

Osteological Peculiarities of *Bufo brongersmai* (Anura: Bufonidae) and Their Possible Relation to Life in an Arid Environment

Massimo Delfino^{1,*}, Stefano Doglio², Zbynek Roček^{3,4}, Daniele Seglie⁵, and Lahcen Kabiri⁶

¹Dipartimento di Scienze della Terra, Università di Firenze, Via G. La Pira 4, I-50121, Firenze, Italy

²Centro Studi e Museo d'Arte Preistorica, Viale Giolitti 1, I-10064, Pinerolo, Italy

³Laboratory of Palaeobiology, Geological Institute, Academy of Sciences, Rozvojová 135, CZ-165 00 Prague, Czech Republic

⁴Department of Zoology, Charles University, Vinicna 7, CZ-128 44 Prague 2, Czech Republic

⁵Dipartimento di Biologia Animale e dell' Uomo, Università di Torino, via Accademia Albertina 17, I-10125 Torino, Italy

⁶Laboratoire LFS [SCEEP], Département de Géologie, Faculté des Sciences et Techniques Errachidia, Université Moulay Ismaïl, BP 509 Boutalamine 52 000 Errachidia, Morocco

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Massimo Delfino, Stefano Doglio, Zbynek Roček, Daniele Seglie, and Lahcen Kabiri (2009) Osteological peculiarities of *Bufo brongersmai* (Anura: Bufonidae) and their possible relation to life in an arid environment. *Zoological Studies* 48(1): 108-119. The morphology of selected isolated skeletal elements of the northwestern African endemic toad *Bufo brongersmai* Hoogmoed 1972 is herein described and compared to those of other *Bufo* species inhabiting the same area and Europe. The osteological morphology of this species clearly differentiates it from others within the genus, and several diagnostic osteological characters are added to the specific diagnosis. In particular, the presence in adult individuals of a rather-large maxillary fontanella, which late in ontogeny is reduced to a few foramina, has not been observed in other species. These fontanellae, as well as the fenestrations on the sphenethmoid, together with other osteological traits, suggest a significant degree of hypo-ossification. This seems likely related to the rapid larval development that allows *B. brongersmai* to achieve higher reproductive fitness than other species in the highly ephemeral waters of the rocky, arid environment it inhabits. Other peculiar osteological traits could be related to the exploitation of small crevices to protect adults from overheating and desiccation. <http://zoostud.sinica.edu.tw/Journals/48.1/108.pdf>

Key words: *Bufo bufo*, *Bufo calamita*, *Bufo mauritanicus*, *Bufo viridis*, Hypo-ossification.

Bufo brongersmai Hoogmoed 1972, commonly called Brongersma's toad or the Tiznit toad, was described as a new species in the early 1970's when Marinus S. Hoogmoed of the National Museum of Natural History in Leiden carefully analyzed some Moroccan populations either previously not identified to the species level or misidentified as the green toad *B. viridis*. The phylogenetic relationships of *B. brongersmai*, initially based on Hoogmoed's statement that it is "related" to the Natterjack toad *B. calamita* and *B. viridis*, were later confirmed by Herrero et al. (1993: 465), who validated its specific status and

presented evidence of "strong karyotypic similarity between *B. viridis* and *B. brongersmai*". Such relationships have been accepted in the general overview of the *B. viridis* complex by Balleto et al. (1999), in an analysis of the variability of *B. viridis* by El-Oualidi and Jaziri (2001), and in a recent review of amphibian phylogeny by Frost et al. (2006; but see "Material and methods" section for further information). On a finer level of analysis, Stöck et al. (2006) placed *B. brongersmai* in the *B. viridis* group but not in the *B. viridis* subgroup.

Originally found at only a few sites in southwestern Morocco and northern parts of the

*To whom correspondence and reprint requests should be addressed. E-mail: massimo.delfino@unifi.it

former Spanish province of Western Sahara, the known range of *B. brongersmai* has now been modified by further research. *Bufo brongersmai* has also been found north of the Grand Atlas mountains, along most of the Moroccan Anti Atlas and could possibly occur in northwestern Algeria close to the Moroccan border (García-París and López-Jurado 1990, Bons and Geniez 1996, Schleich et al. 1996, Geniez et al. 2004). It is a small toad (with a maximum snout-vent length (SVL) of about 50 mm) characterized by extremely fast larval development (in captivity it can be accomplished in 15-20 d; Grillitsch and Grillitsch 1987). *Bufo brongersmai* is thus able to reproduce in temporary puddles and ephemeral brooks that it inhabits in rocky sub-Saharan hilly areas that are nearly devoid of vegetation.

As for most of the African bufonids (see Clarke 2001, and literature therein), only a few papers have been dedicated to its natural history despite its uniqueness (see Bogaerts 2001, Gallix 2002, Guillon et al. 2004). Its osteology is barely known: the only exception being the edentulous condition of its maxillae and vomers reported by Hoogmoed (1972) in the original description.

The goal of the present paper is to describe selected isolated skeletal elements of *B. brongersmai* in order to characterize its skeletal morphology, to discuss the osteology of this species in the context of its peculiar ecology, and to furnish diagnostic characters for the identification of fossil remains that may be discovered in northwestern Africa.

