

REVIEW:

DISCREPANT USAGE OF THE TERM 'OVOVIVIPARITY' IN THE
HERPETOLOGICAL LITERATURE

DANIEL G. BLACKBURN

Department of Biology, Life Sciences Center, Trinity College, Hartford, CT 06106, USA

A broad survey of the literature on reptiles and amphibians reveals that the ambiguous term 'ovoviviparity' has been applied to a variety of reproductive patterns that have little in common. Among these are patterns that can more clearly be referred to as aplacental viviparity, oviparous egg-retention, egg-tending, pseudoviviparity, and lecithotrophy. Some of the uses of 'ovoviviparity' are based on invalid assumptions, and some are mutually exclusive; thus, particular care must be used in interpreting literature reports that lack operative definitions. To minimize confusion, future reports and reviews should avoid 'ovoviviparity' in favour of unambiguous alternatives that explicitly distinguish patterns defined on the basis of reproductive products at deposition from patterns based on sources of nutrients for embryonic development.

INTRODUCTION

Comparative biology seeks to document organismal diversity by distinguishing recurrent themes and common patterns. Fundamental to attempts to recognize patterns that unify species is agreement on a common vocabulary that transcends boundaries of taxon, discipline, and language. Unfortunately, reproductive biology has long been handicapped by several terminological discrepancies, including the use of the term 'ovoviviparity' to describe very different patterns in separate species. Inattention to terminology coupled with the disinclination of many writers to explain their terms has given rise to conceptual confusion, as well as discrepant claims for many species (Blackburn, 1982*a*; 1993*a*). Although one's choice of words to represent reproductive modes is a trivial matter, contradictory terminologies, when overlooked, hinder attempts to recognize and communicate about significant biological phenomena (Packard *et al.*, 1989).

This review has three goals: (1) to document the ambiguous and contradictory ways in which the term 'ovoviviparity' is used in the literature on reptiles and amphibians; (2) to alert researchers to use caution in interpreting reports that do not explain terminological usage; and (3) to encourage avoidance of 'ovoviviparity' and its cognates in favour of clearer alternatives that are now available.

PROVISIONAL TERMINOLOGY

Because this paper deals with the application of terms to reproductive concepts and patterns, a provisional vocabulary is necessary for the sake of communication. I will follow common usage in employing 'egg-laying reproduction' in its literal sense, i.e. in reference to species that reproduce by laying unhatched eggs that complete their development in the external environment. This category includes species

with external fertilization, as well as those with internal fertilization in which some development precedes oviposition (e.g. Shine, 1983; Braña, Bea, & Arrayago, 1991), the reproductive product being an 'egg' rather than an autonomous, free-living offspring. 'Live-bearing' is used to describe species in which the female retains the eggs to term in her reproductive tract and bear fully-developed, autonomous offspring (neonates, larvae, or metamorphosed young). For most purposes, cases in which the young are still surrounded by an eggshell or jelly coat at birth but quickly break through these egg investments can also be considered 'live-bearing'. The terms 'oviparous' and 'viviparous' frequently are applied to 'egg-laying' and 'live-bearing', respectively (e.g. Fitch, 1970; Tinkle & Gibbons, 1977). This terminology is discussed further below.

PAST USES OF 'OVOVIVIPARITY'

'Ovoviviparity', including its adjective form ('ovoviviparous') and non-English equivalents (e.g. 'ovoviviparité', 'ovoviviparie'), is a term with a long, varied history (Bertin, 1952; Bauchot, 1965; Luckett, 1977; Mackie, 1978; Wourms, 1981; Guillette, 1981, 1982; Blackburn, 1985*a*; Smith, 1986*a*). No form of the word appears in certain early, important works in zoology and embryology (Malpighi, 1672; Collins, 1685; Cuvier, 1802; Lamarck, 1809), and its origins appear not to have been traced. Bellairs (1970) speculated that the word was first used to describe reptiles that ovulated large yolks and gave birth to their offspring. Such may be the case, for by the 1830's, the term was being applied to lizards, snakes, and urodeles in which the young develop within the female reproductive tract and are born alive (Dumeril & Bibron, 1834; Owen, 1834*a*; Bonapart, 1837). Richard Owen (1834*b*) explicitly used the adjective 'ovoviviparous' to describe animals that give birth to their offspring yet never form a placenta, a pattern that he erroneously at-

tributed to the monotreme and marsupial mammals. However, the term was by no means universally accepted, and some herpetological works of the 19th century noted difficulties in distinguishing 'ovoviviparity' from the commonly accepted categories of 'oviparity' and 'viviparity' (Haacke, 1885).

In the 20th century, the term 'ovoviviparity' has been used to represent a variety of reproductive patterns. The chief feature that these patterns have in common is that eggs begin to develop in some sort of association with one of the parents; however, the nature and duration of this association varies, as does the parent with which the association occurs. In the herpetological literature, the term 'ovoviviparity' has been used to represent at least five distinct reproductive patterns. Because formal definitions are seldom offered in sources using the word, these patterns are described below to provide operative meanings (i.e. usages) for the term.

