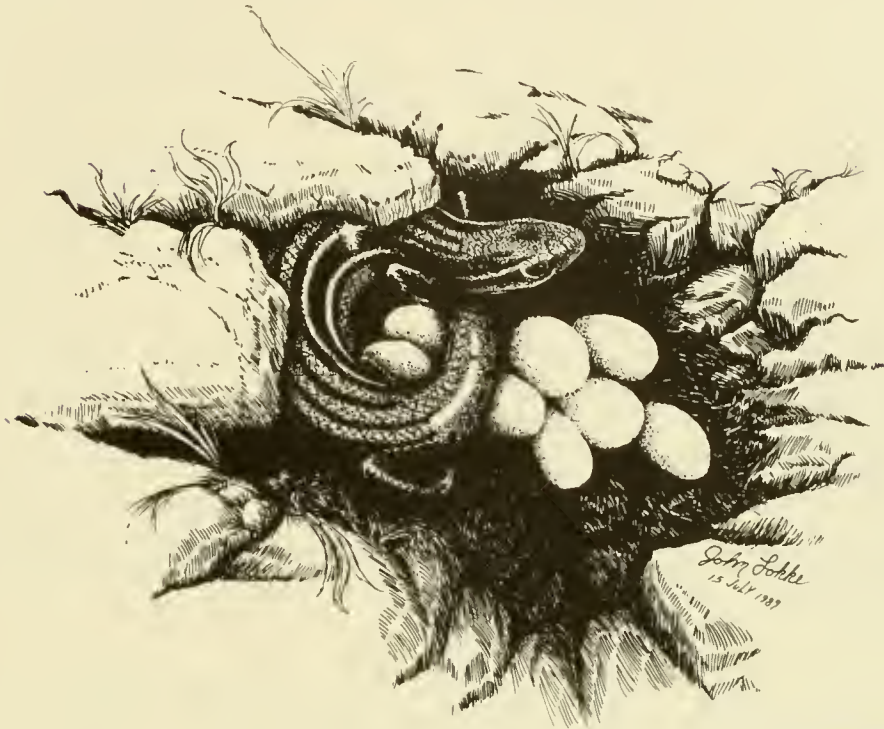


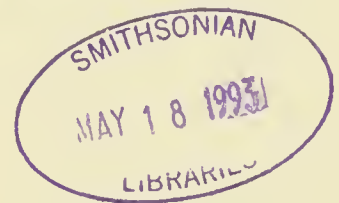
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A CATEGORIZATION AND BIBLIOGRAPHIC SURVEY
OF PARENTAL BEHAVIOR IN
LEPIDOSAURIAN REPTILES



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INTRODUCTION

Parental behavior is a significant aspect of the life history of a wide variety of animal taxa. Parental behavior is common to the vertebrate classes Osteichthyes (Blumer, 1979, 1982; Perrone and Zaret, 1979; Baylis, 1981; Gittleman, 1981; Gross and Sargent, 1985), Amphibia (McDiarmid, 1978; Wells, 1981; Nussbaum, 1985; Duellman and Trueb, 1986), and universal within the Aves (Kendeigh, 1952; Skutch, 1957, 1976; Welty, 1982; Silver et al., 1985) and Mammalia (Kleiman and Malcolm, 1981; Dewsbury, 1985; Kleiman, 1985; Malcolm, 1985). In contrast, relatively few reptiles exhibit parental behavior (Tinkle and Gibbons, 1977; Shine and Bull, 1979; Shine, 1985, 1988). Parental behavior is common in living crocodylians (Greer, 1970, 1971; Lang, 1987; Shine, 1988) and also may have been common in extinct archosaurs (Horner and Makela, 1979; Coombs, 1982; Horner, 1982, 1984, 1987; Horner and Gorman, 1988) and cynodonts (Graves and Duvall, 1983; Duvall, 1986). Accounts of parental behavior in four turtle species (Gopherus agassizii: Barrett and Humphrey, 1986; G. flavomarginatus: Carr, 1952; Janulaw and Appleton cited in Morafka, 1982; Appleton, 1986; Ernst and Barbour, 1989; Manouria emys: Louwman, 1982; McKeown et al., 1982; Trachemys stejnegeri malonei: Hodsdon and Pearson, 1943) are remarkable, because turtles generally lack any form of parental behavior (Shine, 1988; Ernst and Barbour, 1989). The purpose of this review is to survey the various categories of parental behavior reported for lepidosaurians (lizards, snakes, amphisbaenians and a rhychocephalian) and to provide an extensive bibliography as a guide to current and future researchers.

The phrase "parental care" refers to all nongametic and postfertilization contributions of parents to the survival of their offsprings (Wittenburger, 1981; Blumer, 1982) and is construed by some (Williams, 1966; Baylis, 1981; Keenleyside, 1981; Gross and Sargent, 1985; Congdon, 1989; Spotila and O'Connor, 1989) to include viviparity and other physiological contributions. I use the phrase "parental behavior" to limit the scope of this survey to all behavioral contributions by the parent to offspring survival after oviposition or parturition. Behaviors associated exclusively with oviposition and nest construction are not included in this survey; they are probably common to most oviparous lepidosaurians (Hahn, 1909; Hilzheimer, 1910; Blanchard, 1933; Carl, 1944; Carpenter, 1966; Platt, 1969; Rand and Rand, 1976; Duvall et al., 1979; Jones and Guillette, 1982; Green and Pauley, 1987).

The term "brooding" describes behaviors of the parent while attending the nest and progeny (sensu Somma, 1988; also see Pope, 1961; Peters, 1964; Carpenter and Ferguson, 1977). Thus, brooding does not include territorial, nest-site defense wherein the parent remains at a distance from the nest, and not in or on the nest or progeny, as seen in some iguanine and gekkonid lizards, and the tuatara.

HISTORICAL ASPECTS

The oldest conceivable documentation of parental behavior in a lepidosaurian is in the book of Isaiah, 34:15 (McDowell et al., 1982) written some time between 745-350 BC (Asimov, 1968). In this account, the Hebrew word "lilith," at one time interpreted as an owl (Strong, 1961; Asimov, 1968), is referred to as the "arrow snake." This vernacular name may have referred to the boid Eryx jaculus (Topsell, 1608; White, 1954). Since E. jaculus is viviparous, the snake reputed to "lay eggs and hatch, and gather them under her shadow" (McDowell et al., 1982) may refer to an oviparous snake or be erroneous, if not simply a fable.

Much of the pre-Twentieth century natural history literature indicates that many authors believed parental behavior was universal in snakes (Aristotle, [d. 322 BC]; Nicander of Colophon [135-133? BC]; Gesneri, 1551-1587; Topsell, 1608; Chateaubriand, 1827; Sundowner, 1895, 1902). The Second Voyage of Sinbad the Seaman, written in the 8th century AD (Burton, 1885-1888), is an example of early fiction that mentions a giant snake (undoubtedly a python) brooding its eggs. The "cockatrice" or "basilisk" was reputed to brood her eggs (Gesneri, 1551-1587; Topsell, 1608). It is likely that this mythical beast was a fantastical description of a cobra, either Ophiophagus hannah or a species of Naja (White, 1954; also see descriptions by Pliny the Elder, [d. AD 79]; Gesneri, 1551-1587; Topsell, 1608). Similarly, brooding was attributed to the "asp" (= Naja haje?) and the "dipsas" (= Bungarus sp.?; White, 1954) by Nicander. Modern documentation confirms that these taxa brood their eggs (Table VI).