MATERIALS AND METHODS

The anatomical description is based on 5 dried disarticulated skeletons. Four specimens (2 females and 2 males; CeSMAP-H 1-4) came from a perennial spring at 1675 m in elevation in the middle of the Jbel Sarhro range (Morocco, Anti Atlas), about 20 km south of the town of El Kelaa M'Gouna, in the prefecture of Ouarzazate. The 5th specimen, a male MNCN-H 21564, came from Agadir, Morocco; it had been kept for an unknown period in captivity. The SVL of the CeSMAP specimens ranges 34-39 mm, whereas that of the MNCN specimen is larger but not known with precision (not reported on the label). Notwithstanding that the SVLs of the CeSMAP specimens are significantly smaller than the maximum size observed by Hoogmoed (1972; 51 mm for males and 48 mm for females), the fact that

females had fully developed eggs in the abdominal cavity and males had nuptial pads clearly indicates their adult condition and sexual maturity.

Frost et al. (2006) erected the new genus *Pseudepidalea* in order to preserve the monophyly of members of the *B. viridis* group and therefore proposed, among others, the new combination *Pseudepidalea brongersmai* (Hoogmoed 1972). However, due to the fact that such a nomenclatural change is irrelevant to the main conclusions of this research, not to mention that *B. bufo* and *B. viridis* spontaneously produce viable hybrids (Bressi et al. 2000), the traditional nomenclature is adopted here, pending further support for the distinction at the generic rank of these taxa (see Wiens 2007, for general considerations). The anatomical nomenclature follows Sanchiz (1998) and Bailon (1999). The morphology of western Palaearctic species was assessed based on comparative specimens listed in the "Appendix" and on the basis of the following papers: Thireau and Marolle (1968), Sanchiz (1977), Bailon (1999), and Ratnikov (2001).

Collection acronyms are reported in the "Appendix".

RESULTS

Morphological Description

The following descriptions consider neither the general morphology of each single skeletal element nor the basic geometric relationships among different elements, because it is assumed that *B. brongersmai* has the same basic structure exhibited by other members of this genus (as absence of teeth on the premaxillae, maxillae, and vomers; and the number of presacral vertebrae). The descriptions focus on significant traits (such as the presence/absence or position of ridges and pits) of the skeletal elements that lead to the peculiar morphology of this species. Due to the fact that *B. brongersmai* is considered to be phylogenetically related to *B. viridis* (see above), the morphology of the latter is used for comparisons.

Premaxillae: The pars facialis is relatively robust, rather wide and long, and therefore more similar to that of *B. viridis* than to that of *B. bufo*. The left premaxilla of specimen CeSMAP-H 4 has a tiny hole piercing the base of the pars facialis.

Maxillae: The processus palatinus is distinctly reduced so that it is never visible in lateral view. The maxillae of specimens CeSMAP-H 1-4 are characterized by having a relatively large longitudinally elongated and irregular fontanella in the lateral wall, located dorsal to the lamina horizontalis and anteriorly to the processus palatinus, in the area of the fossa maxillaris (Figs. 1a, b). Such a fontanella is comparatively larger in the smallest available specimen, CeSMAP-H 4 (Fig. 1c), than in the largest one CeSMAP-H 2 (Fig. 1d), where it is surrounded by small irregular “foramina”. Its former presence in specimen MNCN-H 21564 is evidenced by the presence of 3 “foramina” on the right maxilla (Fig. 1e) and 1 on the left maxilla.

Nasals: The lateral process (processus paraorbitalis) is distinctly shorter and stouter than in *B. viridis* and *B. bufo*.

Frontoparietals: Each frontoparietal is fused with the corresponding prootic. The anterior part of the frontoparietals is always reduced to a narrow process, medially fimbriated along the margo sagittalis, so that the 2 elements are not in contact medially, and a large frontoparietal fenestra is

present (Fig. 2a). On the dorsal surface, the medial crest is not developed and there is no trace of dermal ornamentation. The occipital canal has smooth rims and is barely visible in the smallest specimens. On the ventral surface, the limits of the incrassatio frontoparietalis are so weakly developed as to be nearly invisible.

Prootics: There are no ridges on the dorsal surface of these elements (Fig. 2a). The foramen ovale on the lateral descending lamina of the prootics is particularly large and elongated.

Exoccipitals: The main peculiarity of the exoccipitals concerns the position of the occipital condyle: contrary to all *Bufo* species used here for comparison, such a structure is not close to the ventromedial edge of the bone, but is significantly far from it (Fig. 2b); a similar condition occurs in the genus *Hyla* (where occipital condyles are only slightly more separated), and it is related to the condylar type of the atlas (see below). The foramen perilymphaticum and the foramen jugulare are very wide (wider than in *B. viridis*), so that the latter is largely visible in posterior view.

