

Gape size and evolution of diet in snakes: feeding ecology of erylinc boas

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Abstract

The Macrostromata accounts for more than 85% of extant snakes and is characterized by increased mobility of the jaws and increased gape size. We used stomach contents of museum specimens and specific literature records to describe the food habits of a basal clade of macrostomatans – the erylinc boas (Erycinae) – with an emphasis on the North American *Charina bottae*. Mammals, lizards, birds, and squamate eggs composed 66%, 17%, 7%, and 5%, respectively, of the prey of *C. bottae*. Smaller *C. bottae* fed on squamate eggs and lizards, whereas larger snakes added mammals and birds to their diet, and ceased to take squamate eggs. Ten of 12 snakes with multiple prey had eaten nestling birds or mammals, and snakes that ate multiple prey were not significantly larger than those that had single prey. *Charina trivirgata* and *C. reinhardtii* also prey on mammals, whereas species of *Eryx* feed mainly on mammalian prey, but also eat lizards and occasionally birds. Evolutionarily more basal groups of snakes primarily feed on elongate prey, which suggests that innovations of the feeding apparatus of macrostomatans allowed these snakes to eat heavier and bulkier prey, particularly mammals. Erycines appeared and diversified at approximately the same geological time as rodents, suggesting that rodents perhaps constituted an abundant prey resource that favoured the diversification of early macrostomatans.

Key words: Boidae, *Charina*, *Eryx*, feeding ecology, fossil record, gape size

INTRODUCTION

For gape-limited predators such as snakes that swallow their prey whole, foraging success (i.e. mass eaten per unit time) likely increases with maximum ingestible prey size, other factors being equal (Forsman & Lindell, 1993). Consequently, selection on traits influencing swallowing performance has probably been strong throughout the evolutionary history of snakes, as implied by the various morphological adaptations facilitating the ingestion of larger prey by more recently evolved ophidian clades (Greene, 1983a; Pough & Groves, 1983; Cundall, 1987; Rieppel, 1988; Cundall & Greene, in press). Studying the feeding biology of a particular group of snakes in a phylogenetic context and with an adequate fossil record should help elucidate factors that significantly influenced the evolutionary

history of the group. With that broader goal, we used stomach contents of museum specimens and a survey of literature records to describe the feeding ecology of erylinc boas, a basal clade of macrostomatans.

Extant snakes are divided into two major clades: Scolecophidia (blindsnakes of three families) and Alethinophidia (all other snakes; Fig. 1). Macrostromata accounts for approx. 95% of Alethinophidia and comprises boas and sand boas (Boidae), pythons (Pythonidae), Round Island boas (Bolyeriidae), dwarf boas (Tropidophiidae), Australasian filesnakes (Acrochordidae), vipers and pitvipers (Viperidae), stiletto snakes (Atractaspididae), racers, ratsnakes, water-snakes, etc. (Colubridae), and cobras, mambas, coralsnakes, seasnakes, etc. (Elapidae). The clade is characterized by, among other traits, morphological synapomorphies correlated with increased mobility of the jaws and increased gape size (Rieppel, 1988; Cundall & Greene, in press), hence the name Macrostromata ('big mouth').

Species of Erycinae, currently classified within Boidae (Fig. 1), are found in North America, Europe, Asia, and Africa. Traditional taxonomic treatments recognized two monotypic genera (*Charina*, *Lichanura*) in North