Pattern 1 involves internal fertilization and partial development of the eggs within the maternal reproductive tract. The eggs at oviposition contain visible embryos, and continue their development in the external environment, where they eventually hatch. 'Ovoviviparity' has been applied to this pattern in egg-laying squamates (e.g. McPhee, 1959; Brattstrom, 1964; Duda & Koul, 1977; Lemus, Illanes, Fuenzalida, Paz de la Vega & Garcia, 1981) as well as amphibians (e.g. von Wahlert, 1953; Grandison, 1978; Wake, 1980); some authors have applied additional criteria as well (see below). This usage has a long, respectable history; it extends to the early part of this century (Rollinat, 1904), and is found in both pioneering and modern works on development (Hrabowski, 1926; Weekes, 1930; Lemus, Martín, Blánquez, Fuenzalida & Illanes, 1984). In contrast, many recent authors have labelled this pattern as a form of 'oviparity' (e.g. Tinkle & Gibbons, 1977; Shine & Bull, 1979; Shine, 1985) and occasionally, 'viviparity' (Turner, 1947).

Pattern 2 is restricted to anamniotes, because the site of metamorphosis is central to its recognition. Fertilization is internal, and the eggs develop in the maternal reproductive tract no further than a premetamorphic stage; thus, the young at birth are larvae that metamorphose in the external environment. These larvae either hatch from the egg membranes before birth or immediately thereafter; thus, unlike Pattern 1, this pattern operationally can be considered a form of 'live-bearing' reproduction, as described above. Among amphibians, this form of reproduction is found in many populations of the urodele *Salamandra salamandra* (Joly, 1968; Fachbach, 1969, 1976). Although usually termed 'viviparity', this pattern often has been referred to as 'ovoviviparity' in literature on *Salamandra*, to distinguish it from maternal retention of the young through metamorphosis (Fachbach, 1969; Özeti, 1979; Warburg, Degani & Warburg, 1979).

Pattern 3 is a form of live-bearing reproduction in which nutrients for development are supplied by the yolk of the oocyte, rather than by an alternative source. Other potential sources of developmental nutrients in live-bearing amphibians and reptiles include placental membranes, oviductal secretions, and sibling yolks or embryos (Amoroso, 1952; Wake, 1977*a,b*, 1982, 1985, 1993; Xavier, 1977; Blackburn, 1985*a*, 1993*b*; Jones & Baxter, 1991). The term 'ovoviviparity' has been applied to live-bearing species in which the organic nutrients for development are of vitelline origin, in literature on both squamates (e.g. Domergue, 1959; Smith, Sinelnik, Fawcett, & Jones, 1972) and amphibians (Salthe & Mecham, 1974; Wake, 1978; Greven, 1980; Duellman, 1992). In other recent literature, live-bearing species often have been termed 'viviparous' regardless of the sources of developmental nutrients (e.g. Fitch, 1970; Packard, Tracy & Roth, 1977; Marini, Trevisan & Benassi, 1983; Jones & Baxter, 1991).

Pattern 4 is similar to the previous pattern, but focuses on the presence or absence of anatomical features presumed to affect physiological exchange between foetal and maternal tissues. Thus, early sources often applied 'ovoviviparity' to live-bearing squamates in which any trace of an eggshell (shell membrane) is grossly visible around the oviductal egg during gestation (Harrison & Weekes, 1925; Kasturirangan, 1951*a*; Miller, 1959; Bellairs, 1970), the rationale being that even a thin shell would limit physiological exchange. According to this usage, truly 'viviparous' squamates are those live-bearing forms in which an eggshell disappears during gestation or is never deposited (Weekes, 1929; Kasturirangan, 1951*b*).

A similar approach has been to classify as 'ovoviviparous' any live-bearing squamates lacking placental organs that accomplish physiological exchange (Jacobi, 1936; Matthews, 1955; Smith *et al.*, 1972; Guillette, 1981). However, recent researchers have seriously questioned whether any live-bearing squamates lack functional placentas (Guillette, 1982; Smith, Preston & Smith, 1983; Blackburn, 1985*a*, 1992, 1993*b*), and this criterion seems to have fallen into disuse (Smith, 1986*a,b*; Guillette, 1987; Jones & Baxter, 1991).

Pattern 5 is represented by the unusual reproductive habits of certain egg-laying anurans. Eggs are fertilized externally, and subsequently are cared for by one of the parents. Eggs are brooded in the stomach, vocal sacs, or depressions in the dorsal integument, or carried on the back or legs. In some species, the parent carries hatched tadpoles on its dorsum. Such forms of parental care have been widely documented and described; for recent reviews see Salthe & Mecham (1974), Wake (1982), and Duellman (1992). These anuran patterns have been referred to as forms of 'ovoviviparity' by several authors (e.g. Amoroso, 1952; Salthe & Mecham, 1974), although others have described them

as 'oviparity' (Webster & Webster, 1974) and 'viviparity' (Matthews, 1955, 1958; Jones & Baxter, 1991).

