

First fossil representative of the salamander crown-group from a Gondwanan continent: *Pleurodeles* cf. *waltl* from the Quaternary of Morocco

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Abstract. No fossil belonging to the Caudata crown-group has been hitherto described from a former Gondwanan continent. We report the first known extinct member of the caudate crown-clade from Africa, i.e. a Gondwanan territory. It belongs to the Recent genus *Pleurodeles* (Salamandridae) and is referred to as *Pleurodeles* cf. *waltl*. The fossils come from the Pleistocene of Morocco. They show that *Pleurodeles* (likely *P. waltl*) has been present in Africa for at least two million years and that anthropogenic dispersal is not the cause of its presence in this continent.

Keywords: Africa, Amphibia, biogeography, Caudata, palaeontology, *Pleurodeles*.

Introduction

Salamanders, i.e. caudate amphibians, make up a primarily Laurasian group. Out of Laurasia, they have reached only the northern, generally northernmost, parts of three former Gondwanan continents: South America, Africa (sensu African Plate, i.e. Middle East included), and India. Caudates likely originated in Laurasia (Milner, 1983), but the history of colonization of Gondwanan areas remains entirely unknown. A few early forms (Cretaceous in age) were reported from Gondwanan continents (South America and Africa), but they are all basal caudates and they did not settle in these continents (Nevo and Estes, 1969; Rage, Marshall and Gayet, 1993; Evans, Milner and Werner, 1996; Rage and Dutheil, 2008).

The caudates that inhabit former Gondwanan areas today are all members of advanced fam-

ilies (Salamandridae and Plethodontidae) belonging to the caudate crown-group (Vicites, Peng and Wake, 2009), but we do not know when they entered there. South America and India did not produce fossils belonging to the caudate crown-group. Such fossils were briefly reported, but not described and/or discussed, from Africa only. They all come from Morocco and they were referred to as indeterminated Salamandridae from the early Pleistocene of Irhoud Ocre in an unpublished study (Jaeger, 1975) and *Pleurodeles* sp. (Salamandridae) from the late Pleistocene and Holocene of El Harhoura 2 (Stoetzel, 2009; Stoetzel et al., 2010).

Here, we report on and describe these Pleistocene fossils with the addition of material from Sidi Abdallah, another Pleistocene Moroccan locality. All fossils belong to *Pleurodeles*. The osteology of all currently recognized species of *Pleurodeles* is incompletely known; therefore, our objective is not to confidently identify the fossils at species level, but to report on the only Gondwanan fossils belonging to the crown-group salamander and to evaluate their impact on the previously suggested hypotheses explaining the presence of *Pleurodeles* on both sides of the Gibraltar Strait.

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Material

The material is only comprised of vertebrae coming from three fossiliferous localities in Morocco (Irhoud Ocre, Sidi Abdallah, El Harhoura 2). The fossil vertebrae were compared to those of living salamandrids, more specifically to those of *Pleurodeles waltl* and *P. nebulosus* because it clearly appears that they are referable to *Pleurodeles*. The skeletons of *P. waltl* used for comparisons are from individuals coming from Madrid and Toledo Provinces, central Iberian Peninsula (MNCN 16168, 16169, 16173 to 16176, 19658), Sevilla and Cádiz Provinces, southern Iberian Peninsula (MNHN-AC SPOT 11665, 11666), from unknown provenances in the Iberian Peninsula (two unnumbered specimens, personal collection of SB), and from the Tangier Peninsula, Morocco (MNHN-AC SPOT 11662 to 11664). *P. nebulosus* is represented by skeletons of two individuals coming from Algiers, Algeria (MNHN 1992.0112) and Tabarca, Tunisia (MNHN-AC 2010-1).

The fossils are curated in the Université des Sciences et Techniques du Languedoc (USTL), Montpellier, France, and in the Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), Rabat, Morocco. The extant material is housed in the Museo Nacional de Ciencias Naturales (MNCN), Madrid, Spain, and in the Muséum National d'Histoire Naturelle (MNHN), Paris, France.

The fossil bearing localities

The three fossiliferous sites are located in northeastern Morocco (fig. 1). Irhoud Ocre is a locality from the early Pleistocene, whose geological age appears to be close to 2 million years (Ma) (Geraads, 2002). Sidi Abdallah is also of early Pleistocene age, but it is not so old as Irhoud Ocre (D. Geraads, pers. com.). Renaud, Benammi and Jaeger (1999) suggested a 1.5 Ma geological age for this locality. El Harhoura 2 includes several fossiliferous levels of different ages. *Pleurodeles* has been found in levels ranging from ca 100 000 (late Pleistocene) to 5800 years (Holocene) (Stoetzel et al., 2010).