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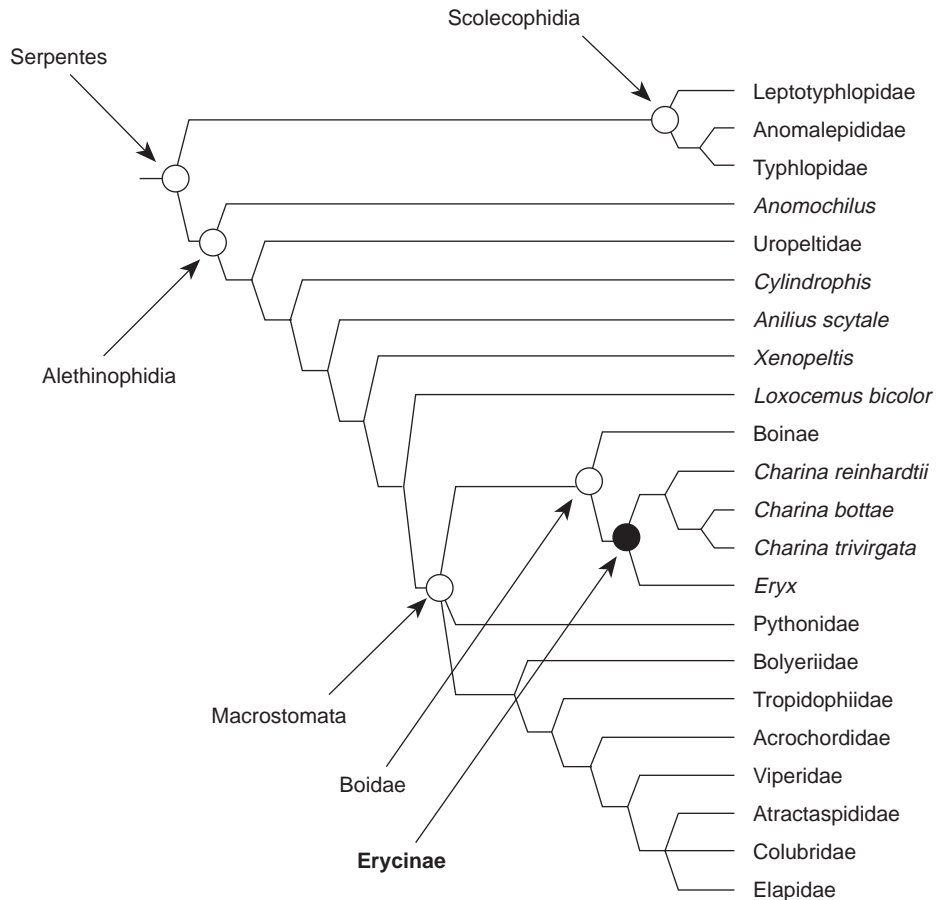


Fig. 1. Phylogenetic relationships among extant snakes, emphasizing those of erycine boas, *Charina* and *Eryx* (after Cadle, 1988; Cundall, Wallach & Rossman, 1993; Kluge, 1993).

America, with Old World species placed in one or two genera (an all-encompassing *Eryx* or a restricted *Eryx* with *Gongylophis* to accommodate the species *conicus*, *colubrinus*, *muelleri*, and *whitakeri*; Das, 1991; Tokar, 1995, 1996). Kluge (1993) documented 16 synapomorphies placing the Calabar burrowing 'python' (traditionally placed in the monotypic *Calabaria*) within the Erycinae, and argued for the recognition of two named clades of erycines: *Eryx* to include the Old World sand boas (see also Szyndlar & Schleich, 1994); and *Charina* to include the North American forms plus *C. reinhardtii* (Calabar burrowing boa), a taxonomic arrangement we follow herein (Fig. 1).

The two species of New World erycines, *Charina bottae* and *C. trivirgata*, are allopatric in western North America. *Charina bottae* (rubber boa) occurs from south-western Canada to southern California in the United States, and eastward from western California to northern Wyoming and Colorado (Stewart, 1977). Rubber boas occur in grassland, chaparral, and woodland (Nussbaum, Brodie & Storm, 1983). They are good swimmers, burrowers, and climbers, and are largely crepuscular and nocturnal, but can also be active during the daytime (Ross, 1931; Stebbins, 1954; Peterson & Dorcas, 1992). *Charina trivirgata* (rosy boa) ranges from

southern California to the tip of Baja California, and eastward to western Arizona and the state of Sonora in northwestern Mexico (Yingling, 1982). Rosy boas occur in deserts and rocky shrubland and can be active at night, dusk, or in the daytime (Klauber, 1931; H. W. Greene, pers. obs.). *Charina reinhardtii* inhabits forested habitats of equatorial west and central Africa (Kluge, 1993). Fourteen species of *Eryx* (sand boas) occupy primarily deserts and steppes (although *E. conicus* also occurs in luxuriant forests) from northern and western Africa, northward to the Balkan peninsula and northern coasts of the Caspian Sea in eastern Europe, and eastward throughout India, Sri Lanka, western China and Mongolia (Wall, 1911; Sorensen, 1988; Kluge, 1993). Adult erycines are typically <1 m in total length, although the maximum size for the extant species is approximately 1.3 m and 1.14 kg (for *E. johnii*; Chari, 1950).