CONTRADICTIONARY CRITERIA AND THEIR CONSEQUENCES

Reproductive patterns that have been represented by the term 'ovoviviparity' have little in common. They include species with internal as well as external fertilization, and species in which the reproductive product exiting the female is an immature, developing egg and those in which it is a fully-developed neonate. In some patterns, the eggs develop in the maternal oviducts whereas in another, eggs develop externally, but the hatchlings are carried on the back of the male parent. Some of the patterns have been defined with a focus on the reproductive product itself, whereas others are distinguished on the basis of the source of nutrients for development, two distinct parameters whose conflation arguably has obscured patterns of reproductive evolution (Blackburn, 1992).

Some criteria for application of the term are based on invalid assumptions. For example, in *Pattern 4* above, one rationale for distinguishing live-bearing squamates as 'ovoviviparous' (as opposed to 'viviparous') when a shell membrane occurs is that this structure is presumed to limit or prevent significant physiological exchange between maternal and foetal tissues. However, because a shell membrane is deposited around the egg in all live-bearing squamates that have been examined (Yaron, 1985; Blackburn, 1993*b*), no such distinction can be made. Moreover, although the shell membrane usually thins during gestation in live-bearing forms, it typically persists until birth (Heulin, 1990), including in certain species with significant physiological exchange between maternal and foetal tissues (Hoffman, 1970; Stewart, 1989, 1990; Stewart, Blackburn, Baxter, & Hoffman, 1990). The dubious assumption that some live-bearing squamates lack placental organs is discussed above.

Some of the criteria for 'ovoviviparity' apply to a limited range of species. Among these criteria is presence of an eggshell in a live-bearing form (*Pattern 4*), which is applicable to squamates and marsupials, but allows no discrimination among amphibian and osteichthyan species. Similarly, that pattern's focus on placental formation ignores the array of non-placental sources of extravitelline nutrients found among anamniotes (e.g. Wourms, 1981; Wake, 1982, 1993). Likewise, the focus on pre-metamorphic larvae in *Pattern 2* may be of use in reference to *Salamandra*, but is of little value for amniotes, chondrichthyans, or even other amphibians. Other criteria for application of the term are so broad as to obscure important distinctions. For example, given that embryonated eggs are deposited by most or all egg-laying squamates (Shine, 1983) as well as by monotremes (Hughes & Carrick, 1978), these species would all be classified as 'ovoviviparous'

by the criteria of *Pattern 1*. In addition, by extension of the criteria of *Pattern 5*, 'ovoviviparity' would apply not only to the anurans described above, but also to monotremes, many egg-laying teleosts, and arguably, crocodylians and birds.

Given the varied, discrepant application of 'ovoviviparity', use of the term has the potential to produce much confusion. Nevertheless, few sources provide definitions or explanations (for exceptions, see Wake, 1982, 1993; Angelini & Ghiara, 1984; Mossman, 1987), perhaps under the assumption that widely-used terms are universally understood. Without detailed information, however, statements in the literature that a particular species is 'ovoviviparous' carry little meaning. Unfortunately, researchers who routinely apply the term to taxa that they study are not always aware of incongruent uses to which the same term has been put in other taxa. For example, although the adjective 'ovoviviparous' is often taken to be synonymous with 'live-bearing' in reference to squamates, in one of its common applications the former term is actually a variant of 'egg-laying' reproduction. One result has been contradictory claims about reproductive habits in various species of egg-laying squamates (Blackburn, 1985*a,b*). Similar terminological discrepancies are suspected in literature on other species for which contradictory reports are available (Blackburn, 1993*a*). Such terminological issues cannot be ignored if we wish to communicate accurately about reproductive patterns (Packard *et al.*, 1989).

TERMINOLOGICAL ALTERNATIVES

Considering the contradictory usage of the word 'ovoviviparity', one possible solution might be to develop a new definition for the term and to encourage its careful application. However, such does not seem to be a viable option. The word has nearly lost the potential to impart meaning; confusion surrounding its use offers little prospect for establishing it as an unambiguous part of our biological vocabulary. Etymologically, the word lacks coherence; it seems to be a hybrid of the common terms 'oviparity' and 'viviparity', despite the fact that each of the patterns represented by 'ovoviviparity' is a subset either of egg-laying or of live-bearing reproduction. An additional problem is that most uses of the term attempt to distinguish a distinct category within biological continua, and therefore are difficult to apply to actual species. For these and other reasons, various reviewers (e.g. Bertin, 1952; Bauchot, 1965; Blackburn, 1982*b*, 1992; Smith, 1986*a*; also see Angelini & Ghiara, 1984) have recommended that the term be deleted from the modern biological lexicon. Such a course is consistent with the trend away from use of the term, especially evident in literature on squamates and fishes during the past decade.