Snakes have long been credited with the ability to swallow their young to protect them from danger (Topsell, 1608; Carver, 1778; Mease, 1807; Holmes, 1823; Hunter, 1824; Chateaubriand, 1827; Gosse, 1851; Rivers, 1874; Stanley, [19??]; Burroughs, 1908; Meek, 1946). Earliest accounts of this behavior are found in hieroglyphics attributed to the ancient Egyptians circa 2300 BC (Speck, 1923). So prevalent was (and still is!) this belief, that it was incorporated into early fiction, including the pre-Elizabethian poem, The Faerie Queene (Spenser, 1590). This alleged behavior, attributed not only to snakes but also to the lizard, Lacerta vivipara (Hopley, 1882), has been reviewed and discussed by numerous authors for more than 300 years (Browne, 1646; White, 1787; Hopley, 1882; Noble, 1921; Speck, 1921, 1923; Schmidt, 1929; Ditmars and Bridges, 1937; Angel, 1950; Klauber, 1972; Russell, 1983; Shine, 1988). Despite many inquiries into the plausibility of this behavior, no scientific evidence exists for its occurrence (Klauber, 1972; Shine, 1988).

Among saurians, Scincus scincus was reputed to care for its eggs and young (Gesneri, 1551-1587; Topsell, 1608), but no modern observations support this contention (Table V). Hoy (1883) suggested that all lizards brooded their eggs. In all likelihood, his statement is based upon observations of Ophisaurus attenuatus and Eumeces septentrionalis; these are the only egg-brooding lizards that he actually observed (Hoy, 1883). The suggestion that an amphisbaenian broods its eggs (Gesneri, 1551-1587; Topsell, 1608; Aldrovandi, 1640; reviewed in Druce, 1910), has not been verified.

CATEGORIES OF PARENTAL BEHAVIOR

The various categories of parental behavior, as reported in the literature, are listed below. The symbol in parentheses identifies the categories used in Tables I and II. The literature sources are provided in Tables V and VI.

Coil around brood (C): The attendant parent remains coiled around or covers the brood with its body, presumably creating a physical buffer or barrier between progeny and the external environment. This is the most common form of parental behavior.

Nest constructed and maintained (NC): A burrow or brood chamber is constructed by the parent and maintained while attending progeny. Although this usually involves digging a depression or burrow in the substrate, Ophiophagus hannah is known to maintain a relatively complex nest chamber constructed from surrounding vegetation (Wasey, 1892; Oliver, 1956; Leakey, 1969; Whitaker, 1977).

Defense of brood (D): Progeny are aggressively defended by parent in the presence of conspecifics or heterospecifics.

Passive protection (PP): Neonatal vipers may accrue protection from the venomous female, without her exhibiting any overt signs of aggressive behavior (i.e., Crotalus horridus: W. Martin, pers. comm.).

Thermoregulation (T): Attendant parent uses its body to maintain a relatively constant incubation temperature for developing eggs. Most, perhaps all, pythonines are able to become low-grade endotherms while brooding through "shivering thermogenesis," thereby raising the temperature of the female's body and developing eggs above that of ambient conditions (Vinegar et al., 1970; Harlow and Grigg, 1984; Shine, 1988). However, it has been suggested that shivering thermogenesis is not practiced by all species of pythons (Vinegar et al., 1970; Ellis and Chappell, 1987; but see [Orlov], 1986; Shine, 1988). It is also possible that an attendant parent could (1) provide a passive thermal barrier between eggs and the external environment with its body or (2) bask in the sun and transfer radiantly absorbed heat from its body to its eggs (Medsger, 1919, 1932; Noble and Mason, 1933; Cogger and Holmes, 1960). Python eggs, of at least two species, that are not brooded, and subsequently incubated at lower temperatures, take longer to hatch and exhibit a higher rate of developmental anomalies (Vinegar, 1973, 1974; Branch and Patterson, 1975).

Hydroregulation (H): Even though it has never been demonstrated experimentally, hydroregulation has been inferred from some squamates (Fitch, 1954; Somma, 1985b; Bels and Van den Sande, 1986; [Orlov], 1986; York and Burghardt, 1988; Somma, 1989b; Somma and Fawcett, 1989). In addition, tenuous evidence suggests that two species of snakes wet their bodies with water and then lay over the eggs, thereby reducing desiccation (Elaphe obsoleta: J. Lombard, pers. comm.; Trimeresurus wiroti: Mehrtens, 1987).

False brooding (FB): Many species of pythons continue to brood when their clutches are removed prior to hatching (T. Miller, pers. comm.), and a Python molurus has brooded without ovipositing (J. S. Foster, pers. comm.). The nongravid female P. m. bivittatus housed with two gravid conspecifics brooded when the gravid females oviposited and brooded their eggs. This "false brooding" consisted of the python laying in a conical coil and exhibiting shivering thermogenesis (J. S. Foster, pers. comm.; Somma, pers. observ.).

Oophagy (OO): The parent eats eggs or aborted ova. This is a form of parental behavior because it may prevent microbial infection of viable, healthy eggs from adjacent infected eggs (Groves, 1982; Somma, 1989a) or prevent detection of progeny by predators using olfaction (i.e., detection of chemical cues released from rotting eggs or aborted ova) to locate food (Tinkle and Gibbons, 1977; Groves, 1982; Shine, 1988). Earliest observations of this behavior may be found in Hindu scriptures dating back to 600 BC (Rao, 1957).

Removal of nonviable eggs from nest (RE): Nonviable eggs are removed from the nest, presumably at a safe distance from viable eggs. This behavior has been reported only in Python molurus (Griehl, 1982) and perhaps occurs in Gerrhonotus liocephalus (Greene cited in Tinkle and Gibbons, 1977).

Parental care of neonates (CN): A parent remains with and expresses parental behavior toward neonates after hatching or parturition.

Neonates assisted during hatching or parturition (AN): Attending parent assists neonates from eggs, extraembryonic membranes or nest chamber. In Eumeces obsoletus and E. septentrionalis, the mother licks amniotic fluid from neonates' bodies after hatching (Evans, 1959; Somma, 1987c).

Manipulation or retrieval of eggs (ME): Eggs are manipulated within the nest or moved to a new nest site. Eggs that have been removed from the nest may also be retrieved.

Communal care of eggs (CC): Eggs may be deposited in a communal clutch and attended by several unrelated parents. In some situations, this behavior could be interpreted as alloparental care (Banks and Schwaner, 1984; Somma, 1987a).

Neonatal feeding facilitated (FN): A brooding female E. obsoletus avoided taking food items in deference to its young, waiting for them to finish before she fed (Evans, 1959). This behavior has not been observed in other reptiles.

Normally does not exhibit parental behavior (NPB): Parental behavior has been reported (sometimes reliably) for individuals of species that normally abandon their progeny.

Details unknown (DU): Details of parental behavior are not known or not reported.

Reliability uncertain (RU): Reliability of report regarded as uncertain or possibly unreliable due to paucity of information provided or observed by the author.

Erroneous documentation (E): Report considered unsubstantiated due to inadequate information for a species normally lacking parental behavior.

DISCUSSION

Over 6140 extant species of lepidosaurian reptiles are currently recognized (Bellairs, 1986); of these, parental behavior has been reported for 210 species. Only 148 species (82 lizards, 65 snakes, and Sphenodon) are represented by reliable documentation or approximately 2.4% of all lepidosaurians (Table III). These species represent 17 families, excluding the unsubstantiated documentation for the Hydrophiidae, Typhlopidae and the unidentified amphisbaenid family (Tables I, II, III). Parental behavior is common in Eumeces, Phelsuma, Uromastix, anguids, xantusiids, iguanines, oviparous boids, southeast-Asian elapids, oviparous viperids, Elaphe, Farancia, and Psammophylax (Tables I and II). In most species (96%) parental behavior is entirely maternal; however, paternal and biparental behavior have been confirmed (Table IV).