Our goals here are to evaluate variation in taxonomic composition of diets and erycine foraging tactics, with an emphasis on *C. bottae*. We also rely on the excellent fossil record of erycines and of rodents to gain a historical perspective on how prey characteristics may have influenced evolutionary innovations in the trophic apparatus of macrostomatans.

Table 1. Prey eaten by *Charina bottae*. ‘*Perognathus (sensu lato)* sp.’ refers to *Chaetodipus* or *Perognathus (sensu stricto)*. ‘Frequency’ refers to the number of times each prey taxon was found in the entire sample; numbers in parentheses indicate the number of snakes that ate that particular prey

Prey taxon	Frequency	Percentage of total no. of prey	Source
Gastropoda			
Stylommatophora			
Arionidae			
<i>Ariolimax columbianus</i>	1 (1)	1.1	G. Anderson, pers. comm.
Aves			
Passeriformes			
Paridae			
<i>Parus rufescens</i>	6 (1)	6.7	Copper, Ohmart & Dahlsten, 1978
Mammalia			
Insectivora			
Talpidae			
<i>Scapanus latimanus</i>	3 (1)	3.4	This study
cf. <i>Scapanus latimanus</i>	3 (1)	3.4	This study
Unidentified talpid	2 (1)	2.2	This study
Soricidae			
<i>Sorex</i> sp.	2 (2)	2.2	This study; Koch & Peterson, 1995
Rodentia			
Dipodidae			
<i>Zapus princeps</i>	1 (1)	1.1	Stebbins, 1954
Geomyidae			
<i>Thomomys talpoides</i>	5 (1)	5.6	Bartholomew & Lleyson, 1993
Heteromyidae			
<i>Perognathus (sensu lato)</i> sp.	1 (1)	1.1	This study
Muridae			
<i>Microtus californicus</i>	1 (1)	1.1	This study
<i>Microtus longicaudus</i>	1 (1)	1.1	Brunson & Demaree, 1951
cf. <i>Microtus montanus</i>	1 (1)	1.1	Fitch, 1936
<i>Peromyscus maniculatus</i>	6 (1)	6.7	This study
<i>Peromyscus</i> cf. <i>P. maniculatus</i>	4 (1)	4.5	This study
<i>Peromyscus</i> sp.	1 (1)	1.1	This study
Unidentified rodent	13 (5)	14.6	This study; Van Denburgh, 1922; Agerter, 1932; Logier, 1932; Tanner & Tanner, 1939
Unidentified mammal	15 (5)	16.9	This study; Cope, 1900
Reptilia			
Squamata			
Anguidae			
<i>Elgaria coerulea</i>	1 (1)	1.1	P. Gregory, pers. comm.
<i>Elgaria</i> sp.	6 (6)	6.7	This study; Stebbins, 1954
Phrynosomatidae			
<i>Sceloporus occidentalis</i>	4 (2)	4.5	This study; Van Denburgh, 1922
<i>Sceloporus</i> sp.	3 (3)	3.4	This study; Cope, 1900
Unidentified lizard	1 (1)	1.1	This study
Squamate eggs			
1	1 (1)	1.1	This study
2	1 (1)	1.1	This study
4	1 (1)	1.1	This study
6 cf. <i>Sceloporus graciosus</i> eggs	1 (1)	1.1	R. Staub, pers. comm.
Unidentified animal	4 (4)	4.5	This study
Total	89		