How, then, can we represent and communicate about the reproductive patterns listed above? The most promising solution lies in the substitution of alternative

Pattern, description	Recommended term	Examples
(1) Oviposition of developing eggs	oviparity ^a	<i>Liolaemus tenuis</i> ^b , <i>Nectophrynoides malcomi</i> ^c
(2) Live-birth of pre-metamorphic larvae	viviparity	<i>Salamandra salamandra</i> ^d
(3) Live-bearing + mainly vitelline nutrients	lecithotrophic viviparity	<i>Virginia striatula</i> ^e , <i>N. viviparus</i> ^c , <i>S. salamandra</i> ^d
(4) Live-bearing + no placenta; Live-bearing + shell membrane	aplacental viviparity; viviparity	<i>N. viviparus</i> ^c , <i>N. occidentalis</i> ^c <i>Thamnophis sirtalis</i> ^e
(5) Parental care of eggs	egg-brooding	oviparous <i>Eumeces</i> ^b , <i>Alytes obstetricans</i> ^c ,
Parental care of eggs	pseudoviviparity ^f	<i>Gastrotheca</i> ^c , <i>Rhinoderma darwini</i> ^c , <i>Rheobatrachus silus</i> ^c

TABLE 1. Recommended alternatives to the term 'ovoviviparity' in descriptions of amphibians and reptiles. See the text for explanations of the numbered reproductive patterns. Reproductive data on the listed species are available in the following sources: Fachbach (1976), Wake (1980, 1982), Lemus *et al.* (1981), Duellman (1992), Stewart (1989), and Blackburn (1993a, 1994). The term 'matrotrophy' is recommended for substantial provision of extra-vitelline nutrients for development (e.g. *Nectophrynoides occidentalis*, *Salamandra atra*, and certain viviparous caecilians, squamates, and other vertebrates). ^a or 'oviparous egg-retention' when considerable development precedes oviposition; ^b Sauria; ^c Anura; ^d Urodela; ^e Serpentes; ^f see text for application of this term.

terms already in use in the herpetological literature. Most of the reproductive patterns described above are defined either by the type of reproductive product exiting the parent (*Patterns 1, 2, and 5*) or by the sources of nutrients for development (*Pattern 3*). The remaining pattern (*Pattern 4*) is indirectly based on nutritional sources, in that it focuses on features presumed to affect maternal-foetal exchange.

A bipartite terminology that has been introduced to the literature is adequate to represent both of these types of reproductive parameters. To describe the reproductive product deposited by the female (egg vs. neonate), the widely-used terms 'oviparity' and 'viviparity' are applied in their literal senses (e.g., Fitch, 1970; Marini *et al.*, 1983; Braña, 1986; Heulin, 1988), that is, in reference to 'egg-laying' and 'live-bearing' reproduction (as defined above) respectively. Accordingly, 'oviparous' species include those that deposit unfertilized eggs as well as those that lay developing eggs that complete their development in the external environment. By the same token, 'viviparous' species give birth to autonomous, free-living offspring, whatever their state of maturity. In reference to egg-laying squamates in which an unusual amount of embryonic development precedes oviposi-

tion, the term 'oviparous egg-retention' can be useful (Shine, 1983; Blackburn, 1985b). In addition, the term 'ovuliparity' is available to describe a type of oviparous reproduction involving maternal deposition of unfertilized eggs (Bertin, 1952; Blackburn, 1985a), as occurs in agnathans, many anurans and osteichthyans, and certain urodeles.

To represent the sources of nutrients for development, two other terms that were first introduced to the piscine literature (Wourms, 1981) have proven applicable to vertebrates in general (Blackburn, 1982b, 1992, 1994; Stewart, 1989, 1992). 'Lecithotrophy' describes provision of nutrients via the yolk, and 'matrotrophy' describes maternal provision of nutrients during gestation by some other means (e.g. oviductal secretions, placental tissues). These terms are derived from the words *lekithos* (Greek for *egg-yolk*), *mater* (Latin for *mother*), and *trophe* (Greek for *nourishment*). Because lecithotrophic and matrotrophic nutrition represent extremes of a continuum, species can be described according to the relative contributions of nutrient sources. Furthermore, specific types of matrotrophy can be recognized according to whether nutrients are supplied by placental membranes ('placentotrophy'), sibling yolks ('oophagy'), sibling foetuses

('adelphophagy') or maternal secretions that are absorbed ('histotrophy') or ingested ('histophagy') (Wourms, 1981; Blackburn *et al.*, 1985).

The above terminology offers several advantages. First, the adoption of terms that translate literally into their intended meanings minimizes the chances for semantic confusion. Second, because each of the two sets of terms is applied to a different parameter (reproductive product *vs.* nutrient sources), the important distinction between these parameters is made explicit. Thus, species can be described as exhibiting lecithotrophic oviparity, lecithotrophic viviparity (e.g., Stewart *et al.*, 1990; Stewart, 1992), matrotrophic viviparity (Blackburn & Vitt, 1992), and in rare cases, matrotrophic oviparity (Blackburn, 1992). Third, the existence of two sets of terms allows investigators to focus on the feature of interest, while allowing a more complete description as information becomes available. Fourth, unlike other systems, the bipartite system does not presuppose a particular evolutionary sequence, but is flexible enough to recognize that matrotrophy and viviparity can evolve according to different pathways in different taxa. The common assumption that strictly lecithotrophic viviparity (one of the variants of 'ovoviviparity') evolves prior to matrotrophic viviparity appears to be unjustified for both reptiles and mammals, if not other vertebrates (Blackburn, 1985a, 1992). Finally, application to all amphibians and reptiles, of a vocabulary that is achieving acceptance in literature on squamates and the three piscine classes, facilitates species comparisons across the broad spectrum of vertebrate diversity. Detailed criteria for inferring parity modes and sources of developmental nutrients in reptiles, and thereby for applying the proposed terminology to particular species, are explored elsewhere (Blackburn, 1993a, 1994).