The literature in this survey (Tables V and VI) demonstrates a paucity of experimentally obtained data on parental behavior in lepidosaurians (but see Noble and Mason, 1933; Hutchison et al., 1966; Vinegar et al., 1970; Van Mierop and Barnard, 1976_a, 1978; Hasegawa, 1985, Somma, 1985_b; [Orlov], 1986; Ellis and Chappell, 1987; York and Burghardt, 1988; Graves, 1989; Somma and Fawcett, 1989; Vitt and Cooper, 1989; Guillette et al., in review). The majority of the literature is descriptive or anecdotal, and the adaptive functions of this life history trait remain largely conjectural. Furthermore, the only ecological/evolutionary analysis devoted solely to parental behavior in reptiles is provided by Shine (1988; see Lillywhite, 1988).

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The cover illustration depicts a female Eumeces s. septentrionalis from Nebraska brooding eggs. I thank John F. Lokke for creating the original artwork from which the illustration was copied.

TABLE I

Distribution of parental behavior in lizards, amphisbaenians
and a rhynchocephalian

Taxa	Type of parental behavior	Oviparous or viviparous	Maternal, paternal or biparental
Agamidae			
<u>Leiolepis belliana</u>	RU, CN	O	B?
<u>Phrynocephalus</u> sp.	RU, CN	O	B
<u>Uromastix aegyptius</u>	D	O	M
<u>U. ornatus</u>	D, CN	O	M
Anguidae			
<u>Barisia imbricata</u>	AN	V	M
<u>Diploglossus bilobatus</u>	C	O	M
<u>D. delasagra</u>	C	O	P
<u>Elgaria coerulea</u>	AN	V	M
<u>E. multicaudata</u>	C, NC, D, CC	O	M
<u>Gerrhonotus liocephalus</u>	C, OO?, RE?	O	M
<u>Mesaspis moreleti</u>	AN	V	M
<u>Ophisaurus apodus</u>	C, D	O	M
<u>O. attenuatus</u>	C, OO	O	M
<u>O. compressus</u>	C	O	M
<u>O. gracilis</u>	C	O	M
<u>O. harti</u>	C	O	M
<u>O. ventralis</u>	C, ME, OO	O	M
Cordylidae			
<u>Cordylus cataphractus</u>	CN	V	B
<u>C. giganteus</u>	CN	V	M
Gekkonidae			
<u>Ailuronyx seychellensis</u>	C, D, OO, AN?	O	M
<u>Chondrodactylus angulifer</u>	RU, D?	O	M
<u>Eublepharis macularis</u>	RU, D, NPB	O	M
<u>Gekko gekko</u>	C, D, NPB?	O	M, P
<u>G. petricolus</u>	C, D, OO	O	M, P
<u>G. smithii</u>	RU, DU	O	M

<u>Hemidactylus turcicus</u>	D, NPB?	O	M
<u>Hemiphyllodactylus typus</u>	RU, DU	O	M
<u>Naultinus grayi</u>	CN, D	V	B
<u>Phelsuma borbonica</u>	D	O	M
<u>P. dubia</u>	D, OO	O	M
<u>P. flavigularis</u>	D, OO	O	M
<u>P. lineata</u>	D, OO	O	M
<u>P. madagascariensis</u>	D, OO	O	M
<u>P. standingi</u>	ME	O	M
<u>Phyllodactylus lanei</u>	C, CC	O	M
<u>Ptychozoon lionotum</u>	C, D	O	M
<u>Teratoscincus scincus</u>	RU, NPB?	O	M
Iguanidae			
<u>Amblyrhynchus cristatus</u>	D	O	M
<u>Brachylophus fasciatus</u>	D	O	M
<u>B. vitiensis</u>	D	O	M
<u>Conolophus pallidus</u>	D	O	M
<u>C. subcristatus</u>	D	O	M
<u>Crotaphytus collaris</u>	RU, NPB	O	M
<u>Cyclura carinata</u>	D	O	M
<u>C. cornuta</u>	D	O	M
<u>C. cychlura</u>	D	O	M
<u>C. nubila</u>	D	O	M
<u>Iguana iguana</u>	D	O	M
<u>Phrynosoma douglassi</u>	RU, D, NPB	V	M
<u>Sauromalus varius</u>	D	O	M
<u>Sceloporus undulatus</u>	E, CN	O	B
Lacertidae			
<u>Acanthodactylus scutellatus</u>	RU, CN	O	M
<u>Lacerta viridis</u>	D?, ME	O	M
Scincidae			
<u>Calyptotis scutirostrum</u>	ME, NC	O	M
<u>Corucia zebzata</u>	CN, D, AN?	V	M
<u>Cyclodina pseudornata</u>	AN	V	M
<u>Egernia cunninghami</u>	AN, D	V	M
<u>E. striata</u>	RU, CN	V	M
<u>E. whitii</u>	RU, CN	V	?
<u>Emoia cyanura</u>	RU, CC?	O	M
<u>Eumeces anthracinus</u>	C, D, NC, OO	O	M
<u>E. callicephalus</u>	C, OO, NC, ME	O, V*	M
<u>E. chinensis</u>	C, NC	O	M
<u>E. copei</u>	CN	V	M
<u>E. egregius</u>	C, D, NC, CC	O	M
<u>E. elegans</u>	C	O	M
<u>E. fasciatus</u>	CN, C, D, ME, NC, OO, H?, CC	O	M
<u>E. inexpectatus</u>	C, OO, CC	O	M
<u>E. laticeps</u>	C, D, NC, ME, OO, CN, CC	O	M
<u>E. laticutatus</u>	C, CN	O	M
<u>E. lynxe</u>	CN	V	M
<u>E. multivirgatus</u>	C, CN?, CC	O	M
<u>E. obsoletus</u>	C, ME, NC, CN, FN, D, OO	O	M

<u>E. okadae</u>	C, NC, OO, ME, CC	O	M
<u>E. oshimensis</u>	DU	O	M
<u>E. parviauriculatus</u>	CN	O	M
<u>E. quadrilineatus</u>	DU	O	M
<u>E. schneiderii</u>	C	O	M
<u>E. septentrionalis</u>	C, D, NC, H, ME, CN, CC, OO, AN	O	M
<u>E. skiltonianus</u>	C, D, NC, ME, CN?	O	M
<u>E. stimsoni</u>	RU, DU	O	M
<u>E. tetragrammus</u>	C	O	M
<u>E. xanthi</u>	C	O	M
<u>Lampropholis mustelina</u>	ME, NC	O	M
<u>Leiolopisma otagense</u>	AN	V	M
<u>L. smithi</u>	AN	V	M
<u>L. zia</u>	ME, NC	O	M
<u>Mabuya capensis</u>	AN	V	M
<u>M. macrorhyncha</u>	AN	V	M
<u>M. macularia</u>	RU, DU	O	M
<u>Neoseps reynoldsi</u>	C	O	M
<u>Scincus scincus</u>	E?, CN	O	M
<u>Sphenomorphus quoyii</u>	AN	V	M
<u>Tiliqua rugosa</u>	AN	V	M
 Teiidae			
<u>Tupinambis teguixin</u>	C, D, CN?, NC, AN?	O	M
<u>T. rufescens</u>	NC, D?	O	M
 Varanidae			
<u>Varanus gouldii</u>	E, AN	O	?
<u>V. griseus</u>	RU, DU	O	M
<u>V. komodoensis</u>	RU, AN, NPB?	O	M
<u>V. mitchelli</u>	RU, C	O	M
<u>V. salvator</u>	RU, D?, NPB	O	M
<u>V. varius</u>	AN	O	M
 Xantusiidae			
<u>Xantusia henshawi</u>	AN	V	M
<u>X. vigilis</u>	AN	V	M
 Trogonophidae or Amphisbaenidae (?)			
'Amphisbaina' (= unidentified species)	RU, C	O	M
 Sphenodontidae			
<u>Sphenodon punctatus</u>	D	O	M

*One instance of viviparity in E. callicephalus has been reported by Taylor (1985).