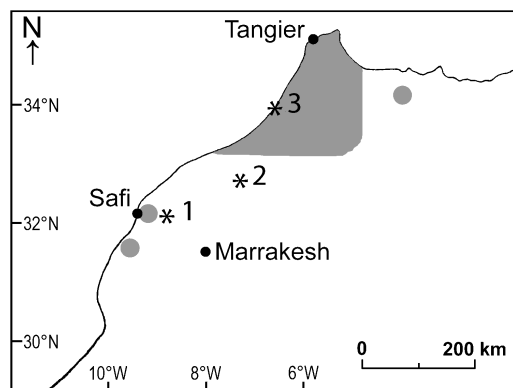


Figure 1. Map of northern Morocco showing the range of extant *P. waltl* (gray areas; from Bons and Geniez, 1996) and localities of extinct *Pleurodeles cf. waltl* (1: Irhoud Ocre, early Pleistocene; 2: Sidi Abdallah, early Pleistocene; 3: El Harhoura 2, late Pleistocene and Holocene).

Systematic account

Salamandridae Goldfuss, 1820

Pleurodeles Michahelles, 1830

Pleurodeles cf. waltl

Referred material: one atlas (USTL, IO 532), 49 trunk (USTL, IO 533-535), one sacral (USTL, IO 536) and one anterior caudal (USTL, IO 537) vertebrae from Irhoud Ocre; one trunk vertebra from Sidi Abdallah (USTL, SBD 2); 16 trunk and one caudal vertebrae from El Harhoura 2 (INSAP, EH2-C6-P12-HK0IH and 16 unnumbered vertebrae).

Description

These vertebrae belong to a mid-sized salamander. The size of dorsal vertebrae (length between pre- and postzygapophyses from 2.1 to 4.9 mm) suggests that the largest individuals reached a total length of about 140 mm.

The atlas is mainly characterized by the presence of a well-developed odontoid process (fig. 2A-C). The two facets of the odontoid process that articulate with the skull are separated, but closely spaced; they occupy an anterior and rather ventral position. In anterior view, the two anterior cotyles are oval, their major axis being weakly oblique on the horizontal. In dorsal aspect, the atlas is comparatively short and constricted. The neural spine is thin and low. On each side, the dorsal surface of the neural arch is limited laterally by a marked anteroposterior crest. In lateral view, the lateral walls are very short; consequently, the postzygapophyses are markedly overhanging. On each side, several foramina open just posterior to the anterior cotyle; among them, the spinal foramen appears to be the largest one that is level with the floor of the neural canal. In ventral view, the haemal keel is well-marked off from the centrum; its lateral margins are concave and they strongly diverge anteriorly. Posteriorly, a foramen opens on either side of the cotyle, at the base of each pedicel. Several irregular foramina pierce the ventral and lateral faces of the atlas.