In Table 1, application of the recommended terminology is illustrated by reference to the reproductive patterns that previously have been labelled as 'ovoviviparity'. As indicated, each of the five patterns can be described by a different set of terms, allowing fine distinctions to be drawn between the species listed.

Two other points deserve mention. The proposed terminology does not explicitly distinguish between populations of *Salamandra* that give birth to larvae and those that give birth to metamorphosed young (see *Pattern 2* above). In the mammalian literature, the terms 'altricial' and 'precocial' describe the state of development of the young at emergence; perhaps application of analogous terms might be useful in descriptions of this urodele genus. The proposed terminology also offers no special recognition of the anuran specializations of *Pattern 5*, which would be classified here as variants of oviparous lecithotrophy. The common term 'brooding' (see Somma, 1988) should be adequate in most cases, with 'egg-tending' and 'parental care' as further alternatives. For anurans in which the eggs are brooded until hatching in the stomach or vocal sacs, the term

'viviparity', by definition, would be deemed inappropriate. However, such species might be referred to as 'pseudoviviparous' (Table 1; Blackburn, 1985a), in recognition of their superficial similarity to species in which the eggs develop to term in the female reproductive tract.

Individual researchers should continue to enjoy the freedom to employ terminologies and classification systems that prove most useful for their own purposes. Nevertheless, conceptual clarity requires explicit attention to the tools of communication, particularly in view of the potential for confusion that has long been presented by use of 'ovoviviparity' and its cognates in the zoological literature.

ACKNOWLEDGEMENTS

Some of the ideas discussed herein have been presented orally at symposia on vertebrate reproductive diversity (Blackburn, 1982b, 1992; Blackburn *et al.*, 1985). I wish to acknowledge John P. Wourms, James R. Stewart, Marvilee H. Wake, Virginia Hayssen, Louis J. Guillelte, Jr., and Julian Lombardi for past discussions of relevant issues, and Tim Halliday, Roger A. Avery, and anonymous reviewers for comments on the manuscript. Background research for this review was conducted with the assistance of library facilities and staff at Cornell University, Vanderbilt University, and Yale University. I also thank Dr. Richard Griffiths, editor of *The Herpetological Journal*, for extending to me the opportunity to contribute this review.

REFERENCES

- Amoroso, E. C. (1952). Placentation. In *Marshall's Physiology of Reproduction*, 127-311. Parkes, A.S. (Ed.). New York: Longmans, Green.
- Angelini, F. & Ghiara, G. (1984). Reproductive modes and strategies in vertebrate evolution. *Boll. Zool.* **51**, 121-203.
- Bauchot, R. (1965). La placentation chez les reptiles. *Ann. Biol.* **4**, 547-575.
- Bellairs, A. d'A. (1970). *The Life of Reptiles*. 2 vols. New York: Universe Books.
- Bertin, L. (1952). Oviparité, ovoviviparité, viviparité. *Bull. Soc. Zool. Fr.* **77**, 84-88.
- Blackburn, D. G. (1982a). Evolutionary origins of viviparity in the Reptilia. I. Sauria. *Amphibia-Reptilia* **3**, 185-205.
- Blackburn, D. G. (1982b). Classification of vertebrate reproductive modes. *Amer. Zool.* **22**, 910.
- Blackburn, D. G. (1985a). *The Evolution of Viviparity and Matrotrophy in Vertebrates, with Special Reference to Reptiles*. Ph.D. Diss., Cornell University, Ithaca, New York.
- Blackburn, D. G. (1985b). Evolutionary origins of viviparity in the Reptilia. II. Serpentes, Amphisbaenia, and Ichthyosauria. *Amphibia-Reptilia* **5**, 259-291.

