



# Present day distribution and historical biogeography of the tribe Ophidiini (Ophidiiformes, Ophidiidae, Ophidiinae) from the East Tropical Atlantic (CLOFETA area) and North-East Atlantic and Mediterranean (CLOFNAM area)

Jesus MATALLANAS<sup>1</sup>, and Margarida CASADEVALL<sup>2</sup>

<sup>1</sup> Unitat de Zoologia, Dept. Biologia Animal, Biologia Vegetal i Ecologia,  
Universitat Autònoma de Barcelona, 08193 Bellaterra, Spain

<sup>2</sup> Corresponding author: M. Casadevall, Unitat de Biologia Animal, Dept. Ciències Ambientals, Universitat de Girona,  
Campus de Montilivi s/n, 17071 Girona, Spain  
Fax: (34) 972 418150; e-mail: camcm@fc.udg.es

**Abstract:** The present day geographic distribution of the Ophidiini tribe (Ophidiidae, Ophidiinae) in the Clofnam (North-Eastern Atlantic and Mediterranean) and Clofeta (Eastern Tropical Atlantic) areas is revised in this paper. Results show that *Parophidion vassali* is not a Mediterranean endemic species, and the presence of *Ophidion barbatum* in the Atlantic is confirmed. Moreover, the paper tries to analyse the historical events which could have caused the present situation of two genera, *Ophidion* and *Parophidion*, both in the Atlantic and in the Mediterranean. Although first fossil records of *Ophidion* and *Parophidion* date from the Pliocene, when considering all the historical events occurred from the existence of the Tethys Sea to the opening of the Atlantic and the Mediterranean formation, a much earlier origin of these genera seems to be more likely. The situation of *Ophidion barbatum* and *O. rochei* in the Mediterranean and Black Sea is also discussed.

**Résumé :** Distribution actuelle et biogéographie historique de la tribu des Ophidiini (Ophidiiformes, Ophidiidae, Ophidiinae) de l'Atlantique orientale tropicale (aire CLOFETA), de l'Atlantique Nord-Est et de la Méditerranée (aire CLOFNAM).

La distribution géographique actuelle de la tribu des Ophidiini (Ophidiidae, Ophidiinae) dans les aires du Clofnam (Atlantique du Nord-Est et Méditerranée) et Clofeta (Atlantique Est tropical) est révisée. Nos résultats vont à l'encontre de l'endémicité de *Parophidion vassali* en Méditerranée et confirment la présence d'*Ophidion barbatum* dans l'Océan Atlantique. De plus, ce travail essaie d'analyser les événements historiques qui pourraient expliquer la situation actuelle des deux genres, *Ophidion* et *Parophidion*, à la fois dans l'Atlantique et en Méditerranée. Bien que les premiers fossiles d'*Ophidion* et *Parophidion* aient été datés du Pliocène, l'ensemble des événements historiques depuis l'existence de la Mer Tethys jusqu'à l'ouverture de l'Atlantique et la formation de la Méditerranée, suggèrent une origine beaucoup plus ancienne des deux genres. La situation d'*Ophidion barbatum* et d'*O. rochei* en Méditerranée et en Mer Noire est aussi discutée.

**Keywords:** Ophidiinae, *Ophidion*, *Parophidion*, distribution, historical events.

## Introduction

The Ophidiiform order is a highly diverse group of approximately 135 genera and between 300 and 400

species. According to Cohen & Nielsen (1978), there are so many species and so little information on their anatomy that several years may pass before a well documented study of their systematics appears.

In this paper, the Ophidiiformes classification proposed by Cohen & Nielsen (1978) and accepted, in general trends, by Schwarzhans (1980), Gordon (1982) and Gordon et al.

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(1984), is followed. According to these scientists, the Ophidiinae are one of the four subfamilies of the Ophidiidae.

Nolf & Steurbaut (1989) stated that the Ophidiinae have existed in neritic deposits since the Eocene; *Lepophidium* appeared in the lower Oligocene and *Ophidion* in the lower Pliocene. Now, according to Lea (1980), the Ophidiinae have a circumtropical and temperate distribution in the continental slope in the world ocean.

The group has recently been revised by Lea (1980) in the Eastern Pacific Ocean; by Gordon (1982) in the Eastern Gulf of Mexico; by Nielsen (1986) in the Clofnam area and by Nielsen (1991) in the Clofeta area.