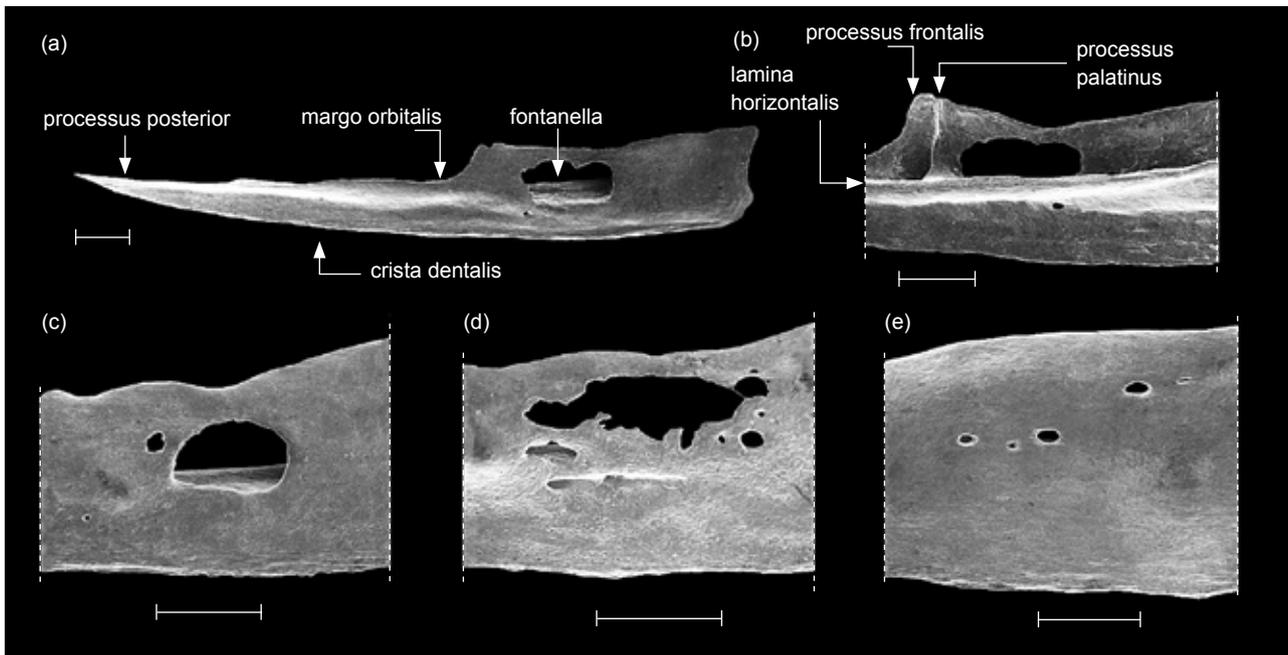


Fig. 1. (a) CeSMAP-H 1, right maxilla in lateral view; (b) CeSMAP-H 1, details of the fontanella on the left maxilla in medial view; note the relationships with the lamina horizontalis and the reduced processus palatinus; (c) CeSMAP-H 4, details of the fontanella on the right maxilla in lateral view; (d) CeSMAP-H 2, details of the fontanella on the right maxilla in lateral view; (e) MNCN-H 21564, details of the vestigial fontanellae on the right maxilla in lateral view. Scale bars = 0.5 mm.

Sphenethmoid: This is slightly wider than long. The development of the dorsal part (i.e., the ossified tectum nasi) varies considerably: it is just a curved strip in CeSMAP-H 3, faintly more developed in specimen CeSMAP-H 4 where an anterior process is present, but significantly more extended in MNCN-H 21564, the largest available specimen. The fenestration within its lateral walls varies: both lateral walls of specimen CeSMAP-H 4 show a wide posterior fenestra that also extends to the ventrolateral surface (Fig. 2c) and a 2nd, much smaller, anterior fenestra is present close to the anteroventral edge of each lateral process (postnasal wall): the rim of the right one is closed, while the rim of the left one is anteriorly open. Specimen CeSMAP-H 3 has a comparatively small fenestra in its right lateral wall, but the left wall is non-fenestrated. Specimens CeSMAP-H 1 and 2 and MNCN-H 21564 show no fenestration or residual foramen either on the lateral or on ventral

walls. The floor of the nasal capsule (solum nasi) is not folded dorsally (producing the so-called sella amplificans) in the CeSMAP specimens, whereas a moderately developed fold is present in MNCN-H 21564 (Fig. 2d).

Pterygoids: These triradiate elements are characterized by a reduced ramus interior, which is stout and much shorter than those of *B. bufo*, *B. calamita*, *B. mauritanicus*, and *B. viridis*.

Squamosals: The anterior (processus zygomaticus) and posterior (processus oticus) processes of the lamella alaris are small and subequal in the smallest specimens, but differ in size in MNCN-H 21564 (Fig. 2e). In the latter, the anterior process is short, slender, and pointed, while the posterior process is both thicker than the anterior one and rounded at its end (approximately like that in *B. viridis*), but not expanded in a dorsally oriented