- Blackburn, D. G. (1992). Convergent evolution of viviparity, matrotrophy, and specializations for fetal nutrition in reptiles and other vertebrates. *Amer. Zool.* **32**, 313-321.
- Blackburn, D. G. (1993a). Standardized criteria for the recognition of reproductive modes in squamate reptiles. *Herpetologica* **49**, 118-132.
- Blackburn, D. G. (1993b). Chorioallantoic placentation in squamate reptiles: morphology, physiology, development, and evolution. *J. Exp. Zool.* **266**, 414-430.
- Blackburn, D. G. (1994). Standardized criteria for the recognition of developmental nutritional patterns in squamate reptiles. *Copeia* (in press).
- Blackburn, D. G. & Vitt, L. J. (1992). Reproduction in viviparous South American lizards of the genus *Mabuya*. In *Reproductive Biology of South American Vertebrates: Aquatic and Terrestrial*, 150-164. Hamlett, W. (Ed.). New York: Springer-Verlag.
- Blackburn, D. G., Evans, H. E. & Vitt, L. J. (1985). Evolution of fetal nutritional adaptations. In *Functional Morphology in Vertebrates*, 437-439. Duncker, H.-R. and Fleischer, G. (Eds.). Stuttgart: Gustav Fischer.
- Bonaparte, C. L. (1837). A new systematic arrangement of vertebrated animals. *Trans. Linn. Soc.* **20**, 247-304.
- Braña, F. (1986). Ciclo reproductor y oviparismo de *Lacerta vivipara* en la Cordillera Cantábrica. *Rev. Espan. Herpetol.* **1**, 273-291.
- Braña, F., Bea, A. & Arrayago, M. J. (1991). Egg retention in lacertid lizards: relationships with reproductive ecology and the evolution of viviparity. *Herpetologica* **47**, 218-226.
- Brattstrom, B. H. (1964). Evolution of the pit vipers. *Trans. San Diego Soc. Nat. Hist.* **13**, 185-268.
- Collins, S. (1685). *A Systeme of Anatomy*. 2 vols. London: Thomas Newcomb.
- Cuvier, G. (1802). *Lectures on Comparative Anatomy* (translation by Ross, W. and Macartney, J.), 2 vols. London: Longman & Reese.
- Domergue, C. A. (1959). Ovoviparité et oviparité chez deux Viperidae du genre *Aspis* (L.). *Bull. Soc. Sci. Nat. Tunis* **9**, 73-74.
- Duda, P. L. & Koul, O. (1977). Ovarian cycle in high altitude lizards from Kashmir. Part II. *Scincella himalayana* (Boulenger). *Herpetologica* **33**, 427-433.
- Duellman, W. E. (1992). Reproductive strategies of frogs. *Scientific American* **July 1992**, 80-87.
- Duméril, A. M. C. & Bibron, G. (1834). *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles*. Vol. 1. Paris: Roret.
- Fachbach, G. (1969). Zur Evolution der Embryonal- bzw. Larvalentwicklung bei *Salamandra*. *Z. Zool. Syst. Evolut.-forsch.* **7**, 128-145.
- Fachbach, G. (1976). Biologie, taxonomie, und phylogenetische Beziehungen der verschiedenen Unterarten von *Salamandra salamandra* im Bereich der Iberischen Halbinsel. *Z. Zool. Syst. Evolut.-forsch.* **14**, 81-103.
- Fitch, H. S. (1970). Reproductive cycles of lizards and snakes. *Univ. Kansas Mus. Nat. Hist., Misc. Publ.* **52**, 1-247.
- Grandison, A. G. C. (1978). The occurrence of *Nectophrynoides* (Anura: Bufonidae) in Ethiopia. A new concept of the genus with a description of a new species. *Monitor. Zool. Ital.* **6**, 119-172.
- Greven, H. (1980). Ultrastructural investigations of the epidermis and the gill epithelium in the intrauterine larvae of *Salamandra salamandra* (L.) (Amphibia, Urodela). *Z. mikrosk.-anat. Forsch., Leipzig* **94**, 196-208.
- Guillette, L. J., Jr. (1981). *Reproductive Strategies and the Evolution of Viviparity in Two Allopatric Populations of the Mexican Lizard Sceloporus aeneus*. Ph.D. Diss., University of Colorado, Boulder, Colorado.
- Guillette, L. J., Jr. (1982). The evolution of viviparity and placentation in the high elevation, Mexican lizard *Sceloporus aeneus*. *Herpetologica* **38**, 94-103.
- Guillette, L. J., Jr. (1987). The evolution of viviparity in fishes, amphibians, and reptiles. In *Hormones and Reproduction in Fishes, Amphibians, and Reptiles*, 523-562. Norris, D. O. and Jones, R. E. (Eds.). New York: Plenum Press.
- Haacke, W. (1885). Über eine neue Art uterinaler Brutflege bei Reptilien. *Zool. Anz.* **8**, 435-439.
- Harrison, L. & Weekes, H. C. (1925). On the occurrence of placentation in the scincid lizard *Lygosoma entrecasteauxi*. *Proc. Linn. Soc. N. S. W.* **50**, 470-486.
- Heulin, B. (1988). Données nouvelles sur les populations ovipares de *Lacerta vivipara*. *C. R. Acad. Sci., Paris (Ser. 3)* **306**, 63-68.
- Heulin, B. (1990). Étude comparative de la membrane coquillière chez les souches ovipare et vivipare du lézard *Lacerta vivipara*. *Can. J. Zool.* **68**, 1015-1019.
- Hoffman, L. H. (1970). Placentation in the garter snake, *Thamnophis sirtalis*. *J. Morph.* **131**, 57-87.
- Hrabowski, H. (1926). Das Dotterorgan der Eidechsen. *Z. Wiss. Zool.* **128**, 305-382.
- Hughes, R. L. & Carrick, F. N. (1978). Reproduction in female monotremes. *Aust. Zool.* **20**, 233-253.
- Jacobi, L. (1936). Ovoviviparie bei einheimischen Eidechsen. *Z. Wiss. Zool.* **148**, 401-464.
- Joly, J. (1968). Données écologiques sur la salamandre tachetée *Salamandra salamandra* L. *Ann. Sci. Naturw. Zool.* **10**, 301-366.
- Jones, R. E. & Baxter, D. C. (1991). Gestation, with emphasis on corpus luteum biology, placentation, and parturition. *Vertebrate Endocrinology: Fundamentals and Biomedical Implications*, vol. 4, part A. New York: Academic Press.
- Kasturirangan, L. R. (1951a). Placentation in the sea snake *Enhydrina schistosa* Daudin. *Proc. Indian Acad. Sci., B.* **34**, 1-32.