The Ophidiinae are highly concentrated on both sides of America, in tropical and temperate waters. In contrast, until now, only the following species have been assigned to the Clofnam area: *Parophidion vassali* (Risso, 1810), *Ophidion barbatum* Linnaeus, 1758 and *O. rochei* Müller, 1845. In the Clofeta area, Nielsen (1991) only recorded *Ophidion barbatum* and *Genypterus capensis* (Smith, 1847). *O. lozanoi* Matallanas, 1990 has also to be included in this area.

Ophidiinae are divided in two tribes: Lepophidiini and Ophidiini. The latter includes five genera: *Parophidion*, *Raneya*, *Chilara*, *Otophidium* and *Ophidion*. Between them, only *Ophidion* and *Parophidion* genera have been assigned, until now, to the Clofnam and Clofeta areas.

The present study has been induced by the incomplete knowledge (only two partial synopsis given by Nielsen, 1981, 1991) of the Ophidiinae from the Central East Atlantic, including the Madeira and Canary Archipelagos and also the Senegal coasts. The objectives are to revise the present day distribution of *Ophidion* and *Parophidion* genera in the Clofeta and Clofnam areas and also to try to analyse the historical events which may have caused the amphioceanic distribution of these two genera.

### Material examined

*Parophidion vassali*: eight specimens (seven from Madeira and one from Canary Islands) from the "Museu Municipal do Funchal" (Madeira, Portugal).

*Ophidion barbatum*: three uncatalogued specimens from the Canary Islands (Departamento de Zoología, Ciencias Marinas, Universidad de la Laguna, Islas Canarias, Spain), some uncatalogued specimens from the Saharan coasts (Institut de Ciències del Mar, Barcelona, Spain), one uncatalogued specimen from the Gulf of Cádiz (Instituto de Ciencias Marinas de Andalucía, Puerto Real, Cádiz, Spain) and specimens from our collection (Universitat Autònoma de Barcelona and Universitat de Girona) from the Western Mediterranean.

*Ophidion rochei*: specimens from our collection (Universitat Autònoma de Barcelona and Universitat de Girona) from the Western Mediterranean.

*Ophidion lozanoi*: Holotype (138 mm SL, Institut de Ciències del Mar, Barcelona, Spain, N° 409/1983) off the Saharan coasts; Paratype (130 mm SL, Station Marine, IFAN - Gorée, Senegal, N° 59.684) off Dakar.

## Results and Discussion

### I. Present day distribution

#### 1) *Parophidion vassali*

According to Nielsen (1986), this species, apparently considered as a Mediterranean relict (Lea, 1980), is found in the Western Mediterranean, from Gibraltar to the Adriatic sea. Fischer et al. (1987) extend its distribution area to the Eastern Mediterranean. Matallanas & Casadevall (1990) found it in Madeira (six specimens) and, on the basis of a figure that Cadenat (1950) ascribes wrongly to *Ophidion barbatum*, they postulate its presence on Senegal coasts. Finally, Azevedo and Heemstra (1995) have recorded this species in the Azores.

We have recently studied a specimen captured by the *Discovery* in the Canary Islands, and its proximity to African coasts supports the possibility of finding *P. vassali* along the whole NW African coast. Actually, A. Brito (pers. com.) has caught specimens of *P. vassali* in the Canary Islands at a depth between 4 and 20 meters. The presence of this species in the Clofeta area has not yet been recorded by Nielsen (1991).

#### 2) *Ophidion barbatum* and *O. rochei*

These two species have often been confused with each other. A recent paper of Casadevall et al. (1996b) has shown a wide variety of morphometric, meristic and anatomical differential characters. We want to emphasize the possession of such a high number of non-overlapping characters when, according to Gordon et al. (1984), in Ophidiiformes, meristic and morphometric data show a broad range of overlapping between several species. Moreover, their habitat, sex-ratio and maximum length in the western Mediterranean are also different (Matallanas & Riba, 1980), and the same will be quoted in relation to its feeding habits (Matallanas, 1980 and 1981).

For Tortonese (1975) and Bauchot & Pras (1980) the presence of *O. barbatum* in the NE Atlantic is doubtful. However, for Nielsen (1986, 1991) the distribution of this species is "Western Mediterranean, from Gibraltar to the Adriatic and Eastern Atlantic from Southern England to Senegal".