TABLE II

Distribution of parental behavior in snakes

Taxa	Type of parental behavior	Oviparous or viviparous	Maternal, paternal or biparental
Boidae			
<u>Aspidites melanocephalus</u>	C, T	O	M
<u>Boa constrictor</u>	RU, C, D, NPB	V	M
<u>Casarea dussemieri</u>	RU, C	O	M
<u>Chondropython viridis</u>	C, T, D, H	O	M
<u>Epicrates cenchria</u>	AN, OO, D, CN	V	M
<u>E. striatus</u>	OO	V	M
<u>E. subflavus</u>	E, C	V*	M
<u>Eunectes murinus</u>	AN, OO	V	M
<u>E. notaeus</u>	AN, OO	V	M
<u>Liasis albertisii</u>	C, D, T	O	M
<u>L. boa</u>	C	O	M
<u>L. childreni</u>	C	O	M
<u>L. fuscus</u>	C, T, D, H	O	M
<u>L. olivaceus</u>	C	O	M
<u>L. papuanus</u>	C, T	O	M
<u>L. perthensis</u>	C	O	M
<u>Morelia amethystina</u>	C, T, CC	O	M
<u>M. bredli</u>	C	O	M
<u>M. spilota</u>	C, T, H, D, NC	O	M
<u>Python anchietae</u>	C, T	O	M
<u>P. curtus</u>	C, T	O	M
<u>P. molurus</u>	C, T, D, FB, RE, CN?, H?, ME	O	M
<u>P. regius</u>	C, T, D, H, ME	O ⁺	M
<u>P. reticulatus</u>	C, T?, D	O	M
<u>P. sebae</u>	C, T?, D, ME, RE	O	M
<u>P. timoriensis</u>	C, T	O	M
'Lilith' or 'arrow snake' (= <u>Eryx jaculus?</u>)	E?, C	V	M
Colubridae			
<u>Ahaetulla nasuta</u>	OO	V	M
<u>Amphiesma stolata</u>	C	O	M
<u>Atretium schistosum</u>	RU, C	O	M
<u>Cemophora coccinea</u>	E, C, OO	O	M
<u>Cerberus rynchops</u>	RU, CN	V	M
<u>Clelia clelia</u>	C, H?	O	M
<u>Coronella austriaca</u>	RU, CN	V	M
<u>Diadophis punctatus</u>	C, NPB, CC?	O	M
<u>Elaphe climacophora</u>	C	O	M
<u>E. flavolineata</u>	C	O	M
<u>E. guttata</u>	RU, C, NPB	O	M
<u>E. obsoleta</u>	C, D, H?, NPB, CC?	O	M, B?
<u>E. quadrivirgata</u>	C, D	O	M
<u>E. quatuorlineata</u>	RU, C, NPB	O	M
<u>E. schrenki</u>	RU, C	O	M

<u>Farancia abacura</u>	C, NC, CN?	0	M
<u>F. erythrogramma</u>	RU, C	0	M
<u>Heterodon platirhinos</u>	E, C, D	0	M
<u>Hydrodynastes gigas</u>	RU, C	0	M
<u>Lampropeltis triangulum</u>	RU**, C, NPB	0	M
<u>Lycodon aulicus</u>	RU, C	0	M
<u>L. striatus</u>	RU, C	0	M
<u>Masticophis flagellum</u>	E, CN	0	B
<u>Natrix natrix</u>	C, D, NPB	0	M
<u>Oligodon taeniolatus</u>	RU, C	0	M
<u>Opisthotropis latouchii</u>	C, H?	0	M
<u>Pituophis catenifer</u>	E, C, D	0	M
<u>Psammophylax rhombeatus</u>	C, CC	0	M
<u>P. tritaeniatus</u>	C	0	M
<u>P. variabilis</u>	C	0 (V)	M
<u>Ptyas korros</u>	RU, C	0	M
<u>P. mucosus</u>	C	0	M
<u>Rhabdophis subminiata</u>	C	0	M
<u>Sinonatrix percarinata</u>	C	0	M
<u>Tropidonophis mairii</u>	C	0	M
<u>Xenochrophis piscator</u>	C, NC	0	M
Elapidae			
<u>Bungarus caeruleus</u>	C	0	M
<u>B. candidus</u>	C	0	M
<u>B. ceylonicus</u>	C, CC?, NC, CN?	0	B?
<u>B. fasciatus</u>	C, CN?	0	M, B?
'Dipsas' (= <u>Bungarus</u> sp.?)	RU, CN?	0	M
<u>Calliophis maculiceps</u>	RU, D?	0	M
<u>Demansia papuensis</u>	RU, DU	0	M
<u>Micrurus fulvius</u>	RU, C, NPB	0	M
<u>M. psyches</u>	RU, DU	0	M
<u>Naja melanoleuca</u>	C	0	M, B?
<u>N. naja</u>	C, D, NC, OO	0	M, B
<u>N. nigricollis</u>	RU, DU	0	M
'Asp' (= <u>Naja</u> <u>haje</u> ?)	RU, D	0	M
<u>Ophiophagus hannah</u>	C, NC	0	M
'Cockatrice' or 'basilisk' (= <u>Ophiophagus</u> <u>hannah</u> or <u>Naja</u> sp.?)	RU, C	0	M
<u>Pseudechis butleri</u>	RU, C, D	0	M
<u>Pseudonaja textilis</u>	RU, C, NPB	0	M
Hydrophiidae			
<u>Pelamis platurus</u>	E, CN, C	V	M
Laticaudidae			
<u>Laticauda colubrina</u>	C, D, CN?	0	M
<u>L. semifasciata</u>	RU, DU	0	?
Leptotyphlopidae			
<u>Leptotyphlops dulcis</u>	C	0	M
<u>L. humilis</u>	E?, C	0	M

Typhlopidae			
<u>Ramphotyphlops braminus</u>	RU, C, NPB	O	M
<u>Rhinotyphlops caecus</u>	RU, DU	O	M
Viperidae			
<u>Agkistrodon contortrix</u>	RU, CN, D	V	M
<u>A. piscivorus</u>	RU, CN, D?	V	M
<u>Calloselasma rhodostoma</u>	C, H, D	O	M
<u>Causus rhombeatus</u>	C	O	M
<u>Crotalus sp.</u>	RU, CN	V	M
<u>C. adamanteus</u>	E?, CN, D	V	M
<u>C. atrox</u>	CN, PP	V	M
<u>C. horridus</u>	CN, PP	V	M
<u>C. viridis</u>	CN, D, PP	V	M
<u>Deinagkistrodon acutus</u>	C	O	M
<u>Lachesis muta</u>	C, D	O	M
<u>Porthidium nummifer</u>	RU, CN	V	M
<u>Sistrurus catenatus</u>	RU, CN	V	M
<u>Trimeresurus kaulbacki</u>	DU, D?	O	M
<u>T. monticola</u>	C, D	O	M
<u>T. okinavensis</u>	C, D	O (V)	M
<u>T. wiroti</u>	C, H?	O	M
<u>Vipera aspis</u>	RU, CN, PP?	V	M
<u>V. berus</u>	CN, PP	V	M

*This species is viviparous (Lynn and Grant, 1940), not oviparous as reported by Gosse (1851). Perhaps Gosse confused an oviparous colubrid for E. subflavus.

**Female L. triangulum remain coiled around their eggs for a brief period after oviposition in order to compress them into an adherent mass before abandoning them (McCauley, 1945; Green and Pauley, 1987). This may account for the considerable number of references (Table VI) suggesting that this species broods its eggs.

+There is an unverified report of viviparity in P. regius (Anonymous, 1941).

