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## *Pythonodipsas* and *Spalerosophis*, Colubrid Snake Genera Convergent to the Vipers

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Two colubrid genera, *Pythonodipsas* and *Spalerosophis*, share many derived character states with vipers. Fragmentation of head plates accounts for much of the similarity between these colubrids and vipers. Because primitive vipers do not have fragmented head plates, we conclude that *Pythonodipsas* and *Spalerosophis* have converged on viper morphology, perhaps independently. *Pythonodipsas* has evolved unique palatine "fangs" and both taxa use constriction to subdue prey.

THE quest for the ancestral stock of the Viperidae (protoviper of Kardong, 1979) has been a favorite pastime for herpetologists. Such an adventure was the investigation of the phylogenetic position of the primitive viper *Azemiops feae* (Liem, Marx and Rabb, 1971) in the hope that it would suggest how early colubroids might have given rise to the vipers.

The monotypic colubrid genus *Pythonodipsas* came to our attention as a possible protoviper (Marx and Rabb, 1970: 546). We indicated that the examination of *Pythonodipsas* "confirmed a

peculiar viperid resemblance indicated by the correlation of derived states of external characters." This unusual snake was reported by FitzSimons (1962:182) as viper-like. He noted, "This, at least until recently, rare and little known snake, appears to be confined to the open country of our dry west. In life it is very adder-like in appearance and habits, and is frequently mistaken for such in the field" (Fig. 1). Perhaps the most remarkable feature of *Pythonodipsas* is the extremely enlarged palatine "fang" (Fig. 2), a development unparalleled in

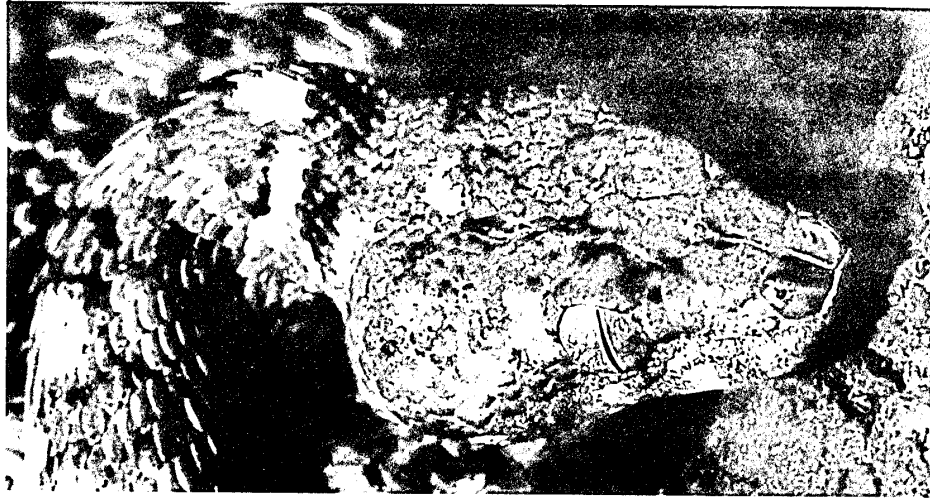


Fig. 1. A live *Pythonodipsas carinatus* (Field Museum of Natural History—FMNH 210073). Photo by Harry Greene.

other snakes. These “fangs” are solid and ungrooved and might be used to snare prey, rather than for venom delivery. In the course of our character survey we discovered another colubrid snake with many viper-like characteristics, *Spalerosophis* (Marx, 1959). We have also made some observations of prey handling behavior in *Pythonodipsas*.

We found that *Pythonodipsas carinata* and *Spalerosophis diadema* are more similar to vipers than are any other species of Colubroidea that we examined. These colubrids may represent either extreme convergence to vipers or they may actually be related to vipers and serve as a model for the ancestral protoviper. In either case these taxa deserve studies of morphological function since they seem to be on the threshold of the viperid morphological adaptive zone.