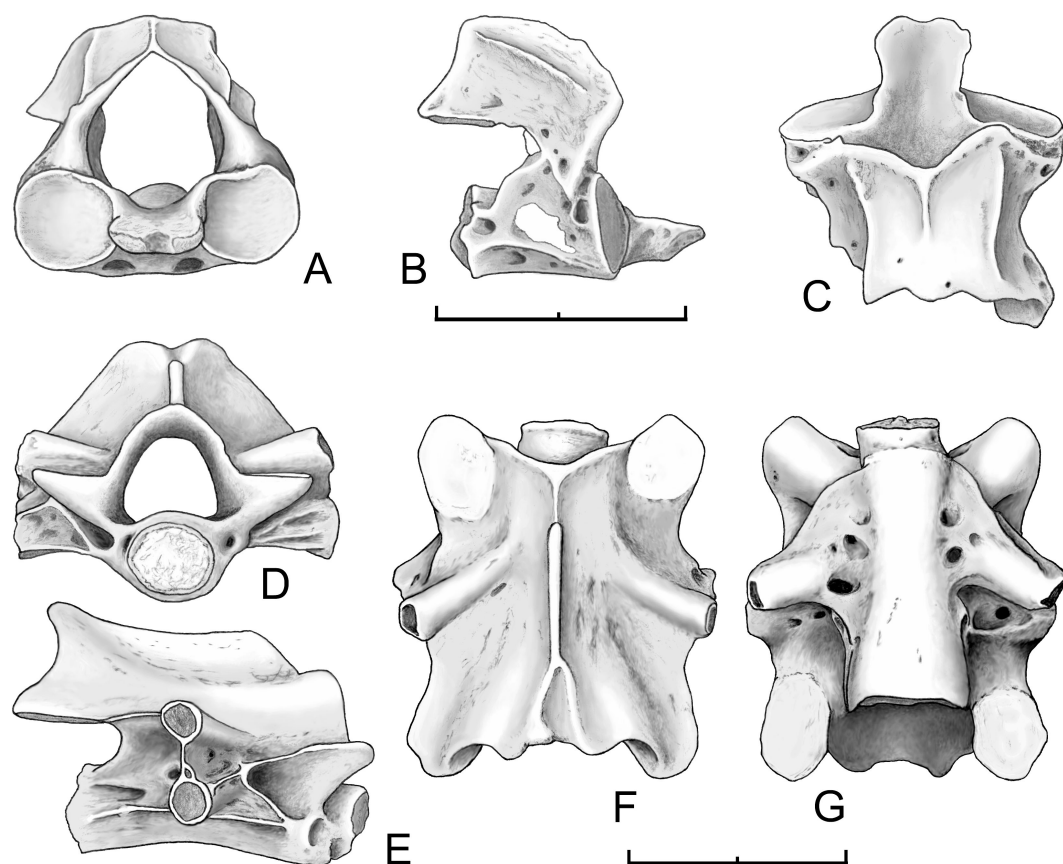


Figure 2. *Pleurodeles* cf. *waltl* from the early Pleistocene of Irhoud Ocre. A-C: atlas (USTL IO 532) in anterior (A), right lateral (B) and dorsal (C) views. D-G: dorsal vertebra (USTL IO 533) in anterior (D), right lateral (E), dorsal (F) and ventral (G) views. Each scale bar: 2 mm.

The dorsal vertebrae come from the three localities. Their morphology is quite homogenous and there is no difference between the localities, except the slightly larger size of the vertebrae from the late Pleistocene and Holocene of El Harhoura 2. The vertebrae are longer than wide and opisthocelous (fig. 2D-G). The condyles lack a precondylar constriction. The neural spine is elongate, but it does not reach the anterior and posterior limits of the neural arch. It is thin and its dorsal border lacks dermal productions. Anteriorly, the neural spine has a moderate height; posteriorly, it grades into the rising neural arch that becomes level with the top of the spine. Consequently, whereas the neural spine has an anterior, posteriorly inclined border, it does not have a posterior border. The

rib-bearers are bicipital, the dorsal and ventral ones being united by a bony lamina up to their lateral tips. On each side, the two rib-bearers are approximately horizontal, but slightly divergent; they are clearly directed posterolaterally. The anterior zygapophyseal ridge extends posteroventrally to connect either the bony lamina uniting the two rib-bearers or the ventral rib-bearer. The posterior zygapophyseal ridge contacts the posterior margin of the dorsal rib-bearer, therefore it is horizontal; the ridge extends along the whole length of the dorsal rib-bearer. In dorsal or ventral aspect, the posterior zygapophyseal ridge does not form a marked notch posterior to the dorsal rib-bearer. In lateral view, the anterior ventral crest is often forked, the anterior ventral crest s.s. retaining its nor-

mal position while an additional crest extends posterodorsally to connect either the dorsal margin of the ventral rib-bearer or the anterior zygapophyseal crest. A broad and deep depression is bound dorsally by the anterior zygapophyseal crest and ventrally by the anterior ventral crest or by the additional ventral crest, where present. Two foramina generally open in the bottom of this depression, close to the base of the rib-bearers. On the posterior half of the lateral wall of the vertebra, three foramina generally open: the 'central' foramen appears to be the spinal foramen. In anterior view, the neural arch is vaulted and approximately triangular. On each side, a paracotylar foramen opens at the base of the prezygapophysis. In posterior view, the neural spine does not appear. The degree of vaulting of the neural arch varies according to the position of the vertebra in the vertebral column, but the neural arch remains always clearly vaulted. In ventral view, the centrum appears more or less cylindrical and its ventral surface is smooth. It is weakly constricted in its middle part. It is

well-limited laterally in its posterior part only; as a result of the presence of anterior ventral crests, its lateral limits are blurred anteriorly. The anterior ventral crests do not extend largely and they have sigmoid anterior borders; anteriorly, they may approach the base of the condyle. The posterior ventral crests are scarcely developed or even absent; thus, in the posterior part of the vertebra, the centrum is clearly separated from the ventral rib-bearer by a broad and deep embayment or notch. The number of subcentral foramina varies.