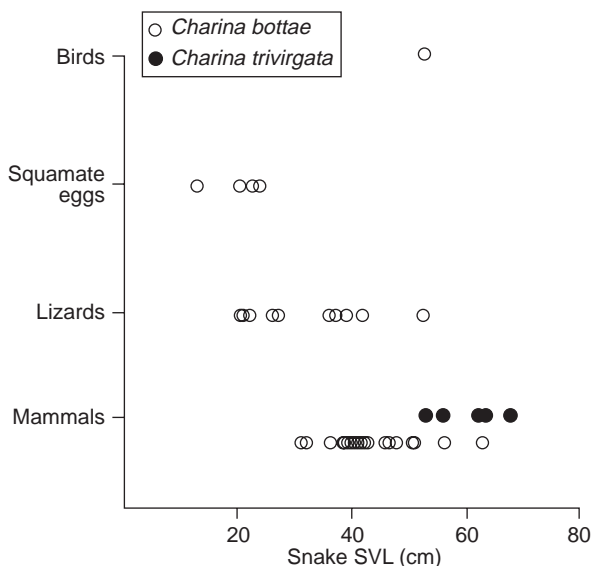
METHODS

We examined 249 and 84 specimens of *Charina bottae* and *C. trivirgata*, respectively, in the California Academy of Sciences (CAS), San Francisco and the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley. We checked for stomach contents by making a midventral incision in preserved specimens,

avoiding only type specimens and fragile individuals. Whenever possible, for each snake with prey we recorded locality data, body size (snout–vent length – SVL \pm 1 cm), body mass (\pm 0.1 g), and minimum number of items in the stomach. All squamate eggs in a single stomach were counted as one item because they may represent a feeding event at the same site and because sometimes their exact number was impossible

Table 2. Records of *Charina bottae* that consumed multiple prey

Museum catalogue number/source	Snake snout–vent length (cm)	No. of prey
CAS 28323	52.2	2 <i>Sceloporus occidentalis</i>
Van Denburgh, 1922	–	2 <i>Sceloporus occidentalis</i>
Copper <i>et al.</i> , 1978	52.8	6 <i>Parus rufescens</i>
MVZ 193419	39.7	3 <i>Scapanus latimanus</i>
CAS 201590	56.0	3 cf. <i>Scapanus latimanus</i>
MVZ 61915	50.9	2 unidentified talpids
CAS-SU 4189	39.2	6 <i>Peromyscus maniculatus</i>
MVZ 140672	31.8	4 <i>Peromyscus</i> cf. <i>P. maniculatus</i>
Bartholomew & Lleyson, 1993	40.0	5 <i>Thomomys talpoides</i>
Van Denburgh, 1922	–	6 unidentified rodents
Logier, 1932	–	2 unidentified rodents
Tanner & Tanner, 1939	–	3 unidentified rodents

**Fig. 2.** Relationship between prey category and snake body size (SVL) in *Charina bottae* ($n = 41$) and *C. trivirgata* ($n = 7$).

to determine. Direction of ingestion (inferred from orientation in the stomach) and order of ingestion of multiple items were recorded as far as possible. Taxonomic identifications were made by comparison with specimens in the MVZ, whenever possible with specimens from the same county or state from which the snake was taken. Partially digested prey, especially those representing mammals, were carefully examined for diagnostic elements. Hair mats frequently contained complete or partial dentitions or isolated teeth that could be identified to genus or species. We weighed snakes and their intact or slightly digested prey after blotting and draining them briefly on paper towels to remove excess fluid.

Our data set also incorporates published dietary records (Table 1). We took care to account for redundancy among literature records (Cope, 1900 with Shaw & Campbell, 1974), and excluded accounts of prey taken in captivity (Lewis, 1946; Linder, 1963; Shaw & Campbell, 1974; Peabody, Johnson & Brodie, 1975) or under otherwise artificial circumstances (Borell, 1931;

Macey, 1983). Values given are means ± 1 SD and P -values are 2-tailed.