#### MORPHOLOGICAL CHARACTER ANALYSIS

In the following section we undertake a five step character analysis:

- 1) We begin by identifying the derived character states that are found in *Pythonodipsas* using the criteria and tabulations of Marx and Rabb (1972).
- 2) Next, we establish which colubroid taxa are most similar to *Pythonodipsas* in derived character states and determine the magnitude of these similarities.
- 3) Focusing on these taxa, we ask which characters are responsible for the most striking instances of overall similarity in derived

states. This identifies a subset of derived states in *Pythonodipsas* that are candidates for homology or homoplasy (i.e., convergence) with other taxa.

- 4) Next, we ask whether this subset is peculiar to species occupying a particular habitat or zoogeographic area.
- 5) Finally, we ask whether this subset of derived states represents a functional system(s) that is likely to evolve independently or whether it reflects common ancestry. We first identify complexes of associated characters. Are characters in the subset associated with each other and/or with other characters? Do these character associations make functional sense?

This five step procedure is then repeated with *Spalerosophis*.

The data for this study are the same used in an analysis of the phyletics of 50 snake characters represented in 508 species of 245 genera from all six families and subfamilies of Colubroidea (Marx and Rabb, 1972).

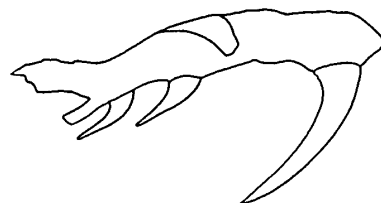


Fig. 2. Medial view of left palatine bone of *Pythonodipsas carinatus*—FMNH 170024.

TABLE 1. NUMBER OF SPECIES OF COLUBROIDEA SHARING DERIVED CHARACTER STATES WITH *Pythonodipsas carinatus*.

	No. of species	Number of shared derived character states										
		0	1	2	3	4	5	6	7	8	9	10-14
Colubridae	312	129	122	42	14	4				1		
Elapidae	68	24	26	16	2							
Hydrophiidae	42	14	19	3	4	1	1					
Azemiopinae	1			1								
Viperinae	34		3	1	9	5	7	6	3			
Crotalinae	45		1	1	4	2	5	9	18	4	1	
<i>Atractaspis</i>	5	3	1	1								
Total no. of species	507	170	172	65	33	12	13	15	22	4	1	

In a comparison of shared, derived character states, *Pythonodipsas* is more similar to many species and genera of the viperid stock (viperines and crotalines) than it is to out-group colubrids, elapids or hydrophiids. Only *Spalerosophis diadema* shares as many derived states with vipers. The similarity of *Pythonodipsas* to vipers is apparent when this genus is compared to the total sample of 507 other species of Colubroidea, representing six families and subfamilies (Table 1).

Twenty-eight % (14) of the examined characters in *Pythonodipsas* occur in derived states

(Marx and Rabb, 1972) and these derived character states are listed in Table 2. This fourteen character array was compared with that of other species of Colubroidea. Our analysis is restricted to taxa sharing seven or more derived character states with *Pythonodipsas* and *Spalerosophis*, since there is a gap between these taxa and those sharing four or fewer derived character states (Table 1). The 27 species sharing seven or more derived character states with *Pythonodipsas* are listed in Table 2. The viperid species in this list represent three different stocks of viperines, taxa from the Palearctic and

TABLE 2. DERIVATIVE CHARACTER STATES PRESENT IN *Pythonodipsas carinatus* AND THEIR FREQUENCY DISTRIBUTION IN COLUBROIDEA SPECIES<sup>1</sup> SHARING SEVEN OR MORE DERIVATIVE CHARACTER STATES WITH *P. carinatus*.