We have studied specimens of *O. barbatum* from the Canary Islands, Senegal, Saharan coasts and from the Gulf of Cádiz, which confirms its Atlantic distribution.

In contrast, *O. rochei* seems to be confined to the Mediterranean, Adriatic and Black Sea (Fischer et al., 1987).

### 3) *Ophidion lozanoi*

Is another species of Ophidiinae recently described (Matallanas, 1990) from NW African specimens. This species has four gillrakers, 24-26 pectoral fin rays, palatine teeth in four rows and the rostral spine larger than the one of *O. barbatum*. *O. lozanoi* is also probably distributed in the SW Mediterranean since Dieuzeide et al. (1955) mentioned specimens of *O. barbatum* with scales from the occiput to the dorsal fin origin, which is a diagnostic character for *O. lozanoi*. This NW African ophidiine has not yet been recorded by Nielsen (1991) in the Clófeta area.

In summary, we can confirm that *P. vassali* is not a Mediterranean endemic species because it has been found in the North and Central East Atlantic too. There is no doubt that *O. barbatum* is also an Atlantic species and finally, *O. lozanoi*, recently described from the NE Atlantic, is probably also a SW Mediterranean species.

## II. Historical biogeography

According to Nolf & Steurbaut (1989), Atlantic Ophidiiforms probably appeared in the Cretaceous and achieved their greatest diversity in the Paleogene Tertiary (especially in the Eocene and the Oligocene). Otolith fossil records analysed by these authors dated the origin of some species of Ophidiiforms. The first genus that seems to have appeared is *Genypterus* (Oligocene), followed by *Lepophidium* (Miocene), while *Ophidion* appeared between the Pliocene and the Quaternary (Table 1). The first fossil records for *Ophidion* were found in the neritic deposits of the Pliocene (approx. 5.2 M.Y.A.). Unpublished data from strata near the Mio-Pliocene include fossil records of *Parophidion schmidtii* (Woods & Kanazawa) (see Nolf & Steurbaut, 1989).

Ophidiiforms from the West coast of America are also considered to be Atlantic in origin because the eastern Pacific barrier totally separates them from Indo-Pacific fauna. According to Lea (1980), the nine *Ophidion* species of the eastern Pacific are endemic in this region.

In general, as Ekman (1953) pointed out, there seems to be a lower affinity between fish species on either side of the Atlantic than between those on the two Central American coastlines. There is a high similarity between fish species on the Atlantic and Pacific coasts where there is a large number of common families and genera. This may be due to the fact that although these areas are now separated by the Central American barrier, the latter did not emerge till the Pliocene. White (1986) dates the appearance of the first Central American isthmus in the Paleocene, at the same time as the

formation of the Mediterranean; this isthmus then submerged until the Pliocene when it re-emerged permanently. Submergence facilitates faunal exchange between eastern Pacific and the Caribbean in the two ways. For White (*op.cit.*), for example, the submergence of the isthmian link between North and South America allowed westward dispersal of the Caribbean lineage of the Atheriniform subfamily Atherinopsinae, back into the Pacific, and a similar pattern was observed by Howes (1991) with the Merlucciidae.

For Ekman (*op.cit.*), communication between both sides of America has been absolutely impossible since the isthmus of Panama joined both parts of America together, so that only exceptionally old species, which existed prior to this, now live on both sides of Central America. Therefore, the presence of species of the *Ophidion* genus on both sides of the isthmus implies that the genus already existed when this barrier finally re-emerged. Furthermore, there are no references to any species that is distributed on both sides of the isthmus of Panama. This was also found by Robins & Lea (1978) in the case of *Lepophidium*: stocks became isolated with the emergence of Central America in the Tertiary and no common species of the genus can be found on both sides of the barrier.

As for the Atlantic species, in agreement with Ekman (1953), because of the existence of the mid-Atlantic barrier, ampho-Atlantic connection is very slight; only a few of the present day species have managed to migrate from one side to the other. There is no available information about *Ophidion lozanoi* habits, but *O. barbatum* and *O. rochei* are benthonic and sand-dwelling species with crepuscular habits, which bury themselves during day-light in the sand and leave their refuge at night or in the first hours of the day to feed (Matallanas & Riba, 1980). It is difficult to imagine how species with such behaviour could have crossed the Atlantic. Thus, we suppose that they were already located on the eastern coast when final circulation in this sea was established.