On the sacral vertebra (fig. 3A, B), the rib-bearers are more robust than those of dorsal vertebrae. The anterior ventral crest is lacking or very weak. A lamina partly covers the anterior depression; as a result the latter appears as two, anterior and posterior, apertures. In addition, the neural arch is less vaulted. Spinal foramina are present.

One anterior caudal vertebra from Irhoud Ocre is available. It differs from those from the dorsal region in lacking developed dorsal rib-

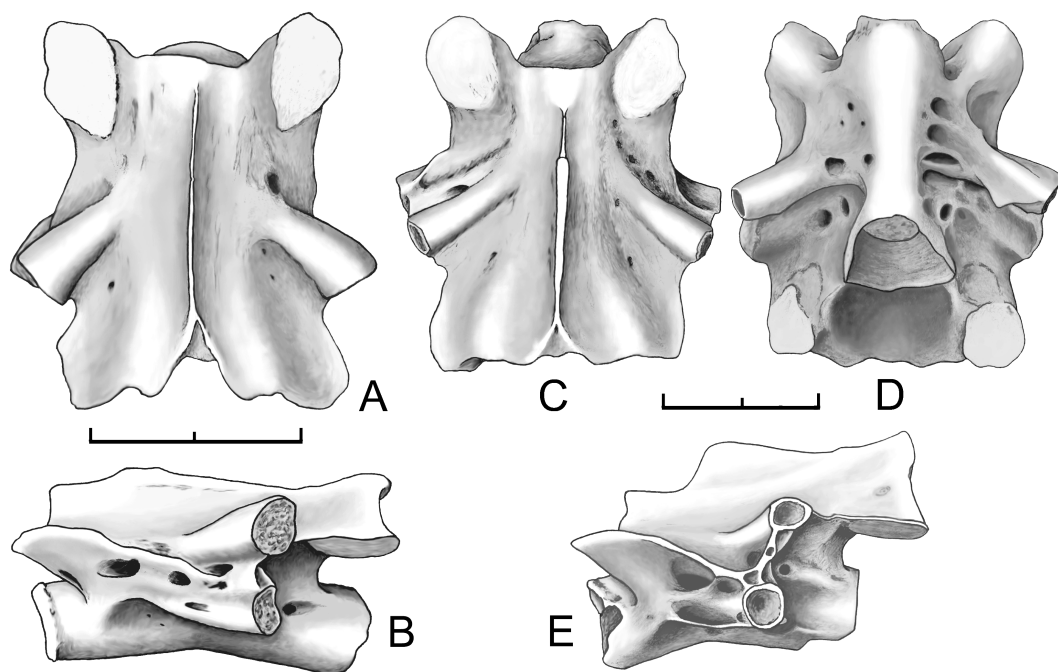


Figure 3. *Pleurodeles* cf. *waltl*. A-B: sacral vertebra (USTL IO 536) from the early Pleistocene of Irhoud Ocre in dorsal (A) and left lateral (B) views. C-E: dorsal vertebra (INSAP, EH2-C6-P12-HKOIH) from the late Pleistocene of El Harhoura 2 in dorsal (C), ventral (D) and left lateral (E) views. Each scale bar: 2 mm.

bearers. Only the ventral rib-bearer is developed and cylindrical, the dorsal one is a lamina that results from the coalescence of the anterior and posterior zygapophyseal crests. As a consequence, the anterior zygapophyseal crest does not slant posteroventrally; it is horizontal. Spinal foramina are present. The vertebra lacks haemapophyses.

A posterior caudal vertebra from El Harhoura 2 represents the only remain from the Holocene level. It differs from the anterior caudal in bearing haemapophyses and in having transverse processes Z-shaped in lateral aspect. In addition, the anterior and posterior zygapophyseal crests contact the top of the transverse processes, the neural spine is tall and the neural arch vaulted.