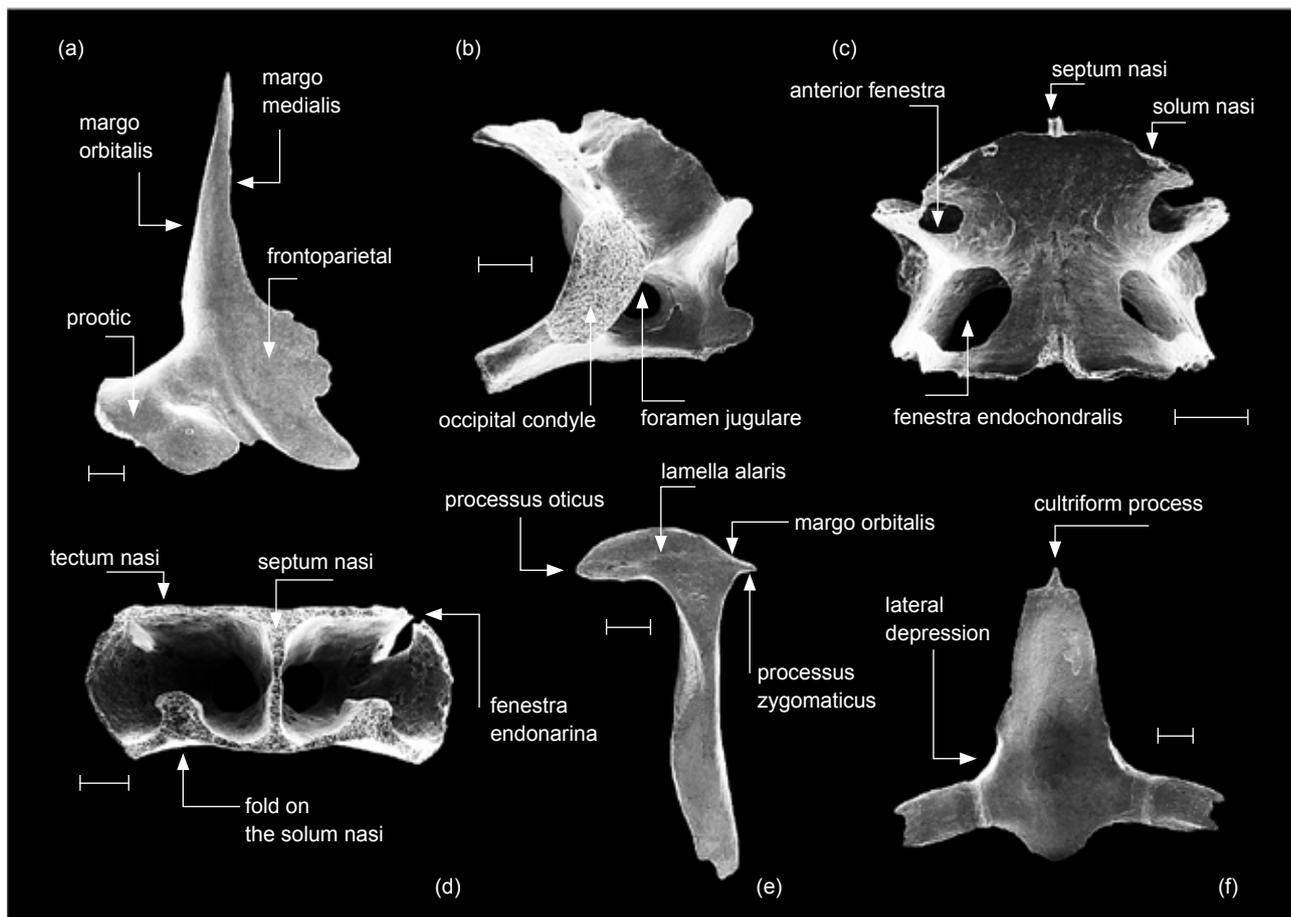


Fig. 2. (a) CeSMAP-H 1, left frontoparietal and prootic in dorsal view; (b) MNCN-H 21564, right exoccipital in posterior view; (c) CeSMAP-H 4, sphenethmoid in ventral view; (d) MNCN-H 21564, sphenethmoid in anterior view; (e) MNCN-H 21564, right squamosal in lateral view; (f) CeSMAP-H 2, paraspheonoid in ventral view. Scale bars = 0.5 mm.

lamina as in *B. bufo*.

Parasphenoid: The cultriform process (pars medialis) is rather stout because its base is wide and the process is rather short. On the ventral surface of the corpus parasphenoideum, there are no transverse ridges. Two lateral depressions are present at the base of the cultriform process (Fig. 2f).

Angulosplenials: The coronoid process is medio-laterally narrowed and so flattened that it develops in a nearly horizontal plane.

Scapulae: A distinct lamina (crista anterior) is developed on the anterior margin (margo anterior),

so that the outline of the anterior region of the bone is rather convex (Fig. 3a) and not concave as is usual in *B. viridis*. The lamina reaches the tip of the pars acromialis, and in some specimens, it produces a tiny apical point (as is the case with specimen CeSMAP-H 3). The supraglenoidal fossa is absent.

Coracoids: These elements have a particularly slender and long shaft.