Character	State	Description	Shared no. of species (max. 27)
7 <sup>2</sup>	2*2	Loreals more than 3	27
9	2*	Anterior temporals more than 3	27
12	2*	Eye not in contact with supralabials	27
1	2*	Dorsal head scalation with some small scales	26
31	2*	Palatine-pterygoid articulation: both bones notched, a saddle joint	25
48	2	Palatine teeth reduced in number	23
11	2	Supralabials increased in numbers	18
24	3	Subcaudals single	12
32	3	Medial wing of prefrontal small	7
17	2*	Dorsal scales smooth and keeled, intraspecific variation	1
47	4*	Enlarged maxillary teeth anterior and posterior	1
5	5	Nostril positioned dorsal in nasal shield	0
40	6	Two compound processes, medial larger	0
46	4	Maxillary fangs posterior, grooved laterally	0

<sup>1</sup> Species sharing 7 derivative states are Colubridae: *Spalerosophis diadema*; Viperinae: *Atheris superciliaris*, *Echis carinatus*, *Vipera xanthina*; Crotalinae: *Bothrops lansbergii*, *B. nummifer*, *Crotalus adamentus*, *C. atrox*, *C. cerastes*, *C. mitchelli*, *C. pusillus*, *C. ruber*, *Lachesis mutus*, *Trimersurus albolabris*, *T. flavoviridis*, *T. monticola*, *T. macrosquamatus*, *T. okinavensis*, *T. puniceus*, *T. stejnegeri*, *T. sumatranus*, *T. wagleri*; sharing 8 derivative states are Crotalinae: *Bothrops dunni*, *B. newi*, *B. schlegeli*, *Crotalus viridis*; sharing 9 derivative states are Crotalinae: *Bothrops godmani*.

<sup>2</sup> Marx and Rabb, 1972.

\* = present in *Spalerosophis diadema*.

TABLE 3. ASSOCIATION OF CERTAIN DERIVED CHARACTER STATES OF *Pythonodipsas carinatus* WITH CHARACTERS AS RECORDED IN MARX AND RABB, 1972.

Character-State <sup>1</sup> (No. of states per character)	9-2 (3)	12-2 (3)	1-2 (5)	48-2 (3)	24-3 (3)	31-2 (4)	11-2 (4)
1 <sup>2</sup>		1	—	1		1	
—		9	9	9		9	
2		2	2	2			
16		16	16				
17		17	17				17
14		14	14				
12		—	12	12			
31			31		31	—	
33		33					
40			40		40		
11		11					—
		38	38				
		48	48	—			
			7		7		
						4	4
						21	21
					46	46	
						41	
				32	32		
				22			
					13		13
					36		
					20		
					28		
	19						

<sup>1</sup> After Marx and Rabb, 1972.

<sup>2</sup> Character number, *Ibid.*

Ethiopian regions (Marx and Rabb, 1965) and a variety of ecological situations (arid land *Echis carinatus*, non-arid *Viper xanthina* from more mesic habitats and the swamp viper *Atheris superciliaris*). The same results apply to the crotalines: representatives from both the Old World and New World, unrelated stocks (rattlesnakes and nonrattlesnakes) and arboreal and terrestrial types from a variety of habitats (desert, forest, etc.). If there is no character convergence, we could conclude that *Pythonodipsas* shares a most recent ancestor with the general viperid stock rather than with any modern viperid genus or subfamily.

The character states shared with the 27 species are not restricted to a few of these taxa (Table 2). Nine of the 14 character states are shared by more than half of the species and so these account for the most striking instances of overall similarity in derived states. Thus, most of the derived character states (64%) are common to many or all of these species, suggesting

that many of the derived states were present in a common viperid ancestor. There is no ecological pattern in the array of shared, derived character states. Species with this array may be terrestrial, arboreal, aquatic or fossorial. Likewise there is no geographic pattern, except that character state 24-3 is associated with Old World colubrids.

The associations between the commonest derived (apomorphic) character states and all fifty characters reported in Marx and Rabb (1972) are tabulated in Table 3. From the pattern of association we can determine whether these derived states vary independently or covary as character complexes which might represent functional systems. Character association was assessed using a total sample of 313 colubrid species, that constitutes an outgroup to viperids. We examined derived states of different characters pairwise by constructing  $2 \times 2$  contingency tables and used a chi square test for positive association (Marx and Rabb, 1972).