RESULTS

Forty *Charina bottae* (SVL = 39.2 ± 10.6 cm, range = 12.7–56.0 cm, $n = 40$; body mass = 54.3 ± 37.8 g, range = 3.5–150.1 g, $n = 40$), 16.1% of the specimens we examined, contained 54 at least partly identifiable prey items. Including 35 published and unpublished dietary records (from 17 snakes), 59 (66.3%) of 89 prey eaten by *C. bottae* were mammals, 17 (16.9%) were 'lizards' (i.e. squamate reptiles other than snakes and amphisbaenians), six (6.7%) were birds, four (4.5%) were squamate eggs, one (1.1%) was a slug, and four were unidentified animals (Table 1; the high number of unidentified lizards, birds, and mammals is the result of stomach contents that consisted exclusively of a few scales, feathers, or clumps of hair with no cranial material). Published dietary records for which we could not determine the frequency of consumption by *C. bottae* included *Elgaria coerulea* (northern alligator lizard), unidentified birds, *Eutamias* sp. (chipmunks), and *Zapus princeps* (jumping mouse; Weeks & Davis, 1963). Shrews have been noted to be commonly eaten by rubber boas (Nussbaum *et al.*, 1983), but we found two records only among 89 prey. Forty-five (78.9%) of 57 *C. bottae* with food contained a single prey, four (7.0%) snakes had two items, three (5.3%) had ingested three prey, one (1.8%) had four, another one had five, and three rubber boas contained six prey each (Table 2). Twelve of 48 (25%) snakes large enough (i.e. SVL ≥ 29.2 cm) to eat mammals or birds had multiple prey. There was no significant difference in body size between snakes that had a single prey (SVL = 38.1 ± 11.4 cm, range = 12.7–62.6 cm, $n = 37$) and those that contained multiple prey (SVL = 45.3 ± 8.7 cm, range = 31.8–56.0 cm, $n = 8$; single-factor ANOVA, $F_{(1,43)} = 2.83$, $P = 0.10$). There was a significant difference in SVL among rubber boas that ate mammals (SVL = 44.2 ± 7.4 cm, range = 31.0–62.6 cm, $n = 26$), lizards (SVL = 32.2 ± 10.6 cm, range = 20.5–52.2 cm, $n = 10$), and squamate eggs



Fig. 3. *Charina bottae* (MVZ 193419), snout–vent length 39.7 cm, 52.5 g, from California (USA), with three broad-footed moles (*Scapanus latimanus*). Numbers next or attached to individual prey (or remains) indicate the order in which they were ingested.

(SVL = 19.7 ± 4.9 cm, range = 12.7–23.6 cm, $n=4$; single-factor ANOVA, $F_{(2,37)} = 20.18$, $P < 0.0001$; Fig. 2), and multiple comparison tests indicated that the differences among the three groups of snakes were significant.

Sixteen prey were swallowed head-first and six were ingested tail-first (16/6: [predicted] 11/11, G -test of independence with Williams' correction, $G = 2.34$, 1 d.f., $P = 0.13$). Three lizards were ingested head-first and two were ingested tail-first, in comparison with 13 mammals swallowed head-first and four ingested tail-first (Fisher's exact test, $P = 0.59$).

We could only reliably estimate prey mass of six nestling deer mice *Peromyscus maniculatus* (individual prey masses = 4.2, 5.4, 5.9, 6.0, 5.9, 6.0 g) eaten by a single *C. bottae* (CAS-SU 4189, 51.7 g). Relative prey mass (prey mass/snake mass) for the combined mice was 0.65. Prey mass of two of three *Scapanus latimanus* (broad-footed mole) taken by another *C. bottae* (MVZ 193419, 52.5 g; Fig. 3) was 4.9 and 5.6 g, which, assuming that the first item swallowed had a mass equal to the average of that of the other two moles, suggests that relative prey mass for the three prey was approximately 0.3.

Eight *Charina trivirgata* (SVL = 59.7 ± 5.7 cm, range = 53.0–67.7 cm, $n = 7$; body mass = 170.7 ± 39.4 g, range = 129.1–243.7 g, $n = 7$), 9.5% of the speci-

mens we examined, contained single mammalian prey: one *P. maniculatus*, one *Dipodomys* sp., one *Perognathus (sensu lato)* sp., two unidentified rodents, and three unidentified mammals. Three prey were swallowed head-first and one was ingested tail-first. The only published dietary records we found for *C. trivirgata* were one adult *Dipodomys* sp. (kangaroo rat), one sciurid rodent (ground squirrel), four young rabbits in the same snake (Merker & Merker, 1995), and an unidentified mammal (Klauber, 1933). Thus, 12 *C. trivirgata* contained 15 prey, all mammals. Records of natural diet for two *C. reinhardtii* include only nestling murid rodents, one *Dasymys incomtus* (shaggy swamp rat) in one snake, and two *Hybomys univittatus* (one-striped forest mouse) in another (Gartlan & Struh-saker, 1971).