Humeri: When compared to the humeri of *B. viridis*, the most remarkable characteristic of *B. brongersmai* humeri is their overall slenderness and the fact that they are rather straight (not as curved as those of *B. viridis*). The crista ventralis

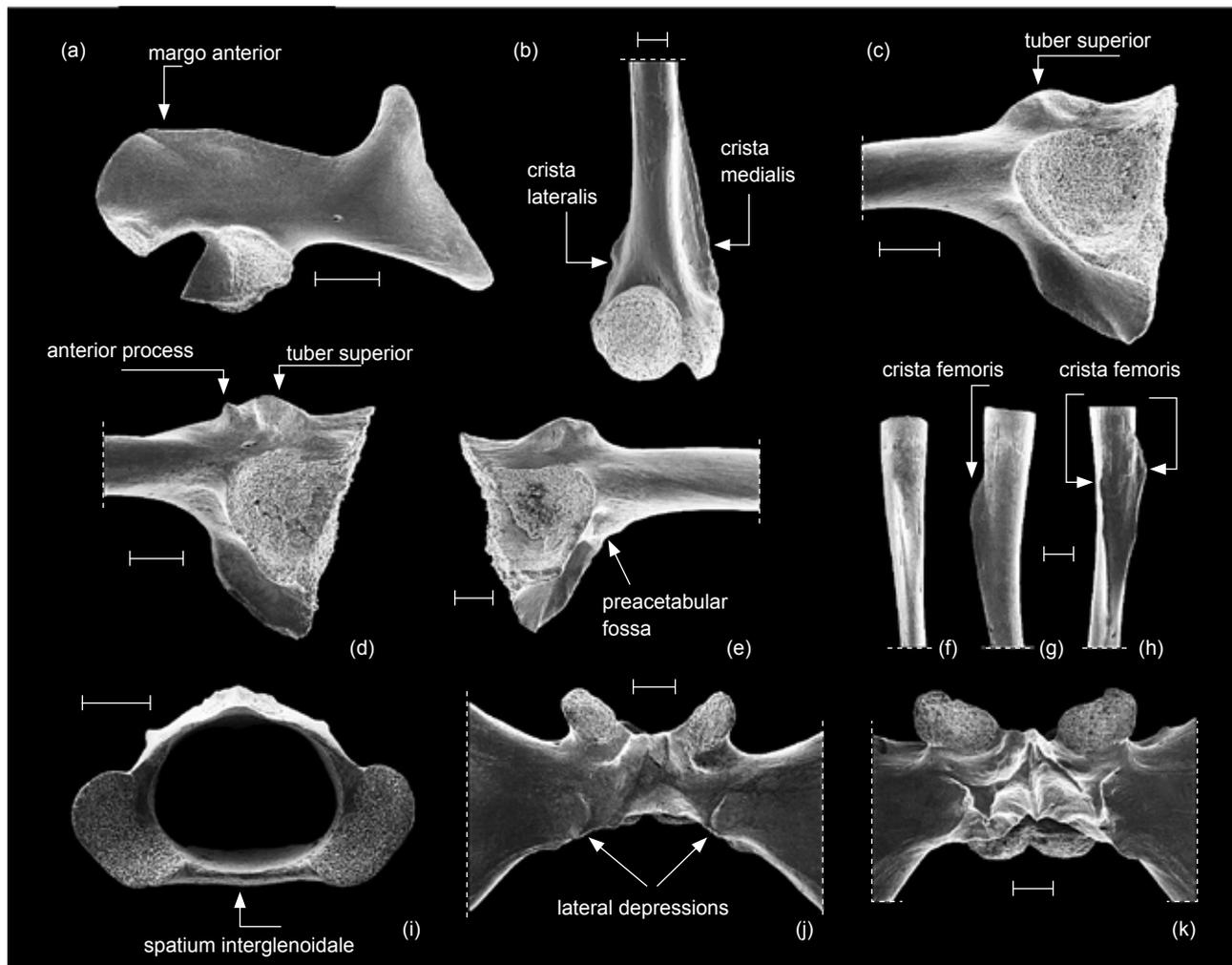


Fig. 3. (a) CeSMAP-H 1, left scapula in external view; (b) CeSMAP-H 4, right humerus in ventral view; (c) CeSMAP-H 1, left ilium in lateral view; (d) CeSMAP-H 4, left ilium in lateral view; (e) MNCN-H 21564, right ilium in lateral view; (f) CeSMAP-H 1; right femur in anterior view; (g) CeSMAP-H 1, left femur in dorsal view; (h) MNCN-H 21564, right femur in anterior view, note the presence of a secondary crest; (i) CeSMAP-H 2, atlas in anterior view; (j) CeSMAP-H 2, details of sacral vertebra in dorsal view; (k) MNCN-H 21564, details of sacral vertebra in dorsal view. Scale bars = 0.5 mm.

is fairly thin and tall. An evident crista medialis and a hint of a crista lateralis are present in male humeri only (Fig. 3b).

Radioulnae: A small, elongated tubercle in the proximal part of the crista radii of specimen MNCN-H 21564 is most likely an aberration.

Iliia: The tuber superior is prominent and robust in all available specimens and usually shows an anterior process (or tubercle) the size and shape of which vary considerably. The anterior tubercle is rather rounded and weakly expressed in CeSMAP-H 1 (where the hint of a tubercle visible on the right element is nearly absent on the left one; Fig. 3c), but clearly evident and pointed in CeSMAP-H 4 (Fig. 3d). Specimen MNCN-H 21564 has a robust tuber devoid of any anterior tubercle, but retains an anterior thickening marked by a posterior shallow groove (Fig. 3e). The ilial shaft (pars cylindriciformis) is rod-like and has no trace on its lateral surface of the longitudinal ridge called the “calamita ridge” (sensu Sanchiz 1977). The preacetabular fossa is absent from some specimens (as in CeSMAP-H 1), rough-hewn in others (as in CeSMAP-H 2), and clearly evident in the larger MNCN-H 21564 (Fig. 3e). In all CeSMAP specimens, the anterior edge of the ventral acetabular expansion (pars descendens) is more developed in the anterior direction than in *B. viridis*, so that its ventral sector has a markedly convex outline; such convexity is underdeveloped in MNCN-H 21564 (compare Figs. 3c, d with 3e).