TABLE 4. NUMBER OF SPECIES OF COLUBROIDEA SHARING DERIVED CHARACTER STATES WITH *Spalerosophis diadema*.

	No. of species	Number of shared derived character states								
		0	1	2	3	4	5	6	7	8-14
Colubridae	312	123	126	39	16	6	1		1	
Elapidae	68	6	43	18	1					
Hydrophiidae	42	2	11	20	5	4				
Azemiopinae	1		1							
Viperinae	34		5	1		6	12	8	2	
Crotalinae	45	1		5	2	3	20	12	2	
<i>Atractaspis</i>	5	1	2	2						
Total no. of species	507	133	188	85	24	19	33	20	5	

Character states 9-2, 12-2, 1-2 and 48-2 tend to covary with one another and with other characters, suggesting a functional unit: all but one are fragmentations of head plates. This fragmentation or shingling of small head scales probably promotes a wider gape. Fragmentation or shingling of various head plates is very rare in colubrids but is common in viperids and boids (Marx and Rabb, 1972).

The other three character states (Table 3) do not appear to covary although each of them shows associations with other characters. These

associations may represent other functional or historical complexes.

Thus, *Pythonodipsas* may be related to vipers since it shares more derived character states with them than with all but one genus of colubrid (*Spalerosophis*). Although these shared derived character states covary and may be functionally related, these states are rare in colubrids.

The osteological architecture for venom injection by viperids has been described many times and has been used to define this mono-

TABLE 5. DERIVATIVE CHARACTER STATES PRESENT IN *Spalerosophis diadema* AND THEIR FREQUENCY DISTRIBUTION IN COLUBROIDEA SPECIES SHARING 7 DERIVATIVE CHARACTER STATES WITH *S. diadema*.

Character <sup>1</sup>	State <sup>1</sup>	Description	Shared number of species (max. 5)
7	2*	Loreal more than 3	5
9	2*	Anterior temporals more than 3	5
12	2*	Eye not in contact with supralabials	5
11	3	Maximum number of supralabials	4
16	3	Maximum number of scale rows at mid-body	4
1	2*	Dorsal head scalation with some small head scales	3
31	2*	Palatine-pterygoid articulation: both bones notched, a saddle joint	3
33	2	Prefrontal with medial dorsal process	2
17	2*	Dorsal scales smooth and keeled, intraspecific variation	1
23	2	Subcaudal shields unkeeled and keeled, intraspecific variation	1
28	3	Vomer ring: lamina fenestrated, a ring complete or lamina deeply emarginated (ring incomplete or part of lamina absent, i.e. intraspecific variation)	1
47	4*	Enlarged maxillary teeth anterior and posterior	1
20	3	Ventral shields increased in number	0
21	3	Ventral shields unkeeled and keeled, intraspecific variation	0

<sup>1</sup> Marx and Rabb, 1972.

\* Present in *Pythonodipsas carinatus*.

TABLE 6. ASSOCIATION OF CERTAIN DERIVED CHARACTER STATES OF *Spalerosophis diadema* WITH CHARACTERS AS RECORDED IN MARX AND RABB, 1972.

Character-State <sup>1</sup>	9-2	12-2	1-2	16-3	31-2
(No. of states per character)	(3)	(3)	(5)	(4)	(4)
	1 <sup>2</sup>	1	—	1	1
	—	9	9	9	9
	2	2	2	2	
	17	17	17	17	
	14	14	14		
	12	—	12	12	
	31		31		—
	33	33			
	40		40		
	11	11		11	
		38	38		
		48	48		
			7		
				20	
				37	
				39	
				47	
					4
					21
					46
					41

<sup>1</sup> After Marx and Rabb, 1972.