The natural diets of species of *Eryx* generally resemble those of the three species of *Charina*. Specific prey items include a gecko, birds, and a naked mole-rat in *E. colubrinus*; a lizard, several birds, and squirrels and other mammals in *E. conicus*; a vole in *E. elegans*; rodents in *E. jaculus*; geckos in *E. jayakari*; a shrew and rodents in *E. johnii*; several lizards, birds, and rodents, and a bat in *E. miliaris*; and lizards, birds, and several rodents in *E. tataricus* (Table 3). Although precise data are lacking, individual *E. conicus* with total lengths as small as 42 cm have eaten adult *Funambulus palmarum*

Table 3. Dietary records for *Eryx colubrinus*, *E. conicus*, *E. elegans*, *E. jaculus*, *E. jayakari*, *E. johnii*, *E. miliaris*, and *E. tataricus*. Source: 1 = Wall, 1911; 2 = Levett-Yeats, 1914; 3 = Powell, 1914; 4 = Pitman, 1958; 5 = Bogdanov, 1962; 6 = Nikol'skii, 1964; 7 = Bogdanov, 1965; 8 = Minton, 1966; 9 = Bogdanov, 1970; 10 = Sharma & Vazirani, 1977; 11 = Khajuria & Agrawal, 1981; 12 = Shammakov, 1981; 13 = Daniel, 1983; 14 = Ataev, 1985; 15 = Gasperetti, 1988; 16 = Prakash, 1988; 17 = Braude, 1991

Prey taxon	Species	Source	Prey taxon	Species	Source
<i>Eryx colubrinus</i>			<i>Eryx miliaris</i>		
Reptilia			Reptilia		
Squamata			Squamata		
Gekkonidae			Agamidae		
<i>Stenodactylus</i> sp.		15	<i>Phrynocephalus helioscopus</i>		5
Aves			<i>Phrynocephalus mystaceus</i>		5, 9
Ciconiiformes			<i>Phrynocephalus interscapularis</i>		12
Charadriidae			<i>Trapelus sanguinolentus</i>		5, 9, 12
<i>Charadrius asiaticus</i>		4	Gekkonidae		
Passeriformes			<i>Crossobamon eversmanni</i>		12
Passeridae			<i>Teratoscincus scincus</i>		5
2 <i>Motacilla aguimp</i>		4	Lacertidae		
Unidentified birds		4	<i>Eremias grammica</i>		5, 12
Mammalia			<i>Eremias scripta</i>		5, 12
Rodentia			Scincidae		
Bathergidae			<i>Eumeces schneideri</i>		5
1 <i>Heterocephalus glaber</i>		17	Aves		
	<i>Eryx conicus</i>		Passeriformes		
Reptilia			Passeridae		
Squamata			<i>Passer domesticus</i>		7
Agamidae			<i>Passer montanus</i>		9
<i>Calotes versicolor</i>		3	<i>Motacilla alba</i>		5, 9
Aves			1 unidentified bird		9
Columbiformes			Mammalia		
Columbidae			Chiroptera		
1 <i>Streptopelia senegalensis</i>		16	1 unidentified bat		7
Passeriformes			Rodentia		
Sturnidae			Dipodidae		
1 <i>Acridotheres tristis</i>		2	<i>Dipus sagitta</i>		5, 7
Sylviidae			Muridae		
1 <i>Turdoides striatus</i>		2	<i>Cricetulus migratorius</i>		5, 7
Upupiformes			<i>Cricetulus</i> sp.		5
Upupidae			<i>Ellobius talpinus</i>		7
1 <i>Upupa epops</i>		2	<i>Meriones libycus</i>		5, 7
Mammalia			<i>Meriones meridianus</i>		9, 12
Rodentia			<i>Mus musculus</i>		5, 7
Sciuridae			<i>Rhombomys opimus</i>		9
2 <i>Funambulus palmarum</i>		1	Sciuridae		
<i>Funambulus</i> sp.		13	<i>Spermophilus</i> sp.		9
1 unidentified mammal		11		<i>Eryx tataricus</i>	
	<i>Eryx elegans</i>		Reptilia		
Mammalia			Squamata		
Rodentia			Agamidae		
Muridae			<i>Stellio lehmanni</i>		14
1 unidentified vole		14	Lacertidae		
	<i>Eryx jaculus</i>		<i>Eremias argus</i>		14
Mammalia			<i>Eremias velox</i>		14
Rodentia			Aves		
Unidentified rodents		6	Passeriformes		
	<i>Eryx jayakari</i>		Fringillidae		
Reptilia			<i>Emberiza bruniceps</i>		9
Squamata			<i>Emberiza</i> sp.		14
Gekkonidae			Passeridae		
<i>Hemidactylus</i> spp.		15	<i>Passer domesticus</i>		9
<i>Stenodactylus</i> spp.		15	Mammalia		
	<i>Eryx johnii</i>		Rodentia		
Mammalia			Dipodidae		
Insectivora			<i>Allactaga elater</i>		7
Soricidae			<i>Dipus sagitta</i>		7
1 juvenile <i>Suncus</i> sp.		8	<i>Pygeretmus pumilio</i>		7
Rodentia			Muridae		
Muridae			<i>Alticola argentatus</i>		7
1 <i>Meriones</i> sp.		10	<i>Cricetulus migratorius</i>		7
Sciuridae			<i>Ellobius talpinus</i>		7
1 unidentified squirrel		3	cf. <i>Ellobius</i> sp.		14
			<i>Meriones libycus</i>		7, 14
			<i>Meriones tamariscinus</i>		7
			<i>Mus musculus</i>		14
			<i>Rhombomys opimus</i>		7, 14
			Sciuridae		
			<i>Spermophilus fulvus</i>		7
			<i>Spermophilus</i> sp.		14

