, 1983). We have presented evidence in earlier papers that geographic and ontogenetic variation in the diet of *C. rhodostoma* is closely and seemingly adaptively associated with geographic and ontogenetic variation in venom composition (Daltry et al., 1996b, 1997).

In the present study, we have also shown that young *C. rhodostoma* commonly eat insectivorous vertebrates, which may help to explain this species' ontogenetic variation in caudal coloration and behavior. The tails of juveniles are yellow and are gently undulated in a manner which attracts other herptiles to within striking distance (Schuett, 1984). The tail even has one or two black "eye-dots" at the distal end; a refinement which, curiously enough, does not appear to have been documented previously. Caudal luring is widespread among, and probably synapomorphic for, the Viperidae (Greene, 1992), and is usually seen in juveniles with brightly colored tails (Neill, 1960; Carpenter and Gillingham, 1990). Neither the luring behavior nor the yellow color or eye-dots on the dorsum of the tail have been recorded in *C. rhodostoma* exceeding 350 mm SVL.

The extent of sex-based differences in the diet of *C. rhodostoma* are harder to determine, owing to the relatively small samples sizes obtained from most populations. Dietary data from Java revealed that males more frequently consumed reptiles, however, perhaps partly because they were generally smaller than females and therefore fewer were capable of tackling rats.

Although, surprisingly, sexual dimorphism in body size was not evident among the present sample from Malaysia and South Thailand, female *C. rhodostoma* are typically larger than males throughout the distribution range (Gloyd and Conant, 1990; Daltry, 1995). The larger body size of female *C. rhodostoma* probably evolved primarily to promote fecundity, but might also have a selective advantage as a means of relieving competition for food between the sexes (Schoener, 1971; Fitch, 1981). Gender-related variation in prey size has also been detected in the sexually dimorphic sea snake *Laticauda colubrina* (Pernetta, 1977) and filesnake *Acrochordus arafuræ* (Houston and

Shine, 1993), but few other studies have explicitly compared the genders.

As well as sexual differences in snake body size, dissimilarities in diet may be causally associated with other gender-related differences in morphology, behavioral ecology, and physiology. Interestingly, there are consistent discrepancies in the venom composition of male and female *C. rhodostoma* throughout Southeast Asia which could affect their ability to subdue and digest different types of prey (Daltry et al., 1996a).

We also obtained evidence that the genders differed in their frequency of feeding according to their reproductive status. Female snakes of many species show reduced foraging activity in comparison with non-gravid mature females, including *Thamnophis elegans* (Fox, 1948), *Crotalus horridus* (Keenlyne, 1972), *Sistrurus catenatus* (Reinert and Kodrich, 1982), *Austrelaps* spp. (Shine, 1987a), *Crotalus viridis* (Macartney, 1989), *Vipera aspis* (Luiselli and Agrimi, 1991), and *Porthidium godmani* (Campbell and Solorzano, 1992). It has been suggested this can simply be attributed to the reduced activity of gravid females which limits their opportunity for encountering prey (Shine, 1980), but this can hardly explain aphagia in an ambush predator such as *Calloselasma rhodostoma*. In fact, Koch (1991) observed that gravid female *C. rhodostoma* refuse food even when placed within striking distance. A more plausible explanation in this case is that the females devote such a high proportion of the body cavity to house the developing clutch that they simply lack room to digest a (typically) large prey animal. Female *C. rhodostoma* produce up to 35 eggs, each of approximately 20 × 30 mm in size (Smith, 1915), which greatly distend the body and cause several major organs to be displaced anteriorly. The females rely upon visceral fat for body maintenance and embryogenesis, and resume feeding shortly after oviposition (Koch, 1991).

During the mating season, adult male *C. rhodostoma* similarly appeared to undergo a period of aphagia. Our radiotelemetry study found that free-living males did not feed during the peak mating season whereas females normally fed once every fortnight until early vitellogenesis (unpubl. data). Because this species typically ingests relatively large prey items, we suggest that feeding could damage the short-term reproductive success of a male by interfering with the locomotory activities associated with locating females, courtship, and contesting with other males (York, 1983, 1984). Reduced feeding among breeding male viperids has previously been reported in, among others, *Vipera berus* (Prestit, 1971) and *V. aspis* (Luiselli and Agrimi, 1991).