Femurs: The crista femoris is laminar, thin, tall and with a nearly straight edge in all CeSMAP specimens (Figs. 3f, g). In specimen MNCN-H 21564, a supplementary smaller crista is developed dorsally to the main one, and the intermediate area is nearly flat (Fig. 3h); both ridges are more robust and apically blunt than the single ridge of the CeSMAP specimens.

Tibiofibulae: The longitudinal ridge on the side of the tibial element is present, but weakly developed.

Atlas: The most relevant feature of the atlas is that the spatium interglenoidale is significantly wider than in the European and northwestern African members of the genus *Bufo*, so that the cotylar type sensu Lynch (1971) is not II but I (Fig. 3i). The centrum is extremely thin and the neural ridges rather weak. In lateral view, it is easy to see that below each postzygapophyseal facet, there

is a circum-zygapophyseal pit from the ventral margin of which originates a posteriorly protruding process (see Sanchiz 1977).

Presacral vertebrae: Vertebrae are particularly dorsoventrally compressed: neural arches are rather flattened and neural canals are markedly wide, much wider than tall. Neural ridges are weakly developed so that in some cases even only a sagittal line or a sagittal convexity is barely visible. Centra are regularly flattened and thin, and the same also holds for the cotyles and condyles. The prezygapophyses of the 2nd presacral vertebra (which articulates with the atlas) are rather reduced in size compared to those of *B. viridis*. A strong process with a truncated apex protrudes anterodorsally from the medial part of the anterior edge of the neural arch. Specimen MNCN-H 21564 has an additional process at the base of each transverse process (more developed on the left side) of the most posterior presacral vertebra.

Sacral vertebra : In anterior and posterior view, the lateral apophyses are nearly horizontal, not weakly tilted dorsally, as is usually the case in other *Bufo* species. In anterior view, the prezygapophyseal facets are only slightly tilted. The cotyle and condyle are wide and respectively not deep or long. The development of the neural ridge varies: it is nearly absent from CeSMAP-H 3 and 4 where there is just a weak sagittal convexity (feebly emphasized by the shallow depressions located medially of each prezygapophyseal facet); in specimens CeSMAP-H 1 and 2, there is a weakly developed “W-shaped” ridge with shallow lateral depressions (Fig. 3j); this “W-shaped” ridge and lateral depressions are much more evident in specimen MNCN-H 21564 (Fig. 3k).

Urostyle: The cotyles are particularly wide and short. Lateral processes are usually absent, but present as an exception in CeSMAP-H 4.

DISCUSSION

The osteology of *B. brongersmai* is so peculiar that it can be used not only to complement the diagnosis of the species, but also to discuss morphological traits possibly related to the exceptional environment inhabited by this species.

Specific status and osteological diagnosis

The osteological analysis presented here fully supports the taxonomic conclusions reached by previous authors. *Bufo brongersmai* is osteologically characterized by the following combination of characters which can be partly attributed to hypo-ossification (skeletal underdevelopment; see below): the presence of a mandibular fontanella in smaller but already sexually mature specimens (the fontanella seems to be reduced by at least to 1 or more foramina late in ontogeny), the palatine process on the maxillae is reduced and not visible in lateral view, the nasal processus paraorbitalis is comparatively short and stout, the frontoparietals are greatly reduced leaving an open medial fenestra, the occipital condyles are far from the medial edge of the exoccipital, the anterior margin of the scapula extends into a lamina, the atlas shows cotylar type I, and the vertebral centra are characteristically flattened.

It should be noted that the internal and external morphological peculiarities characterizing the postmetamorphic stages of *B. brongersmai* are not paralleled in the tadpole: the comparative analysis of the external morphology of *B. brongersmai* tadpoles carried out by Grillitsch and Grillitsch (1987) and Grillitsch et al. (1989) revealed that among other *Bufo* species, *B. brongersmai* is not exclusively characterized by any feature, a fact suggesting "minimal variability in the larval habitat" among different species of *Bufo* (Grillitsch et al. 1989: 228). This is, however, not surprising because earlier developmental stages are generally more uniform than are adults.

Relationships between *B. brongersmai* and *B. viridis*, already suggested on the basis of different analyses (see "Introduction"), are supported by at least 5 shared osteological cranial and post-cranial characters: development of the sella amplificans in the antrum olfactorium of the sphenethmoid, weak development of the otic process of the squamosal, absence of a transverse ridge on the ventral surface of the parasphenoid, development of a process below the postzygapophyseal facet of the atlas, and W-shaped neural ridge (with well-delimited lateral depressions) of the sacral vertebra.

Despite the fact that a certain degree of homoplasy has been reported for the genus *Bufo* (Pauly et al. 2004), it is remarkable that the osteology of *B. brongersmai* clearly links it to *B. viridis*, with no traits univocally shared with the

few other *Bufo* species analyzed during this study. Such a relationship is expected to be confirmed by future studies based on a rigorous phylogenetic approach and on a wider sample of specimens and taxa.