(three-striped palm squirrel; head-body length 12–19 cm, mass 100–160 g), and thus sometimes take prey that approach their own body mass (Wall, 1911).

DISCUSSION

Our study suggests that small *C. bottae* feed primarily on squamate eggs and lizards; larger snakes cease to eat squamate eggs and add birds and various species of mammals to their diets. Similar ontogenetic dietary shifts from ectotherms to endotherms are widespread among other snakes, including various boines (Henderson *et al.*, 1987; Henderson, 1993), pythons (Shine & Slip, 1990), vipers (Fitch, 1960; Shine *et al.*, 1998), colubrids (Mushinsky, Hebrard & Vodopich, 1982; Greene, 1989; Rodríguez-Robles, Bell & Greene, 1999), and elapids (Shine, 1980). Such shifts presumably reflect the absolutely larger gape required to consume even the smallest mammals and birds (e.g. the head of a small *C. bottae* [MVZ 43608], SVL = 29.2 cm, is only 0.7 cm in maximum width). Predation on clumped nestlings is clearly a significant aspect of the foraging biology of adult *C. bottae* (all multiple items in 12 rubber boas were individuals of the same prey species, and in at least seven cases were nestlings), and the collective body mass of a litter may well exceed that of an adult of the same species. The relatively high incidence of tail-first prey ingestion by *C. bottae* perhaps reflects predation on relatively small items, as nestlings have low relative prey mass ratios and small diameters compared to snake head size (cf. Greene, 1976; Rodríguez-Robles & Leal, 1993). Our findings for *C. trivirgata* and Old World erycines imply diets generally similar to that of *C. bottae*, including at least occasional consumption of both nestling mammals and of relatively bulky, heavy prey.

Indirect evidence and fortuitous field observations document both wide-foraging and ambush-hunting tactics among erycines. Nestling birds and rodents are necessarily sedentary, so *C. bottae* and *C. reinhardtii* must encounter those prey by wide-foraging rather than ambush; in fact, these two species have been seen crawling into nests (Ross, 1931; Gartlan & Struhsaker, 1971; Copper, Ohmart & Dahlsten, 1978). An observation of a *C. trivirgata* coiled above a *Neotoma* sp. (woodrat) nest (Klauber, 1924) may imply ambush tactics by rosy boas. *Eryx conicus* and *E. jaculus* use both wide-foraging and ambush tactics in hunting prey – the former species was observed to conceal itself at the base of trees to seize passing palm squirrels, and within a hole to capture doves feeding on a nearby dung heap (Daniel, 1983; Prakash, 1988; Tokar, 1995). Erycines thus may prove fruitful subjects for exploring the costs and benefits of alternative foraging modes (see Huey & Pianka, 1981; Secor & Nagy, 1994), and field studies may determine if these snakes capture agamid lizards and other diurnally active species by ambush-hunting or by wide-foraging for those prey in their nocturnal retreats.