TABLE III

Summary of the number of species and genera exhibiting parental behavior within lepidosaurian taxa (based on Tables I and II)

Taxa	Number* of genera	Number* of species
Squamata	107 (69)	209 (147)
Amphisbaenia	1 (0)	1 (0)
Trogonophidae or Amphisbaenidae (?)	1 (0)	1 (0)
Sauria	48 (36)	104 (82)
Agamidae	3 (1)	4 (2)
Anguidae	6 (6)	13 (13)

Cordylidae	1 (1)	2 (2)
Gekkonidae	11 (7)	18 (13)
Iguanidae	9 (6)	14 (11)
Lacertidae	2 (1)	2 (1)
Scincidae	13 (11)	41 (35)
Teiidae	1 (1)	2 (2)
Varanidae	1 (1)	6 (1)
Xantusiidae	1 (1)	2 (2)
Serpentes	58 (33)	104 (65)
Boidae	10 (7)	28 (24)
Colubridae	25 (14)	36 (20)
Elapidae	8 (3)	14 (7)
Hydrophiidae	1 (0)	1 (0)
Laticaudidae	1 (1)	2 (1)
Leptotyphlopidae	1 (1)	2 (1)
Typhlopidae	2 (0)	2 (0)
Viperidae	10 (7)	19 (12)
Rhynchocephalia	1 (1)	1 (1)
Sphenodontidae	1 (1)	1 (1)

*Number in parentheses represents actual total when erroneous and uncertain accounts are deleted from analysis (see Tables I and II).

TABLE IV

Prevalence of maternal, paternal and biparental behavior in lepidosaurians

Parent exhibiting behavior	Number* of species	Percent* of total
Maternal only	193 (142)	92.0 (96)
Paternal only	1 (1)	0.5 (0.7)
Biparental only	7 (2)	3.0 (1.3)
Maternal and biparental	4 (1)	2.0 (0.7)
Paternal or maternal	2 (2)	1.0 (1.3)
Sex of parent unknown	3 (0)	1.5 (0)

*Number in parentheses represents actual value when erroneous and uncertain sources are deleted from analysis.

TABLE V

Bibliographic sources for reports of lizard, amphisbaenians and
rhynchocephalian parental behavior

Taxa	Sources
Agamidae	
<u>Leiolepis belliana</u>	Boulenger, 1903
<u>Phrynocephalus</u> sp.	Bertin and Burton, 1967
<u>Uromastix aegyptius</u>	Mendelssohn and Bouskila, 1989; H. Mendelssohn, pers. comm.
<u>U. ornatus</u>	Mendelssohn and Bouskila, 1989; G. Perry, pers. comm.; H. Mendelssohn, pers. comm.
Anguidae	
<u>Barisia imbricata</u>	Guillette and Hotton, 1986
<u>Diploglossus bilobatus</u>	Taylor, 1956
<u>D. delasagra</u>	Barbour and Ramsden, 1919
<u>Elgaria coerulea</u>	Stewart in Guillette and Hotton, 1986, and pers. comm.
<u>E. multicarinata</u>	Langerwerf, 1981; Jes, 1987
<u>Gerrhonotus liocephalus</u>	Greene and Dial, 1966; Greene in Tinkle and Gibbons, 1977
<u>Mesaspis moreleti</u>	Greene in Guillette and Hotton, 1986
<u>Ophisaurus apodus</u>	Petzold, 1971; Langerwerf, 1981, 1984; Claffey and Johnson, 1982 _{a, b} ; Huff, 1985
<u>O. attenuatus</u>	?Hoy, 1883; Collins, 1959; Blair, 1961; Fitch, 1970, 1986, 1989; Vogt, 1981
<u>O. compressus</u>	Bartlett, 1985
<u>O. gracilis</u>	Wall, 1908; Smith, 1935; Jayaram, 1974; Daniel, 1983
<u>O. harti</u>	Pope, 1929, 1955
<u>O. ventralis</u>	Noble and Mason, 1932, 1933; Telford, 1952; Vinegar, 1968; Villiard, 1969; Mount, 1975; Somma, pers. observ.
Cordylidae	
<u>Cordylus cataphractus</u>	Branch, 1988; S. Jacobs, pers. comm.
<u>C. giganteus</u>	Patterson and Bannister, 1987; S. Jacobs, pers. comm.
Gekkonidae	
<u>Ailuronyx sechellensis</u>	High, [1976]; Miller, 1980; McKeown and Miller, 1985; Slavens, 1987
<u>Chondrodactylus angulifer</u>	Miller, 1983 _a
<u>Eublepharis macularis</u>	Miller, 1980
<u>Gekko gecko</u>	Honegger, 1969; Koch, 1972; Zaworski, 1987 _{a, c} , 1988; T. Miller, pers. comm.
<u>G. petricolus</u>	Zaworski, 1987 _{a, b}
<u>G. smithii</u>	Tho and Ho, 1979
<u>Hemidactylus turcicus</u>	Somma, pers. obs.
<u>Hemiphyllodactylus typus</u>	Eijsden, 1978
<u>Naultinus grayi</u>	Robb, 1980; J. Fawcett, pers. comm.

- Phelsuma borbonica Miller, 1982
P. dubia Osadnik, 1984
P. flavigularis Osadnik, 1984
P. lineata Osadnik, 1984
P. madagascariensis Osadnik, 1984; Rösler, 1988
P. standlingi Digney and Tytle, 1983
Phyllodactylus lanei Z. Uribe, pers. comm.; A. Ramírez, pers. comm.
Ptychozoon lionotum Waitkus, 1983; Tytle et al., 1987
Teratoscincus scincus Miller, 1983b
- Iguanidae
- Amblyrhynchus cristatus Heller, 1903; Eibl-Eibsfeldt, 1966; Trillmich, 1979; Fitch, 1982; Dellinger, 1989
Brachylophus fasciatus Cogger, 1974; Gibbons and Watkins, 1982
B. vitiensis Gibbons and Watkins, 1982; Gibbons, 1984/85
Conolophus pallidus Christian and Tracy, 1982
C. subcristatus Werner, 1982
Crotaphytus collaris Burt and Hoyle, 1934
Cyclura carinata Iverson, 1977, 1979
C. cornuta Shaw, 1969; Wiewandt, 1977, 1979; Boylan, 1984
C. cychlura Carey, 1975
C. nubila Shaw, 1954; Crutchfield, 1982, 1986; Thompson in Blair, 1983a, b
Iguana iguana Alvarez del Toro, 1960; Mertens, 1960; Wiewandt, 1982; Ellison, 1985
Phrynosoma douglassi Lockwood, 1883
Sauromalus varius Lawler and Jarchow, 1986; Lawler in Gilbert, 1987; Castillo S., 1989
Sceloporus undulatus Hay, 1892
- Lacertidae
- Acanthodactylus scutellatus G. Perry, pers. comm.
Lacerta viridis Mertens, 1960; Burton and Burton, 1984
- Scincidae
- Calyptotis scutirostrum Ehmann, 1988
Corucia zebrata Hediger, 1937, 1986; Slavens, 1983; Honegger, 1985; Mehaffey, 1986; Peterson, 1986; A. Anderson, pers. comm.
Cyclodina pseudornata J. Fawcett, pers. comm.
Egernia cunninghami Niekisch, 1975, 1980; Zimmermann, 1986
E. striata Pianka and Giles, 1982
E. whitii McPhee, 1979
Emoia cyanura J. Fitch in Fitch, 1970
Eumeces anthracinus Clausen, 1938; Dowling, 1950; Hamilton, 1958; Anderson, 1965; Cooper et al., 1973; Collins, 1975
E. callicephalus Campbell and Simmons, 1961; Zweifel, 1962; Williamson, 1986; Tanner, 1987, and pers. comm.
E. chinensis [Wang, 1966]
E. copei L. Guillette, pers. comm.
E. egregius Hamilton and Pollack, 1958; Mount, 1961, 1963; Somma, pers. observ.