Hypo-ossification and its reasons

It is obvious from the osteological account of available specimens of *B. brongersmai* that the skeletons are markedly hypo-ossified, i.e., bones have not attained their ultimate developmental stage. The degree of hypo-ossification is correlated with the size of an individual (and consequently, its individual age), and if hypo-ossification is retained in adults, it can be taken as a feature useful for taxonomic considerations.

Skeletal underdevelopment in *B. brongersmai* is recognized in both endochondral and dermal elements. Hypo-ossification of endochondral elements can be demonstrated in the sphenethmoid by the narrow roof and floor of the nasal capsules (i.e., the tectum and solum nasi, respectively, completed by cartilage in living animals), short septum nasi and lateral processes (the postnasal walls), prolonged by cartilage in living animals, and by various degrees of what we called in the descriptive part above "fenestration" (i.e., those parts which are completed by cartilage in living animals). The large foramen ovale in the prootics (extensively rimmed by cartilage in living animals) may be considered a result of hypo-ossification as well. Also the absence of some morphological features in the presacral vertebrae, corresponding to the juvenile morphology in other related taxa, may be attributed to hypo-ossification.

Skeletal underdevelopment is also expressed in dermal bones. The most remarkable is the presence of fontanellae in the maxillae (Fig. 1), which is, in agreement with the progress of ossification in the course of development, comparatively larger in small (i.e., juvenile) individuals, whereas in larger ones it is less extensive. Also one of the premaxillae was pierced in a similar way, suggesting that these "fenestrae" are completed in living animals by membranous tissues from which dermal bones ossify.

Hypo-ossification of dermal bones may also be demonstrated, similarly to vertebrae, in their limited size and generalized shape which lack morphological details that normally arise in the latest stages of development. This is exemplified

by the small size of the lamella alaris of the squamosal, the small size of the facial process of the premaxilla and of the lateral process of the nasals, and by weakly developed frontoparietal incassation (thickened parts of the frontoparietals which protrude from their inner surface into the foramina in the roof of the braincase).

It is worth noting that in specimens of *B. calamita* and *B. bufo* smaller (SVL < 30 mm) than the *B. brongersmai* specimens described here, there is no evidence of the presence (or prior presence as evidenced by residual foramina) of a maxillary fontanella, nor of fenestrae in the lateral walls of the sphenethmoid; and such features have not been reported for any other extant or fossil anurans. The most plausible explanation for such incomplete ossification is that it represents a way for the larvae to achieve rapid development in temporary water bodies occurring in arid conditions.

The low degree of ossification in metamorphosing larvae, juveniles, and adults, compared to corresponding stages in related taxa, was recognized in *Discoglossus pictus* (Roček, unpubl. observ.), in which complete larval development was observed in laboratory conditions (from fertilized eggs to the end of metamorphosis) within 19 d (at 27°C). The size of metamorphosed juveniles was very small (SVL of < 10 mm), and the skull was still completely chondrified, with no signs of ossification (compare observations of *B. brongersmai* below). This can be considered an adaptation to semiarid conditions in the Mediterranean area, where development must be completed between the first rains in spring and the total disappearance of water bodies available for development of tadpoles few weeks later.

Ecology, size, and osteological peculiarities

During recurrent surveys in the Jbel Sarhro chain (spring and autumn 2003, autumn 2004, and spring 2005), *B. viridis* and *B. mauritanicus* were found in a variety of habitats, but *B. brongersmai* only in rocky and arid environments, close to small pools of temporary rainwater or streamlets originating from a spring, as in the case of the reproductive site from which the CeSMAP specimens described originated (not to mention that *B. brongersmai* was found in places where water was apparently not available, nor signs of its past presence were detected). This site is a perennial spring from which originated, in Mar. 2005, a streamlet that subsequently developed as

a system of small, mostly temporary, pools isolated by sandy areas or connected by shallow rivulets. The streamlet was flanked by chaste trees (*Vitex agnus-castus*), growing quite densely in places, and also by some small cultivated fields along the bottom of the valley. All this was surrounded by arid, rocky slopes with very sparse grassy vegetation (Gramineae) and other herbaceous plants. At this site, *B. brongersmai* is sympatric with *B. viridis*, *B. mauritanicus*, and *Rana saharica*. Visual and acoustic inspection during the day and at night, as well as extensive searching under rocks around the brook inhabited by these populations, revealed that the *B. brongersmai* specimens considerably outnumbered those of the other species. It is worth noting that in the same period, large numbers of *B. mauritanicus*, *Hyla meridionalis*, and *R. saharica* (*B. brongersmai* was not recorded) were breeding in a meander of the river Asif M'Goun, 20 km north of the *B. brongersmai* site. Such a strong difference in terms of environmental conditions and population densities at some sites can be interpreted as a consequence of a higher fitness of *B. brongersmai* in rocky, arid environments. This fitness is at least partly linked to the capability to complete larval development in ephemeral water bodies where the other species reproduce less frequently (i.e., only in particularly rainy years in those habitats) and/or where populations depend on recurrent immigration from "wetter" areas. A key life history trait of *B. brongersmai* seems to be its rapid larval development that allows it to save at least 3-8 wk in comparison to developmental periods of other toads present in Morocco (see developmental data in Schleich et al. 1996). It is interesting to note that Bogaerts (2001) reported a notably longer developmental period in captivity for *B. brongersmai*, possibly related to a lower temperature during development of the eggs. The shortness of the larval period is considered to confer a higher fitness in anurans (Wilbur and Collins 1973), and for *B. brongersmai*, a shortened developmental period is a critical factor in a dry environment where water bodies are ephemeral.