<sup>2</sup> Character number, *Ibid.*

phyletic stock. The two most primitive viperid genera, *Azemiops* and *Causus*, have cranial osteology that unquestionably establishes them as vipers (Liem et al., 1971). Their viperid relationship has never been questioned in the modern literature (Boulenger, 1896 to present). However, they show no fragmentation of head plates, but instead have the usual primitive colubroid complement of large head plates (Marx and Rabb, 1970, 1972). These taxa function as vipers without head plate fragmentation. Fragmentation was apparently a secondary refinement during the evolution of viperids. *Pythonodipsas* has derived fragmentation of head plates, but has palatine "fangs" (Fig. 2) rather than the maxillary fangs characteristic of vipers. Thus, head plate fragmentation probably evolved independently in *Pythonodipsas* and in vipers, perhaps as an adaptation that facilitated the wide gape required for fang erection or the ingestion of large prey. We conclude that the similarities between *Pythonodipsas* and vipers represent convergence. The alternative view,

that *Azemiops* and *Causus* have secondarily consolidated their head plates, seems most unlikely for *Azemiops* and *Causus* have suites of primitive characters (Pope, 1935; Liem et al., 1971). Furthermore, the one viperid in which secondary consolidation of head scales has occurred, *Adenorhinos*, is a highly specialized earthworm feeder and here consolidation involves only lateral head and chin scales (rather than dorsal head plates) and is associated with a general foreshortening of the snout (Marx and Rabb, 1965).

*Pythonodipsas* shares more derived characters with *Spalerosophis diadema* than with any other colubrid in our sample. This non-fanged colubrid (the posterior maxillary tooth is enlarged but lacks a groove) shares seven of its fourteen derived states with the rear-fanged *Pythonodipsas*.

*S. diadema* shares as many derived states as does *Pythonodipsas* with some vipers (Table 4); fourteen of fifty characters are derived. We restrict our analysis, as before, to taxa sharing large numbers of derived character states with *Spalerosophis*. Seven derived states are shared with *Pythonodipsas* (Table 5) and four vipers: *Bitis arietans*, *Echis coloratus*, *Crotalus durissus* and *Crotalus ruber*. These four vipers represent different subfamilies from the Old and New World and they live in a variety of habitats. Furthermore, the seven commonest derived character states are not associated with any zoogeographic area. The habitat distribution of the seven character states show the same variety reported for the *Pythonodipsas* analysis.

The five commonest derived character states were identified and their associations with the total array of fifty characters are tabulated in Table 6. Four character states (9-2, 12-2, 1-2 and 16-3) covary, as does character state 31-2 to a lesser extent. Two of these 9-2 and 12-2 represent fragmentation of head plates, suggesting a functional complex.

Consequently, the derived morphology of the colubrid *Spalerosophis* suggests a relationship with vipers for the same reasons stated for *Pythonodipsas* (many shared derived character states, the suggestion of a functional complex and rarity of states elsewhere in colubrids). However, the combination of maxillary fangs and primitive head scalation in the primitive vipers *Azemiops* and *Causus* indicates that *Spalerosophis*, like *Pythonodipsas*, has independently evolved fragmented head plates. The selective pressures responsible for head scale fragmen-

tation in *Spalerosophis* are not obvious, for its anterior teeth are much smaller than the maxillary fangs of vipers or the palatine "fangs" of *Pythonodipsas*.

Are *Spalerosophis* and *Pythonodipsas* a monophyletic group? These taxa certainly share many derived character states (Tables 2, 5). However, they also differ in a comparable number of derived characters and have never been considered congeneric. For example, *Pythonodipsas* has seven derived character states (5-5, 11-2, 24-3, 32-3, 40-6, 46-4, 48-2) and palatine "fangs" that are not present in *Spalerosophis*. *Spalerosophis* has seven different derived character states (11-3, 16-3, 20-3, 21-3, 28-3, 33-3, 47-4) that are not present in *Pythonodipsas*. Furthermore all but one of the fourteen character states listed above represent different characters. Therefore we cannot conclude from the available evidence whether these taxa are related or convergent.