Results

Opisthocoelous vertebrae occur only in Salamandridae and Plethodontidae. However, while the anterior condyle of plethodontids is formed by calcified cartilage that infills the cotyle, salamandrids have a bony condyle (Wake, 1963; Wake and Lawson, 1973; Souteyrand-Boulenger, 1995). In the fossils, this clearly points to the Salamandridae. Other features of the fossils, although non restricted to salamandrids, are consistent with this assignment: rib-bearers bicipital, united by a bony lamina up to their lateral tips, and spinal nerves exiting intravertebrally in the dorsal, sacral and caudal regions.

A significant character is the orientation of the anterior zygapophyseal crest that slopes posteroventrally to join either the ventral rib-bearer or the lamina that connects the rib-bearers. This feature occurs in salamandrids belonging to the 'group II genera' (Estes, 1981), i.e. *Pleurodelini* (Dubois and Raffaëlli, 2009): the Asian assemblage that includes the living *Tylototriton* (also known from Eocene of Germany; Herre, 1935; Estes, 1981) and *Echinotriton* (included to *Tylototriton*, at the time of Estes' study), the European extinct *Chelotriton* (middle Eocene-

Pliocene; Bailon, 1989; Roček, 1994), and the living *Pleurodeles* that inhabits southwesternmost Europe and northernmost Africa (reported from the Neogene of Europe; see below). Two other genera, *Brachycormus* and *Palaeopleurodeles* that are both extinct (late Oligocene and early/middle Miocene of Germany, respectively) belong to the 'group II' but the condition of their anterior zygapophyseal crest is unknown.

Tylototriton, *Echinotriton*, *Chelotriton* and *Brachycormus* are readily distinguished from the Moroccan fossils in having sculptured dermal plates capping the neural spines (Estes, 1981; Roček, 1996), a character that cannot be checked in *Palaeopleurodeles*. *Tylototriton* and *Echinotriton* further differ from the fossils in having a marked notch in the posterior zygapophyseal crest, posterior to the rib-bearer; *Chelotriton*, *Pleurodeles* and the fossils lack the notch and their posterior zygapophyseal crest largely fills the space posterior to the rib-bearer. In *Brachycormus* and *Palaeopleurodeles*, this character cannot be reliably observed. Finally, the poorly known *Palaeopleurodeles* differs from the fossils by the presence of two lateroventral crests on the ventral face of vertebrae (Estes, 1981). Therefore, within salamandrids of 'group II', only *Pleurodeles* is consistent with the fossils. Aside from taxa belonging to 'group II', the fossils should be compared with *Salamandra*, the only other caudate genus known in Africa. In the latter, the atlas is more elongate and its strong neural spine is anteriorly subdivided into two (Haller-Probst and Schleich, 1994) or three (SB, pers. obs.) anterior ridges, dorsal vertebrae are more depressed and have a lower neural spine, and the anterior zygapophyseal crests are horizontal, joining the dorsal rib-bearers. Therefore, the fossils from Morocco may be referred only to *Pleurodeles*, from which they do not differ.

Assignment to species level cannot be achieved confidently. *Pleurodeles* includes three extant, and no extinct species: *P. waltl* from the Iberian Peninsula and northernmost Mo-

rocco, *P. nebulosus* from northernmost Algeria (except the Edough Peninsula) and northernmost Tunisia, and *P. poireti* restricted to the Edough Peninsula in Algeria (Carranza and Wade, 2004). The vertebral morphology of *P. poireti* remains unknown and it cannot be compared to the fossils. The fossil vertebrae are clearly similar to those of *P. waltl* and they differ from those of *P. nebulosus*. Dorsal vertebrae of *P. nebulosus* are more elongated. The ratio total length to width across prezygapophyses is generally above 1.5 in *P. nebulosus* while it ranges from 1.26 to 1.4 in *P. waltl*; in the fossils it is quite similar to that in *P. waltl* (1.23–1.36). In addition, in *P. nebulosus* the ventral rib-bearer has a posterior small, lamellar and more or less triangular expansion close to its tip; its size varies but it is always present. A similar, but smaller expansion may occur in *P. waltl*, but only in some posterior dorsal vertebrae of adults. Among the fossils, only one vertebra from the late Pleistocene levels of El Harhoura 2 displays such an expansion (fig. 3C-E). Finally, *P. poireti* occupying a very restricted area far from Morocco, we propose as a working hypothesis that the fossils may belong to *P. waltl*, it being understood that no definite identification may be suggested pending the study of vertebrae of *P. poireti* is possible. Therefore, we refer the fossils to as *Pleurodeles* cf. *waltl*.