- E. elegans
E. fasciatus*
- Mell, 1929; Hikida, 1981
 Ditmars, 1904, 1907; Allard, 1909; Ruthven, 1911; Dunn, 1920; Blanchard, 1922; Bishop, 1926; Burt, 1928, 1937; Corrington, 1929; Klots, 1930; Noble and Mason, 1932, 1933; Burt and Burt, 1935, Taylor, 1935; Conant, 1938, 1951; McCauley, 1939, 1945; Cagle, 1940; Anderson, 1942, 1965; McClellan et al., 1943; Minton, 1944, 1972; H. Smith, 1946; Neill, 1948; Evans and Roeker, 1951; Fitch, 1954, 1967; Parmalee, 1955; Kennedy, 1956; Reynolds, 1959; Tinkle, 1959, P. Smith, 1961; Leviton, [1972]; Snyder, 1972; Burghardt, 1973; Mount, 1975; Fitch and von Achen, 1977; Vogt, 1981; Groves, 1982; Lang, 1982, 1983; Cooper et al., 1983; Cooper and Vitt, 1985; Stewart and Duvall, 1985; Vitt and Cooper, 1986, 1989; Green and Pauley, 1987; Johnson, 1987; Cochran, 1989; Somma, pers. observ.
- E. inexpectatus
- Smith, 1946; Duellman and Schwartz, 1958; Hamilton, 1958; Molchos, 1971; ?Loop and Scoville, 1972; Mount, 1975; Vitt and Cooper, 1986; Dundee and Rossman, 1989; Somma, pers. observ.
- E. laticeps
- Hurter, 1911; Noble and Mason, 1932, 1933; Taylor, 1935; Cook, 1943; McClellan et al., 1943; Mansueti, 1948; Martof, 1956; Smith, 1961; Mount, 1975; Johnson, 1979; Moehn, 1980; Schuette, 1980; Ashton and Ashton, 1985; Cooper and Vitt, 1985; Hammond, 1985; Vitt and Cooper, 1985_a, _b, 1989; Green and Pauley, 1987; Johnson, 1987; Meshaka et al., 1988; Somma, pers. observ.
- E. laticutatus
E. lynxe
E. multivirgatus
- Sengoku, 1979; Hikida, 1981; [Mathui, 1985]
 L. Guillette, pers. comm.
 Gehlbach, 1965; Van Devender and Van Devender, 1975; A. Aquino, pers. comm.; J. Lynch, pers. comm.
- E. obsoletus
- Taylor, 1935; Smith, 1946; Fitch, 1955, 1956, 1964, 1967, 1970; Fouquette and Lindsay, 1955; Evans, 1959; Hall, 1972; Hall and Fitch, 1972; J. Lynch, pers. comm.; Somma, pers. observ.
- E. okadae
- [Hikida, 1975]; Sengoku, 1979; Hasegawa, 1984, 1985, and pers. comm.; [Mathui, 1985]
- E. oshimensis
E. parviauriculatus
E. quadrilineatus
E. schneiderii
E. septentrionalis
- Toyama, 1975
 Tanner, 1987, and pers. comm.
 Mell, 1929
 Zimmermann, 1986
 ?Hoy, 1883; Breckenridge, 1941, 1943, 1944; Smith and Slater, 1949; Nelson, 1963; Bredin, 1981, 1989 [pers. comm.]; Lang, 1982, 1983; [Gerholdt], 1984_b; Somma, 1985_a, _b, _c, 1987_a, _b, _c, 1989_a; Somma and Fawcett, 1985, 1989; McAllister, 1987; (reviewed in Somma and Cochran, 1989)

- E. skiltonianus Heller in McClain, 1899**; Van Denburgh, 1922; Woodbury, 1931; Tanner, 1943, 1957
- E. stimsoni Taylor, 1935
- E. tetragrammus Strecker, 1908; Werler, 1951; Behler and King, 1979
- E. xanthi Pope in Schmidt, 1927; Mell, 1929
- Lampropholis mustelina Ehmann, 1988
- Leiolopisma otagense Smithells in Sharrell, 1966
- L. smithii J. Fawcett, pers. comm.
- L. zia Ehmann, 1988
- Mabuya capensis Rose, 1929, 1950; FitzSimons, 1943
- M. macrorhyncha Rebouças-Spieker and Vanzolini, 1978
- M. macularia Daniel, 1983
- Neoseps reynoldsi Telford, 1959
- Sphenomorphus quoyii Shine, 1988
- Scincus scincus Gesneri, 1551-1587; Topsell, 1608
- Tiliqua rugosa Mertens, 1960; Hitz, 1983
- Teiidae
- Tupinambis teguixin Reese, 1922; Krieg, 1925; Fitzgerald et al., 1989, In press
- T. rufescens Fitzgerald et al., 1989, In press
- Varanidae
- Varanus gouldii Berney, 1936
- V. griseus Auffenberg, 1981
- V. komodoensis Lallemand, 1929; Pfeffer, 1959; Auffenberg, 1981
- V. mitchelli Gow in Shine, 1988
- V. salvator Biswas and Kar, 1981
- V. varius Cogger, 1967, and in Shine, 1988; Mertens, 1987; Carter, 1989, and pers. comm.
- Xantusiidae
- Xantusia henshawi Shaw, 1949
- X. vigilis Cowles, 1944; Miller, 1954
- Trogonophidae or Amphisbaenidae (?)
- 'Amphisbaina' (= species?) Gesneri, 1551-1587; Topsell, 1608; Aldrovandi, 1640
- Sphenodontidae
- Sphenodon punctatus Thompson, 1988, and in Shine, 1988 and Heaton-Jones, 1989; Guillette et al., in review

*Prior to 1932, Eumeces inexpectatus and E. laticeps were included within the species E. fasciatus (Cope, 1900; Davis, 1968; Steiner, 1986). The fasciatus group was divided into three species by Taylor (1932a, b, 1935); E. fasciatus, E. inexpectatus and E. laticeps. Consequently, some references pertaining to E. fasciatus prior to 1932 may actually refer to either, E. inexpectatus or E. laticeps.

**Identity of species as described in this account is uncertain. This could refer to Eumeces gilberti; if so, it is the only record of brooding in this species.

TABLE VI

Bibliographic sources for reports of snake parental behavior

Taxa	Sources
Boidae	
<u>Aspidites melanocephalus</u>	Ross, 1978; Boos, 1979; Murphy et al., 1981; Barker, 1982, 1985; Charles et al., 1985
<u>Boa constrictor</u>	Lanworn, 1972; Wells, 1981
<u>Casarea dussumieri</u>	Bloxam, 1984
<u>Chondropython viridis</u>	Kibler in Lederer, 1944; Pope, 1961; Kratzer, 1962; MacKay, 1973; Switak, 1975; Walsh, 1977, [1980]; Ross 1978; Olexa, 1979; Christian, 1981; Engelmann and Obst, 1981; Slavens, 1982, 1983, 1984, 1985, 1987; Hudson, 1983; Van Mierop et al., 1983; Zulich, 1983, 1985; [Orlov], 1986; Wexo, 1987
<u>Epicrates cenchria</u>	Boos, 1976; Brunner, 1979; Groves, 1981; Walsh and Davis, 1984
<u>E. striatus</u>	Huff, 1980; Slavens, 1987
<u>E. subflavus</u>	Gosse, 1851
<u>Eunectes murinus</u>	Neill and Allen, 1962; Holmstrom and Behler, 1981
<u>E. notaeus</u>	Holmstrom, 1981; Slavens, 1985, 1988; Townson, 1985
<u>Liasis albertisii</u>	Kinghorn, 1956; Johnson, 1975; Ross and Larman, 1977; Ross, 1978; Tarbet, 1984; Slavens, 1986; B. Clark, pers. comm.
<u>L. boa</u>	Barker, 1982; Mehrtens, 1987
<u>L. childreni</u>	Ross, 1973, 1980a, 1983; Dunn, 1979a; Sheargold, 1979; Barker, 1982; Slavens, 1988
<u>L. fuscus</u>	Kinghorn, 1956; Gow, 1976; Ross and Larman, 1977; Ross, 1978, 1980b; Boos, 1979, 1983; McPhee, 1979; Barker, 1982; Weidner in Funk, 1982; Orlov, 1982; Bulian and Broer, 1984; Charles et al., 1985; [Orlov], 1986; Mehrtens, 1987; Shine, 1988
<u>L. olivaceus</u>	Kinghorn, 1956
<u>L. papuanus</u>	Tryon, 1985; Tryon and Whitehead, 1988
<u>L. perthensis</u>	Stafford, 1986
<u>Morelia amethystina</u>	Pope, 1961; Ross, 1978; Boos, 1979; McPhee, 1979; Parker, [1982]; Banks and Swaner, 1984; Charles et al., 1985; Grow, 1987; B. Clark, pers. comm.