Larval dispersion is not feasible either, because only *Chilara* and *Parophidion* have a prolonged prejuvenile phase (Lea, 1980). In spite of that, Lea (*op.cit.*) also considered *Parophidion vassali* and *P. schmidtii* as the result of discontinuity to a common transatlantic ancestral population. Probably then, as Ho (1990) supposed for Merlucciidae, the amphioceanic distribution of *Ophidion* and *Parophidion* (in the Atlantic) could be the direct result of the separation of continental shelves by sea floor spreading.

Maldonado (1985) states that most of the major topographic features of the North Atlantic had formed by 40 M.Y.A. However, the Iberian Peninsula and Africa were still significantly separated by a deep channel allowing the connection between the eastern Tethys and the Atlantic.

**Table 1.** Chronology of events leading up to present day configuration of the Mediterranean and the Atlantic.**Tableau 1.** Événements historiques qui ont conduit à la configuration actuelle de la Méditerranée et de l'Atlantique.

PERIOD	TETHYS MEDITERRANEAN / BLACK SEA		ATLANTIC	CENTRAL AMERICAN ISTHMUS	OPHIDIID- FORMES	BIOCHEMICAL DATA
Epoch						
CRETACEOUS	Tethys				Already existed <sup>(3)</sup>	
TERTIARY						
<i>Paleocene</i> 66.5 m.y.a.	Tethys			Emergence of an isthmian link <sup>(1)</sup>		
<i>Eocene</i> 54 m.y.a.					Maximum development of the Order: Eoc.-Oligoc.	
<i>Oligocene</i> 36 m.y.a.			Already formed <sup>(5)</sup>	Submergence <sup>(1)</sup>	<i>Genypterus</i> fossil records <sup>(3)</sup>	
<i>Miocene</i> Middle 15 m.y.a.	Paratethys <sup>(2)</sup>	Mediterranean <sup>(2)</sup>	Basic circulation patterns of modern Atlantic <sup>(5)</sup>		<i>Lepophidium</i> fossil records <sup>(3)</sup>	
Upper 6 m.y.a.	Paratethys freshwater <sup>(2)</sup>	Messinian salinity crisis. Gibraltar strait closed and Mediterranean dried				
5.5 m.y.a.	Paratethys residual basins <sup>(2)</sup>	“Lago Mare” <sup>(2)</sup>				
<i>Pliocene</i> 5.2 m.y.a.	Paratethys became a normal sea for a short time, then freshwater <sup>(2)</sup>	Gibraltar strait opened. Resettlement of marine conditions <sup>(2)</sup> . Mediterranean already formed.		Reemergence of the isthmian link <sup>(1)</sup>	First genus <i>Ophidion</i> fossil records <sup>(3)</sup>	Divergence time between <i>O. barbatum</i> and <i>O. rochei</i> <sup>(4)</sup>
QUATERNARY						
	Mediterranean					
<i>Pleistocene</i> 1.8 m.y.a.	Northern hemisphere glatiations caused oscillations of the sea level <sup>(2)</sup>					
<i>Holocene</i> 10.000 y.a.	Bosfor strait opened and marine water overflowed into the Black Sea <sup>(2)</sup>					

References are taken from: (1) White, 1986, (2) Hsü, 1978, (3) Nolf & Steurbaut, 1989, (4) Casadevall et al., 1996a, (5) Maldonado, 1985.

During the Early to Middle Miocene (20-15 M.Y.A.) overflow water from the Norwegian Sea and Arctic Ocean began to flow in significant quantities into the North Atlantic, creating the basic circulation patterns of the modern Atlantic Ocean (see Table 1).

It must be remembered that Nolf & Steurbaut (1989) situated the origin of these genera in the Pliocene and beginning of the Quaternary. However, the fossil records found by these authors may not have really been the oldest, since, in the light of the aforementioned data, Lea's idea

(1980) situating the origin of the *Ophidion* genus in the Tethys Sea coincides more highly with all these events.