We hope that this study will pave the way for further investigations into the causes of intra-specific variation in ophidian feeding ecology using *C. rhodostoma*. Experimental feeding trials in captivity would help resolve whether diet merely reflects variation in prey availability or, as we suspect, congenital differences in prey choice. This species would be an excellent subject for studying the heritability of prey choice because it is easily maintained, matures at only two years of age in captivity, and females can produce two large clutches of eggs each year (Gloyd and Conant, 1990).

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Chondrocranial Anatomy and Skeletogenesis in *Dendrobates auratus*

RAFAEL O. DE SÁ AND SHANNON HILL

Department of Biology, University of Richmond, Richmond, Virginia 23173, USA

ABSTRACT.—The larval chondrocranium and visceral skeleton of *Dendrobates auratus* is described and compared with those of other dendrobatids. Four characters, i.e., lack of fusion between orbital cartilages and otic capsules, wide processus muscularis palatoquadri, lack of processus pseudopterygoideus, and lack of processus anterolateralis hyalis, represent derived conditions for *Dendrobates* within Dendrobatidae. Cranial and postcranial ossification sequences are reported for *D. auratus* and *Epipedobates tricolor*. Skeletogenesis is earlier in *E. tricolor*, but the overall pattern of ossification is similar in the two species.

RESUMEN.—Se describe el condrocáneo y esqueleto visceral de *Dendrobates auratus* comparándolo con el de otros dendrobatidos. Cuatro características—no fusión de cartílagos orbitales con cápsulas óticas, proceso muscular del palatocadrado ancho, ausencia de proceso pseudopterygoideo, y ausencia de proceso anterolateralis hyalis—representan estados derivados para *Dendrobates*. Se reportan la secuencia de osificación craneal y post-cranial para *D. auratus* y *Epipedobates tricolor*. La osificación es más temprano en *E. tricolor*, pero el patrón general de osificación es similar en las dos especies.

The family Dendrobatidae consists of approximately 157 recognized species clustered in six genera (Frost, 1985; Ford, 1993). The genus *Dendrobates* comprises 47 recognized species whose combined distribution extends from southern Nicaragua throughout South America, reaching Bolivia and Peru. *Dendrobates auratus* (Girard, 1855) is found from southern Nicaragua to Colombia at elevations of 0–800 m.

Chondrocranial anatomy has been reported for only seven species of Dendrobatidae (Haas, 1995), representing about 4% of known species of dendrobatids. Data on skeletogenesis has not been reported for any species in the Dendrobatidae. Herein, we describe the chondrocranial anatomy and ossification sequence of *Dendrobates auratus*. Skeletal development of *D. auratus* is compared with that of *Epipedobates tricolor*.

MATERIALS AND METHODS

Tadpoles were staged following Gosner's table (1960). Specimens were cleared and double-

stained for bone and cartilage using Alizarin Red S and Alcian blue respectively, following the technique of Dingerkus and Uhler (1977). A total of 26 tadpoles of *Dendrobates auratus* (stages 29–44, and one juvenile) and 28 tadpoles of *Epipedobates tricolor* (stages 29–46) were examined. Specimens are deposited in the National Museum of Natural History, Washington D.C. (*Dendrobates auratus* USNM 509456–509482; *Epipedobates tricolor* USNM 509483–509510).

The chondrocranium of *Dendrobates auratus* is described based on a stage 32 tadpole, this corresponds to the latest larval stage before cranial ossification was observed. Terminology follows that of de Sá (1988) and Haas (1995). Observations and illustrations were made using a Wild MC3 stereomicroscope with the aid of a camera lucida attachment.

RESULTS

The lower horny beak of *Dendrobates auratus* larvae is supported by two cartilages infra-