M. bredli
M. spilota

Gow, 1981, 1983
Allan in G. Krefft, 1869; P. Krefft, 1926;
Fleay, 1956; Cogger and Holmes, 1960;
Gow, 1976, 1983; Ross, 1978; Worrel in
Boos, 1979; McPhee, 1979; Harlow in
Shine, 1980; Weidner in Funk, 1982;
Broer, 1983; Burton and Burton, 1984;
Harlow and Grigg, 1984; Charles et al.,
1985; Bels and Van den Sande, 1986; Slip,
1986; Lombard, 1987; Slip and Shine,
1988_a, _b; Anonymous, [19??]

Python anchietae
P. curtus

McLain, 1983; Laszlo, 1984; Branch, 1988
Noble, 1935; Stemmler, 1969; Vinegar et
al., 1970; Reitinger and Lee, 1978;
Katuska, 1983; Stafford, 1986; Trutnau,
1986; T. Weidner, pers. comm.

P. molurus

Bennett, 1824; Lamarrepiquot [=Lamarre-
Piquot], 1835_a; Valenciennes, 1841_a, _b;
Duméril, 1842; Lamarre-Piquot, 1835_b,
1842, 1858_a, _b; Forbes, 1881; Holland in
Hopley, 1882; Marshall, 1893; Pinkert,
1893; Kern, 1907; Wall, 1912, 1921;
Abercromby, 1913; Doflein, 1914; Krogh,
1916; Leigh, 1926, 1936; Lederer, 1928,
1944, 1956; Schlott, 1935; Kopstein,
1938; Patsch, 1943; Smith, 1943; Walker
and Stoddart in Angel, 1950; Deraniyagala
1955; Stemmler-Morath, 1956; Vogel,
[1958?]; Anonymous, 1960_a, Dowling, 1960;
Lutz, 1962; Deoras, 1965; Wendt, 1965;
Hutchison et al., 1966; Yadav, 1967;
Vinegar et al., 1970; Wagner, 1973, 1976;
Coborn, 1975, 1985; Foekema, 1975;
Acharjyo and Misra, 1976; Van Mierop and
Barnard, 1976_a, _b, 1978; Frank, 1977;
Acharjyo, 1978; Getreuer, 1979; Townson,
1980, [1989]; Frye, 1981; Griehl, 1982;
Clark and Tytle, 1983; Gurung, 1983; Van
Mierop et al., 1983; [Gerholdt], 1984_a,
Connors, 1985; Slavens, 1985, 1987, 1988;
Alderton, 1986; Michaels, 1986; Trutnau,
1986; Whitaker and Whitaker, 1986; Clark,
1988; Obst et al., 1988; Schleich and
Kästle, 1988; Cox, 1989

P. regius

Pitman, 1938; Schivre, 1972; Logan, 1973;
Peters, 1976; Boos, 1979; Van Mierop and
Bessette, 1981; Malone, 1982; Orlov,
1982; Lehmann and Lehmann, 1983; Laszlo,
1984; Barten, 1986; [Orlov], 1986;
Trutnau, 1986; Ellis and Chappell, 1987;
Slavens, 1987; Kirschner and Ochsenbein,
1988

P. reticulatus

Abbott in Wray, 1862; Köhler, 1907;
Ditmars, 1910; Hilzheimer, 1910;

P. sebae

Benedict, 1932; Kopstein, 1938; Lederer, 1944, 1956; Taylor, 1965; Honegger, 1970, 1970/71, 1975; Müller, 1970; Vinegar et al., 1970; Foekema, 1971; La Panouse and Pellier, 1973; Johnson, 1977; Trutnau, 1980, 1986; Slavens, 1984
 Günther, 1862; Sclater, 1862; [Günther], 1886; F. FitzSimons, [1912], 1930; Werner, 1930 (in Angel, 1950); Benedict and Mann in Ditmars, 1931; Benedict, 1932; Benedict et al., 1932; Pitman, 1938; Lederer, 1942, 1944, 1956; Broadley, 1959; Anonymous, 1960_{a,b}; Dowling, 1960, 1961; Sweeney, 1961; V. FitzSimons, 1962, 1970; Meyer-Holzappel, 1969; Schütte, 1970; Vinegar et al., 1970; Munnig Schmidt, 1971, 1973; Patterson, 1974; Branch and Patterson, 1975; Broadley and Cock, 1975_{a, b}; Pienaur et al., 1978; Dunn, 1979_b; Slavens, 1985; Trutnau, 1986; Patterson and Bannister, 1987; Branch, 1988; Schleich and Kästle, 1988; Shine, 1988
 Murphy et al., 1978; Barker, 1982

P. timoriensis

'Lilith' or 'arrow snake'
 (= Eryx jaculus?)

Isaiah 34:15, [c. 745-350 BC], (McDowell et al., 1982)

Colubridae

Ahaetulla nasuta

Rieppel, 1970

Amphiesma stolata

Wall, 1911, 1921; Mell, 1929; Daniel, 1983

Atretium schistosum

Murthy, 1986

Cemophora coccinea

Ditmars, 1907

Cerberus rynchops

Whitaker, 1978; Trutnau, 1986

Clelia clelia

Brazil, 1914, and in Roosevelt, 1914

Coronella austriaca

Appleby, 1971

Diadophis punctatus

?McCauley, 1945; Cook, 1954; Fowlie, 1965; ?Brodie et al., 1969; Somma, pers. observ.

Elaphe climacophora

Fukada, 1965

E. flavolineata

Kopstein, 1938

E. guttata

Kelly et al., 1936; Haast and Anderson, 1981; Kent in Shine, 1988; T. Miller, pers. comm.

E. obsoleta

Ditmars, 1907; Medsger, 1919, 1932; ?Netting, 1927; ?McCauley, 1945; Pope, 1946; M. Fisher, pers. comm.; J. Lombard, pers. comm.

E. quadrivirgata

Fukada, 1965; Orlov, 1982

E. quatuorlineata

Vogel, [1958?]