We wish to note that the Indian Ocean colubrid *Dityophis vivax* Günther shows fragmentation of head scales (i.e., subocular scale, small numerous temporals and a small partial suture on each parietal) (Günther, 1881). Future workers may wish to investigate the relationships of this taxon to *Pythonodipsas* and *Spalerosophis*. Parker (1949) has commented on hemipenial similarities between *Pythonodipsas* and *Dityophis*.

#### PREY HANDLING AND DIET IN *PYTHONODIPSAS* AND *SPALEROSOPHIS*

There are only a few observations on the diets of these snakes and both taxa are known to constrict prey. Boulenger (1888) retrieved two geckos (*Afroedura africana*) from the stomach of a *Pythonodipsas* and Mertens (1955) reported that Falk (1921) observed a captive snake constricting and eating a skink (*Mabuya acutilabris*). There are a few records of *Spalerosophis* feeding on small mammals (Anderson, 1898; Wall, 1914; Schmidt and Marx, 1957). H. Greene (pers. comm.) observed *Spalerosophis* constricting mice with its ventral scales facing toward its head (Green and Burghardt, 1978). One cannot conclude that *Pythonodipsas* is a lizard specialist and that *Spalerosophis* is a mammal specialist from these preliminary observations. Both taxa may feed on both lizards and mammals, since this is a common combination of prey among snakes, particularly for constricting colubrids (Arnold, 1972).

*Behavioral observation on Pythonodipsas carinatus*.—An adult *P. carinatus* fed on adult *Anolis carolinensis* on three occasions in the laboratory. Prey handling was observed twice although in both instances prey capture was not observed. On both occasions, the snake constricted the anole with a horizontal coil of two loops, with force applied by the lateral surface of the snake's body and with its ventral scales facing away from its head. This is a common constriction mode employed by colubrids (Greene and Burghardt, 1978). On the first occasion, when observation began the snake had engulfed the anole's head but retained two tight loops about the posterior trunk of the anole. The snake maintained these loops for the next four minutes while proceeding with head-first ingestion. During this interval the anole continued to breathe and clutch a rock with its hind feet. Two min later the snake loosened the constricting coil as it swallowed the trunk. The snake completed ingestion after a total of 12 min had elapsed. On the second occasion the snake was first observed holding the anole's pectoral region in its mouth with one tight and one loose loop just posterior to the snake's head, around the anole's trunk. This posture was maintained for 13 min, when the anole struggled and the snake tightened the first constricting loop. Observations were then interrupted for 15 min but at the end of this interval the snake had completely ingested the anole.

These observations indicate that *Pythonodipsas* constricts prey in a common colubrid style described by Greene and Burghardt (1978). While envenomation may have contributed to prey handling, it did not immediately immobilize the lizards. Instead the lizards continued to struggle for minutes after the initial strike and the snake maintained a constricting coil until ingestion was well advanced. In general, the sequence of events, particularly the long interval of constriction, was similar to prey handling in other rear-fanged snakes that constrict prey (e.g., *Trimorphodon*).

#### THE NEED FOR FUNCTIONAL ANALYSIS OF MORPHOLOGY

The striking convergence of *Pythonodipsas* and *Spalerosophis* with vipers is at first surprising since neither of these snakes envenomates prey with anterior teeth. The viper-like fragmentation of head scales in *Pythonodipsas* may be related to erection of palatine "fangs." The

maxillary fangs of vipers may be used to snare prey, as well as for envenomation, and, likewise, the enlarged anterior maxillary and mandibular teeth of boids and some colubrids may be used to snare prey (Frazzetta, 1966; Kardong, 1979, 1980). Does *Pythonodipsas* snare prey with its solid palatine "fangs?" If it does then these "fangs" must be rotated forward, erected during the strike, for they are recurved and probably incapable of snaring prey in their resting position. The specialized palatine-pterygoid articulation, a flange on the palatine and fragmentation of head plates are compatible with "fang" erection in *Pythonodipsas*, but only detailed observations of live animals can settle the matter. Head scale fragmentation is much less pronounced in *Spalerosophis*, but is nonetheless puzzling as an adaptation for fang erection since this snake has the anterior maxillary and palatine teeth only slightly enlarged. Perhaps head scale fragmentation in *Spalerosophis* and *Pythonodipsas*, as well as in boids and viperids, promotes the wide gape required to engulf large prey.