Comparisons with immediate outgroups, the basal alethinophidians (i.e. *Anomochilus*, uropeltids, *Cylindrophis*, *Anilius scytale*, *Xenopeltis*, *Loxocemus bicolor*; Fig. 1), provide insights into the early evolution of erycines. Most basal alethinophidians have strongly constrained gapes due to retention of a primitive jaw anatomy (Cundall & Greene, in press) and therefore primarily eat elongate prey (e.g. eels, caecilians, limbless squamates, earthworms; Greene, 1983a, 1997; Valls-Moraes & Yuki, 1998). Observations on some successive extant outgroups to Macrostromata (*L. bicolor* – Mora, 1991; scolecophidians – Gehlbach, Watkins & Kroll, 1971; Webb & Shine, 1992; varanoid lizards – Pregill, Gauthier & Greene, 1986) suggest that snakes primitively used wide-foraging rather than ambush-hunting techniques. In contrast, boines, pythons, and more derived lineages (e.g. pitvipers) primarily rely on ambush-hunting (Greene, 1983b; Slip & Shine, 1988; Greene, 1992; Secor & Nagy, 1994) and often take prey that are both heavy and bulky (Greene, 1983b; Shine & Slip, 1990), which implies that those two innovations may have characterized the feeding biology of ancestral macrostomatans. Erycines use both ambush-hunting and the primitive wide-foraging behaviour and take heavy, bulky prey (which sometimes approach the snake's own mass) as well as light-weight, but bulky prey (i.e. nestling mammals and birds). Provided that erycines arose within a clade including boines and pythons (Fig. 1), frequent predation on nestling mammals and reversal to wide-foraging by erycines represent subsequent modifications of the feeding biology characteristic of the earliest macrostomatans.

The fossil record of erycines and rodents is consistent with our scenario of early macrostomatian evolution. The 12 described genera of fossil North American erycines, some of them of questionable status, consist almost entirely of isolated vertebrae or short sequences of articulated vertebrae (Holman, 1979; Harding & Holman, 1982; but see Breithaupt & Duvall, 1986). If *Helagras* is an erycine, the fossil record for this group extends to the Early Paleocene (approx. 65 million years ago [Mya]). *Cheilophis*, *Huberophis*, *Lithophis*, and one species each of *Calamagras* and *Ogmophis* are known from the Eocene (54–38 Mya). A rich erycine fossil history from widely scattered Eurasian and Middle Eastern localities dates from the Eocene (Hoffstetter & Rage, 1972; Milner, 1986; Rage, 1987; Thomas *et al.*, 1991; Rage & Augé, 1993; Szyndlar and Schleich, 1994). The origin of erycines has been disputed, but based on his phylogenetic hypothesis for these snakes, Kluge (1993) suggested that the clade radiated initially in the Old World. Although rodents first appear in the fossil record of many Asian and North American localities in the Late Paleocene (57–54 Mya), phylogenetically-derived biogeographic reconstructions and the occurrence of older basal rodents (or rodent sister taxa, depending upon the definition of Rodentia) in Asia unambiguously support an Asiatic origin for the group (Vianey-Liaud, 1985; Li *et al.*, 1987; Dashzeveg, 1990; Meng *et al.*, 1994; McKenna & Bell, 1997; Beard, 1998).

Available evidence thus indicates a roughly contemporaneous origin for erycine boas and rodents, during widespread conversion from forests to steppes and other more open environments (Behrensmeyer *et al.*, 1992). We suggest that the early radiation of rodents, with their rapid life cycles and exuberant fecundity, may have provided special circumstances of prey size, shape, and abundance that favoured the diversification of the ancestors of modern erycines.

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