E. schrenki

Kudryavtsev and Frolov, 1984

Farancia abacura

Ridgeway, 1883 (in Hay, 1892; Wright and Wright, 1957; Minton, 1972); Meade, 1937, 1940, 1945, 1946; Conant and Downs, 1940;

- Farancia erythrogramma Goldstein, 1941; Cagle, 1942; Reynolds and Solberg, 1942; Cook, 1954; Riemer, 1957; Tinkle, 1959; Hahn and Wilson, 1966; Crawford, 1984; Mehrtens, 1987; Dundee and Rossman, 1989
Heterodon platirhinos Fry in Wright and Wright, 1957; Neill, 1964a; Ashton and Ashton, 1981
Hydrodynastes gigas Hay, 1892, 1893; Hahn 1909
Lampropeltis triangulum Vogel 1964
Lycodon aulicus Ditmars, 1907; Noble, 1920; Babcock, 1929; Anonymous, 1940; Minton, 1972; Minton and Minton, 1973; Marsec in Shine, 1988
L. striatus Herklots, 1935
Masticophis flagellum Wall, 1921
Natrix natrix Meek, 1946
Oligodon taeniolatus Stradling in Hopley, 1882; Gallwey, 1932; Berridge, 1935; Smith, 1951; Parker, 1963; Appleby, 1971
Opisthotropis latouchii Daniel, 1983
Pituophis catenifer Pope, 1929
Psammophylax rhombeatus Carl, 1944
P. tritaeniatus F. FitzSimons, [1912]; V. FitzSimons, 1962, 1970; Le Roux, 1964; Bourquin, 1970; Visser, 1971; De Waal, 1978; Branch, 1981, 1988; Broadley, 1983; Jacobsen, 1985; Trutnau, 1986; Patterson and Bannister, 1987
P. variabilis Sweeney, 1961; Isemonger, 1968; Branch, 1981; Hedges, 1983; Patterson and Bannister, 1987
Ptyas korros Spawls in Broadley, 1977
P. mucosus Mell, 1929
Rhabdophis subminiata Wall, 1907, 1921; Mell, 1929; Kopstein, 1938; Daniel, 1983
Sinonatrix percarinata Mell, 1929
Tropidonophis mairii Pope, 1929, 1935
Xenochrophis piscator ?Sundowner, 1895*, 1902; Bredl in Shine, 1988
 Abercromby, 1913; Mell, 1929; Whitaker, 1978; Daniel, 1983; Whitaker and Whitaker, 1986
- Elapidae
Bungarus caeruleus Wall, 1921; Daniel, 1983; Whitaker and Whitaker, 1986
B. candidus Mell, 1929; Shaw and Shebbeare, 1931; Soderberg, 1973
B. ceylonicus Green, 1905
B. fasciatus Evans, 1905; Wall, 1921; Mell, 1929; Soderberg, 1973; Yahya, 1985
 'Dipsas' (= Bungarus sp.?) Nicander of Colophon [135-133? BC]
Calliophis maculiceps Frith, 1977 (also illustrated in Phelps, 1981)
Demansia papuensis Parker, [1982]

- Micrurus fulvius
M. pysches
Naja melanoleuca
N. naja
- 'Asp' (= Naja haje?)
N. nigricollis
Ophiophagus hannah
- 'Cockatrice' or 'Basilisk'
 (= Ophiophagus hannah or
Naja sp.?)
Pseudechis butleri
Pseudonaja textilis
- Hydrophiidae
Pelamis platurus
- Laticaudidae
Laticauda colubrina
L. semifasciata
- Leptotyphlopidae
Leptotyphlops dulcis
L. humilis
- Typhlopidae
Ramphotyphlops braminus
Rhinotyphlops caecus
- Viperidae
Agkistrodon contortrix
A. piscivorus
Calloselasma rhodostoma
- Campbell, 1973
 Mole, 1924
 Tryon, 1979; Dowling, 1986
 [Appuhamy, 1810] (see Deraniyagala, 1955);
 Fayrer, 1870; Kipling, 1894+; Wall, 1921;
 Mell, 1929; Jennison, 1931; Kopstein,
 1938; Smith, 1943; Simmon, 1944; Tweedie,
 1954; Deraniyagala, 1955; Rao, 1957;
 Duckett, 1964; Deoras, 1965; Petzold,
 1968; Miller, 1970; Campbell and Quinn,
 1975, Daniel, 1983; Whitaker and
 Whitaker, 1986
 Nicander of Colophon [135-133? BC]
 Håkansson, 1981
 Fayrer, 1870; Nicholson, 1870; Wasey, 1892;
 Evans, 1903; Joynson, 1917; Wall, 1924;
 Berridge, 1935; Mustill, 1936; Smith,
 1936; Oliver, 1956; Leakey, 1969; Ionides
 and Leakey in Soderberg, 1973;
 Burchfield, 1977; Whitaker, 1977, 1978;
 Reitingger and Lee, 1978; Daniel, 1983;
 Gurung, 1983; Whitaker and Whitaker,
 1986; Dattatri, 1987; Mehrtens, 1987;
 Shine, 1988
 Gesneri, 1551-1587; Topsell, 1608
 Fitzgerald and Mengden, 1987
 Fleay, 1943; Edwards and Wells in Shine,
 1988; Shine, 1989
- Bertin and Burton, 1967
- Semper, 1881; ?Sundowner, 1895, 1902*;
 Smedley, 1931; Neill, 1964_b, Taylor, 1965
 Herre and Rabor, 1949
- Hibbard, 1964
 Whitfield, 1983++
- Mell, 1929
 Bogert, 1940
- Anderson, 1942; Fitch, 1960; Kennedy, 1964
 Wharton, 1960, 1966
 Smith, 1915, 1943; Tweedie, 1954; Leakey,
 1969; Campden-Main, 1970; Reitingger and
 Lee, 1978; Liat, 1982; York and
 Burghardt, 1988; Gloyd and Conant, 1989

<u>Causus rhombeatus</u>	F. FitzSimons, [1912]; Woodward, 1933; Sweeney, 1961; Broadley, 1983
<u>Crotalus</u> sp.	Audubon, 1909
<u>C. adamanteus</u>	Meek, 1946
<u>C. atrox</u>	Price, 1988
<u>C. horridus</u>	Anderson, 1942, 1965; Lokke, 1985; Martin, 1986 _{a,b} , 1989, and pers. comm.; ?Bartlett, 1987; ?Brown, 1987; ?Reinert and Zappalorti, 1988
<u>C. viridis</u>	Gloyd, 1937; Jackley and Shelton in Klauber, 1972; Duvall et al., 1985; Graves, 1988, 1989
<u>Deinagkistrodon acutus</u>	Fleck, 1987
<u>Lachesis muta</u>	Mole, 1924, and in Ditmars, 1910; Donisthorpe, 1947; Ramsey and Travis, 1960; Wehekind, 1960; Emsley, 1977; Caycedo, 1978; Frieberg, 1982
<u>Porthidium nummifer</u>	Picado T., 1931
<u>Sistrurus catenatus</u>	Greene and Oliver, 1965; ?Vogt, 1981; Reinert and Kodrich, 1982
<u>Trimeresurus kaulbacki</u>	Obst et al., 1988
<u>T. monticola</u>	Leigh, 1910; Pope, 1929, 1935
<u>T. okinavensis</u>	?Fukada, 1964; Koba et al., 1970
<u>T. wiroti</u>	Mehrtens, 1987
<u>Vipera aspis</u>	Lanworn, 1972; Naulleau, 1987; Dowling, 1986
<u>V. berus</u>	Brittain, 1866 (in Hopley, 1882); Service, 1902; Smith, 1951; Appleby, 1971; Street, 1979; Naulleau, 1987

*It is not known what species Sundowner actually observed but T. mairii and L. colubrina seem likely candidates. The credibility of Sundowner's [= Tichborne, H. (sic?)] (1895, 1902) observations are at best questionable, and mostly fabricated (Johnson and Smith, 1985). Nevertheless, it is likely that he also observed Australian pythons (species unspecified) brooding their eggs (Sundowner, 1895, 1902).

+Although a work of fiction, Kipling (1894) was one of the earliest published accounts of brooding in Naja naja (mistakenly referred to as Ophiophagus hannah) in English. He based his story, "Rikki-tikki-tavi," on a personal communication from an anonymous herpetologist (Kipling, 1894).

++Whitfield's (1983) mention of brooding in L. humilis is likely a mistaken reference to Hibbard's (1964) observations on L. dulcis.

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