The imposing suite of predatory adaptations in *Pythonodipsas* underscores the need for more ecological information. This snake apparently snares prey with its palatine "fangs" and then restrains struggling prey by constriction while envenomating with its grooved posterior maxillary teeth. Even the simpler combination of constriction with envenomation by rear fangs is extremely unusual and found only in a few colubrid taxa like *Trimorphodon*. This elaborate combination of prey handling devices in *Pythonodipsas* may simply be a unique alternative solution to the general problem of subduing potentially dangerous prey, but it might be a special solution to particular ecological circumstances. Perhaps this snake must deal with geckos that are prone to escape capture by tearing their skins (Bustard, 1970:57; Mertens, 1960:107; R. Huey, pers. comm.). Or perhaps the enlarged palatine "fangs" and enlarged opposing teeth on the mandible are used to trap struggling prey in the mouth, as proposed by H. W. Greene (pers. comm.) for *Psammodynastes*. It would be very informative to observe *Pythonodipsas* feeding on its natural African prey.

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## Age, Growth and Early Life History of the Waccamaw Darter, *Etheostoma perlongum*

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**The examination of scales, otoliths and length frequency histograms indicates that *Etheostoma perlongum* is an annual darter. Adults die soon after spawning. Growth is rapid. Darters reach half average adult size between four and eight weeks. Females attain most of their adult size by month 5, and males continue to grow through month 9 (with the exception of "stunted" males in the population). Fertilized eggs are spherical, 1.2 mm in diameter, and hatch between 120 and 168 hours at 20-23 C in aquaria. Laboratory reared larvae show a full complement of 38 myomeres by 4.9 mm SL, and become juvenile by 10.2 mm SL.**

DETAILS of the life history, especially age and growth information, of many of the nearly 130 described percid fishes of the tribe Etheostomatini are poorly known. Some studies of the fishes of the genus *Percina*, including age and growth information, are reported by Page and Smith (1970, 1971), Page (1978) and Thomas (1970). Other reports of age information of fishes in the genus *Etheostoma* include the subgenera: *Catonotus* (Lake, 1936; Karr, 1964; Page, 1974, 1975; Page and Burr, 1976; Flynn and Hoyt, 1979); *Etheostoma* (Fahy, 1954; Lachner et al., 1950); *Hololepis* (Braasch and Smith, 1967; Schmidt, 1979); *Oligocephalus* (Pflieger, 1978); *Microperca* (Burr and Page, 1978, 1979); and *Nothonotus* (Raney and Lachner, 1939).

Length frequency histograms have been used to determine age classes of darter species by Fahy (1954), Flynn and Hoyt (1979), Lachner

et al. (1950), Raney and Lachner (1943) and Starnes (1977).

Difficulties in the scale method of aging fish were discussed by Carlander (1974) and problems caused by little variation in seasonal water temperature were alluded to by Starnes (1977), however, the scale method of age determination has been used successfully on darters. The first study of this type was done by Raney and Lachner (1943) who reported that *E. longimanum* lives two years and *E. olmstedii* lives two to four years.

Darters known that may not survive to a second breeding season are those of the subgenus *Microperca*. The oldest reported specimens of *E. microperca* are two years (Winn, 1958). Burr and Page (1979) reported that only 17.6% of males and 25.7% of females of *E. microperca* survive to a second growing season. *Etheostoma proeliare* is also shortlived. The oldest reported