- Kasturirangan, L. R. (1951b). The allantoplacenta of the sea snake *Hydrophis cyanocinctus* Daudin. *J. Zool. Soc. India* **8**, 277-289.
- Lamarck, J.-B. M. (1809). *Philosophie Zoologique*. Dentu: Paris.
- Lemus, D., Illanes, J., Fuenzalida, M., Paz de la Vega, Y. & Garcia, M. (1981). Comparative analysis of the development of the lizard *Liolaemus tenuis tenuis*. I. A series of normal post-laying stages in embryonic development. *J. Morph.* **169**, 337-349.
- Lemus, D., Martín, R., Blánquez, M. J., Fuenzalida, M. & Illanes, J. (1984). Estudio comparado del desarrollo embrionario de especies ovíparas y una ovovivípara (*Gallus gallus*, *Coturnix c. japonica* y *Liolaemus tenuis t.*). *Zbl. Vet. Med. C. anat. Histol. Embryol.* **13**, 252-260.
- Luckett, W. P. (1977). Ontogeny of amniote fetal membranes and their application to phylogeny. In *Major Patterns in Vertebrate Evolution*, 439-516. Hecht, M.K., Goody, P.C. and Hecht, B.M. (Eds.). New York: Plenum Press.
- Malpighi, M. (1672). *De Formatione Pulli in Ovo*. Bononiae.
- Mackie, G. L. (1978). Are sphaeriid clams ovoviviparous or viviparous? *Nautilus* **92**, 145-147.
- Marini, M., Trevisan, P. & Benassi, M. (1983). Rohon-Beard neurons in viviparous and oviparous urodeles. *Boll. Zool.* **50**, 207-216.
- Matthews, L. H. (1955). The evolution of viviparity in vertebrates. *Mem. Soc. Endocrinol.* **4**, 129-148.
- Matthews, L. H. (1958). Viviparity in *Gastrotheca* (Amphibia: Anura), and some considerations of the evolution of viviparity. *Bull. Soc. Zool. Fr.* **82**, 317-320.
- McPhee, D. R. (1959). *Some Common Snakes and Lizards of Australia*. Brisbane: Jacaranda Press.
- Miller, M. R. (1959). The endocrine basis for reproductive adaptations in reptiles. In *Comparative Endocrinology*, 499-516. Gorman, A., (Ed.). New York: Wiley.
- Mossman, H. W. (1987). *Vertebrate Fetal Membranes*. Brunswick, New Jersey: Rutgers University Press.
- Owen, R. (1834a). On the generation of the marsupial animals, with a description of the impregnated uterus of the kangaroo. *Phil. Trans.* **123**, 333-364.
- Owen, R. (1834b). On the ova of the *Ornithorhynchus paradoxus*. *Phil. Trans.* **123**, 555-566.
- Özeti, N. (1979). Reproductive biology of the salamander *Mertensiella luschani antalyana*. *Herpetologica* **35**, 193-197.
- Packard, G. C., Tracy, C. R. & Roth, J. J. (1977). The physiological ecology of reptilian eggs and embryos, and the evolution of viviparity within the class Reptilia. *Biol. Rev.* **52**, 71-105.
- Packard, G. C., Elinson, R. P, Gavaud, J., Guillette, L. J., Jr., Lombardi, J., Schindler, J., Shine, R., Tyndale-Biscoe, H., Wake, M. H., Xavier, F. D. J., & Yaron, Z. (1989). How are reproductive systems integrated and how has viviparity evolved? In *Complex Organismal Functions: Integration and Evolution in Vertebrates*, 281-293. Wake, D. & Roth, G. (Eds.). Dahlem Conference Report, Chichester: J. Wiley & Sons.
- Rollinat, R. (1904). Observations sur la tendance vers l'ovoviviparité chez quelques Sauriens et Ophidiens de le France centrale. *Mém. de la Soc. Zool. Fr.* **17**, 30-41.
- Salthe, S. N. & Mecham, J. S. (1974). Reproductive and courtship patterns. In *Physiology of the Amphibia*, vol. 2, 309-521. Lofts, B. (Ed.). New York: Academic Press.
- Shine, R. (1983). Reptilian reproductive modes: the oviparity-viviparity continuum. *Herpetologica* **39**, 1-8.
- Shine, R. (1985). The evolution of viviparity in reptiles: an ecological analysis. In *Biology of the Reptilia*, 605-694. Gans, C. & Billet, F. (Eds.). New York: Wiley & Sons.
- Shine, R. & Bull, J. J. (1979). The evolution of live-bearing in lizards and snakes. *Amer. Nat.* **113**, 905-923.
- Smith, H. M. (1986a). "Ovoviviparity": spurious for ectotherms. *Bioscience* **36**, 292.
- Smith, H. M. (1986b). Terminology of reproductive parities. *Bull. Maryland Herpetol. Soc.* **22**, 19-20.
- Smith, H. M., Sinelnik, G., Fawcett, J. D. & Jones, R. E. (1972). A unique reproductive cycle in *Anolis* and its relatives. *Bull. Phila. Herpetol. Soc.* **20**, 28-30.
- Smith, H. M., Preston, M. J. & Smith, R. B. (1983). The history of the concept of viviparity in the alligator lizard genus *Barisia*. *Herp. Rev.* **14**, 34-35.
- Somma, L. A. (1988). Comments on the use of the term "brooding" to describe parental behavior in squamate reptiles. *Amphibia-Reptilia* **9**: 89-91.
- Stewart, J. R. (1989). Facultative placentotrophy and the evolution of squamate placentation: quality of eggs and neonates in *Virginia striatula*. *Amer. Nat.* **133**, 111-137.
- Stewart, J. R. (1990). Development of the extraembryonic membranes and histology of the placentae in *Virginia striatula* (Squamata: Serpentes). *J. Morph.* **205**, 33-43.
- Stewart, J. R. (1992). Placental structure and nutritional provision to embryos in predominantly lecithotrophic viviparous reptiles. *Amer. Zool.* **32**, 303-312.
- Stewart, J. R., Blackburn, D. G., Baxter, D. C. & Hoffman, L. H. (1990). Nutritional provision to the embryos in *Thamnophis ordinoides* (Squamata: Colubridae), a predominantly lecithotrophic placental reptile. *Physiol. Zool.* **63**, 722-734.
- Tinkle, D. W. & Gibbons, J. W. (1977). The distribution and evolution of viviparity in reptiles. *Misc. Publ. Mus. Zool. Univ. Mich.* **154**, 1-55.
- Turner, C. L. (1947). Viviparity in teleost fishes. *Sci. Monthly* **65**, 508-518.
- von Wahlert, G. (1953). Eileiter, Laich, und Kloake der Salamandriden. *Zool. Jahrbuch* **73**, 276-310.