Based on mitochondrial DNA sequences, Carranza and Arnold (2004) and Veith et al. (2004) suggested that two clades may be distinguished within *P. waltl*: one would be comprised of populations from western and central Iberian Peninsula and another clade would include populations from southern and eastern Iberian Peninsula plus those from Morocco. Our study of the vertebral morphology of *P. waltl* did not disclose significant intraspecific differences.

Discussion

The biogeographic history of *Pleurodeles* is debated. The only consensus is that this taxon originated in Europe. Veith et al. (2004) stated

that the oldest *Pleurodeles* dates from ca 23 Ma (earliest Miocene), which is an error (confusion with *Palaeopleurodeles*, which is however only 17–15 Ma old?). In fact, the earliest *Pleurodeles* (an unstudied, presumed new species) was reported by Böhme and Ilg (2003) from the middle Miocene (ca 15–13.5 Ma) of Valalto 1A (Spain); however, the fossil is not described. At species level, only *P. waltl* was identified. The earliest representative of *P. waltl* comes from the late Pliocene (ca 3.2–2.5 Ma) of Las Higuieruelas, Spain (Martín and Sanchiz, 2010). Younger records from the Iberian Peninsula were reported by Gleed-Owen (2001), Barroso-Ruiz and Bailon (2003, 2006) and Martín and Sanchiz (2010).

Several biogeographical scenarios were proposed about the origin and dispersals of *Pleurodeles*, more specifically *P. waltl*, on both sides of the Gibraltar Strait. According to Carranza and Arnold (2004), the first split (by ca 5.3 Ma) within *Pleurodeles* separated *P. waltl* that occupied the Iberian Peninsula from the North African lineage (*P. poireti* and *P. nebulosus*, the latter not yet recognized in the article). Subsequently, in the Iberian Peninsula, *P. waltl* was divided by 3.2–2 Ma into western plus central populations on one hand and southern plus eastern ones on the other hand. North African populations of *P. waltl* would have originated from the southern and eastern Iberian assemblage; consequently, the species would have crossed the sea after the disappearance of the last terrestrial connection, therefore Carranza and Arnold suggested that the dispersal was perhaps of anthropogenic origin. As far as the initial dichotomy within *P. waltl* (western + central populations vs southern + eastern + Moroccan ones) is concerned, Batista, Harris and Carretero (2004) proposed a date (3.5 Ma) approximately similar to that suggested by Carranza and Arnold (2004). Veith et al. (2004) suggested a different history for *P. waltl*. They suggested that this species took advantage of the Messinian event to reach North Africa by about 5.6 Ma and that, subsequently but at an

unknown date, this African lineage entered back Iberia where it settled in the southern and eastern regions. About this dispersal from Africa to Europe, they considered the role of anthropogenic dispersal possible.

The presence of *Pleurodeles* (likely *P. waltl*) about 2 Ma ago at Irhoud Ocre is consistent with both hypotheses. However, if the species is really *P. waltl*, then this age discards anthropogenic dispersal from Europe to Africa as conceived possible by Carranza and Arnold (2004), but it may be compatible with such dispersals between Africa and Europe at a younger date, as conjectured by Veith et al. (2004).

Conclusion

Because of the lack of osteological referential on North African salamanders, the identification of the studied Moroccan fossils cannot be definitely confirmed at specific level. However, they doubtless belong to the genus *Pleurodeles* and appear to belong or to be close to the species *P. waltl*. Whatever the species identification of these remains and their impact on the biogeographic history of *Pleurodeles*, it should be mainly noted that these fossils are the only known extinct representatives of the Caudata crown-group from former Gondwana.

Acknowledgements. We are grateful to J.J. Jaeger (University of Poitiers), and to the Archaeological Mission "El Harhoura-Témara" (Ministère des Affaires Etrangères et Européennes, France – Ministère de la Culture, Morocco) directed by R. Nespoulet (MNHN, Paris) and M.A. El Hajraoui (INSAP, Rabat), who permitted us to study the fossil material. D. Donaire (Jerez de la Frontera) and D. Geraads (CNRS, Paris) helped in various ways. Two anonymous reviewers made helpful suggestions.

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Received: November 30, 2010. Accepted: February 18, 2011.