The present day distribution of the *Ophidion* genus is highly concentrated on the eastern and western coasts of America, in tropical and temperate regions, and species are highly diversified. In fact, according to Robins et al. (1986), Boschung (1992), and Robins (in press), the following western Atlantic species have been identified (many still poorly defined): *O. grayi* (Fowler, 1948); *O. holbrooki* (Putman, 1874); *O. lagochila* (Böhlke & Robins, 1959); *O. marginatum* (De Kay, 1842); *O. nocomis* Robins & Böhlke, 1959 (known only from the Bahamas to Puerto Rico); *O. selenops* Robins & Böhlke, 1959 (known only from South Carolina to the southeastern Gulf of Mexico) and *O. welshi* (Nichols & Breder, 1922). Another species cited is *O. beani* Jordan & Gilbert, 1883, whose scientific name is being changed (Robins et al., 1986).

The gap that exists between the number of species on both Atlantic coasts may have been caused by the intense cooling of the climate which took place in the Pliocene (Late Tertiary) once the Atlantic had opened and the Mediterranean had formed. According to Ekman (1953), the two sides of the Atlantic were equally subject to this cooling and, as a result, many northern species migrated southwards in search of warmer waters. Eastern coast species migrated to African coasts and many Indo-Pacific species disappeared, thereby considerably impoverishing this side of the Atlantic. Ekman (*op.cit.*) states that the tropical climate and fauna reappeared more quickly on the eastern coast of the Atlantic, on the boundary between the Pliocene and Early Quaternary, and this may have allowed species of the *Ophidion* genus to diversify more rapidly.

The situation of the Mediterranean in relation to *Ophidion barbatum* and *O. rochei* must also be taken into consideration. In agreement with Hsü (1978), approximately 6 M.Y.A. (Upper Miocene) the movement northwards of the African plate created an isthmus that closed the Mediterranean, producing the Messinian crisis, during which the Mediterranean began to progressively dry up, forming a few isolated salty lakes, called the 'Lago Mare' (approx. 5.5 M.Y.A.). The re-emergence of the Panama isthmus in the Pliocene coincided chronologically with the re-opening of the Mediterranean approximately 5.2-5 M.Y.A., when the Strait of Gibraltar, a permanent connection between the Atlantic and the Mediterranean, was formed. At this time, marine animals were again able to restock the Mediterranean (see Table 1), and invasions from whether tropical or boreal faunas, following the alternation of glacial and interglacial quaternary phases, was possible (Quignart, 1978). From then, nearly all Mediterranean habitats have been colonized by Atlantic species (Briggs 1974, Por 1989).

A recent study (Casadevall et al., 1996a) calculated the genetic distance between *O. barbatum* and *O. rochei* using electrophoretic analysis. A divergence time of 5.0 - 5.2 M.Y.A. was obtained between the two species. A further study is necessary to confirm these results, but, considering this first estimation, the divergence time coincides with this resettlement of marine conditions. If we assume the genus as having originated before the Messinian crisis, our hypothesis is that this phenomenon allowed allopatric conditions for divergence between a more western (or Atlantic) population (the present *O. barbatum* species) and a more eastern population (the present *O. rochei* species). Tortonese (1985) favours the idea of Tethyan "paleoendemics" surviving the Messinian salinity crisis, which completely isolated the Mediterranean basin. Then, *O. rochei* could have a population which was relegated during the crisis to the eastern Mediterranean basins, or an eastern Atlantic population which may have occupied the Mediterranean more quickly than the other when the Strait was opened. This would also account for their present distribution. Similarly, Howes (1991) propose that the presence of north-eastern Atlantic gadoid species and their relatives in the Mediterranean suggests that these taxa are recent invaders from the Atlantic.

Borsa et al. (1986) consider that some species of boreal affinity, motivated by some of the recent glacial periods (the Pleistocene), could have entered the Mediterranean from the Atlantic when climatic conditions were colder. When *O. barbatum* entered the Mediterranean, *O. rochei* would have been sufficiently differentiated so as not to allow re-homogenization. According to the same authors, this may have occurred in the subspecies *Platichthys flesus*.

As far as the presence of *O. rochei* in the Black Sea is concerned, the species probably invaded the Black Sea after these events occurred, because no permanent link was established with the Mediterranean until the early Quaternary. Previously the Black Sea had been subject to periods of desiccation which did not allow its fauna to develop permanently (Ekman, 1953).

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