- Wake, M. H. (1977a). The reproductive biology of caecilians: an evolutionary perspective. In *The Reproductive Biology of Amphibians*, 73-101. Taylor, D. H., Guttman, S. I. (Eds.). New York: Plenum Press.
- Wake, M. H. (1977b). Fetal maintenance and its evolutionary significance in the Amphibia: Gymniophona. *J. Herpetol.* **11**, 379-386.
- Wake, M. H. (1978). The reproductive biology of *Eleutherodactylus jasperi* (Amphibia, Anura, Leptodactylidae), with comments on the evolution of live-bearing systems. *J. Herpetol.* **12**, 121-133.
- Wake, M. H. (1980). The reproductive biology of *Nectophrynoides malcomi* (Amphibia: Bufonidae), with comments on the evolution of reproductive modes in the genus *Nectophrynoides*. *Copeia* **1980**, 193-209.
- Wake, M. H. (1982). Diversity within a framework of constraints. Amphibian reproductive modes. In *Environmental Adaptation and Evolution*, 87-106. Mossakowski, D., and Roth, D. G., (Eds.). Stuttgart: Gustav Fischer.
- Wake, M. H. (1985). Oviduct structure and function in non-mammalian vertebrates. In *Functional Morphology in Vertebrates*, 427-435. Duncker, H.-R., and Fleischer, G. (Eds.). Stuttgart: Gustav Fischer.
- Wake, M. H. (1993). Evolution of oviductal gestation in amphibians. *J. Exp. Zool.* **266**, 394-413.
- Warburg, M. R., Degani, G. & Warburg, I. (1979). Ovoviviparity in *Salamandra salamandra* (L.) (Amphibia, Urodela) from Northern Israel. *Vie Milleu* **28/29**, 247-257.
- Webster, D. & Webster, M. (1974). *Comparative Vertebrate Morphology*. New York: Academic Press.
- Weekes, H. C. (1929). On placentation in reptiles. I. *Proc. Linn. Soc. N. S. W.* **54**, 34-60.
- Weekes, H. C. (1930). On placentation in reptiles. II. *Proc. Linn. Soc. N. S. W.* **55**, 550-576.
- Wourms, J. P. (1981). Viviparity: the maternal-fetal relationship in fishes. *Amer. Zool.* **21**, 473-515.
- Xavier, F. (1977). An exceptional reproductive strategy in Anura: *Nectophrynoides occidentalis* Angel (Bufonidae), an example of adaptation to terrestrial life by viviparity. In *Major Patterns in Vertebrate Evolution*, 545-552. Hecht, M. K., Goody, P. C. and Hecht, B. M. New York: Plenum Press.
- Yaron, Z. (1985). Reptile placentation and gestation: structure, function, and endocrine control. In *Biology of the Reptilia*, vol. 15., 527-603. Gans, C. and Billet, F. (Eds.). New York: Wiley & Sons.

Accepted: 17.11.93