In anurans, the length of the larval period may be positively correlated with size at metamorphosis, but some cases of negative correlations have been reported in the literature (see for example, Newman 1988 and Reques and Tejedo 1995). Few data concerning the size at metamorphosis are available for *B. brongersmai*. Schleich et al. (1996) reported an SVL of about 30 mm at metamorphosis, but the smallest

specimens found during the present research at the site south of El Kelaa M'Gouna had an SVL of 22 mm (note that it was a breeding specimen and therefore not a neo-metamorphosed toadlet), and Bogaerts (2001) provided comparative data of captive specimens whose SVLs at metamorphosis varied from 8 to 12 mm. Even if more data (duration of the larval period and size at metamorphosis) from wild specimens should be collected before drawing a conclusion, the apparent small size of the neo-metamorphosed toadlets may be related to the extremely reduced larval period. As a comparison, it is worth noting that Schleich et al. (1996) indicated that *B. mauritanicus*, a much larger species, has a length at metamorphosis of about 23-28 mm (with an adult SVL of about 160 mm; and a development period of about 6 wk).

It can be assumed that in *B. brongersmai*, the increase in fitness related to the reduced duration of larval development is not lowered by eventual drawbacks emanating from the small size at metamorphosis. There are contrasting data and interpretations concerning the relationships between size at metamorphosis and fitness in arid environments. Size (both for neo-metamorphosed specimens and adults) can be a relevant factor for survival in desert anurans, because it is positively correlated with resistance to dehydration, but at the same time, it is negatively correlated with chances of finding suitable shelter from overheating and aridity (see among others, Nevo 1972, Wilbur and Collins 1973, Tandy et al. 1985, Newman and Dunham 1994, Castellano et al. 2000, Kutrup et al. 2005). In *B. brongersmai*, a significantly smaller size of neo-metamorphosed and fully grown specimens is apparent when compared, for example, to the sympatric *B. viridis* (with a maximum SVL of 51 mm in the former species and 107 mm in the Libyan populations of the latter species; data from Schleich et al. 1996, and references therein) and *B. mauritanicus* (see data above). The potential disadvantage conferred by a small size (i.e., greater risk of desiccation) may be compensated for by the ability to find more-hospitable shelters in deeper, and therefore moister, sectors of crevices. That the habitation of such crevices is a key character of the evolutionary history of *B. brongersmai* is clearly supported by osteological characters like the flattening of the vertebrae, the horizontal development of the sacral lateral apophyses, the strong reduction in the ridges on the vertebral neural arches, and possibly also the atlas cotylar type that is typical of climbing

taxa (as tree frogs of the genus *Hyla*).

If the ecological success of *B. brongersmai* is so closely related to its ability to inhabit rocky and arid environments with highly ephemeral water bodies, it is tempting to consider these and other unique skeletal traits as being adaptive to such a hostile environment. It seems reasonable to suppose that the presence of osteological simplifications in *B. brongersmai* implies a decreased energy investment in building the skeletal element. Therefore it could tentatively be suggested that such peculiarities allow for more-economical metabolic costs during later stages of larval morphogenesis resulting to a shortened period of larval development. These speculations cannot be directly proven within the framework of this study, but they will hopefully stimulate further research.

CONCLUSIONS

The analysis of isolated skeletal elements of *B. brongersmai* allowed the identification of several osteological peculiarities that clearly differentiate this species from all other western Palearctic *Bufo* species. At the same time, these osteological characters indicate a close relationship with *B. viridis*, supporting the phylogenetic relationships currently recognized based on molecular sequence data.

It is here proposed that fenestrae in some cranial elements (maxilla and sphenethmoid), the wide frontoparietal fenestration, and some degree of simplification of the entire skeleton (general lightening and absence or reduction of ridges) contribute towards shortening the late premetamorphic and metamorphic stages, as they slightly lower the energetic needs of the toadlet. By shortening the aquatic phase of the life history and hence its dependence on water, its reproductive fitness in ephemeral waters in the arid environments of northwestern Africa can be said to be increased. Some osteological traits, such as the atlas cotylar type and the orientation of the sacral lateral apophyses, are hypothesized to be related to its exploitation of small crevices for protection against overheating and desiccation.

The diagnostic osteological characters here defined for *B. brongersmai* on the basis of isolated skeletal elements frequently found in Quaternary assemblages (maxilla, frontoparietal, exoccipital, scapula, and atlas in particular) will hopefully allow the identification of fossil remains

from northwestern Africa that could contribute to unraveling the origin and biogeography of this species.

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APPENDIX. Acronyms and list of reference specimens (all skeletal preparations)

CeSMAP, Centro Studi e Museo di Arte Preistorica, Pinerolo, Italy; DSTF, Dipartimento di Scienze della Terra, Firenze, Italy; MNCN, Museo Nacional Ciencias Naturales Madrid, Spain.

Bufo brongersmai - CeSMAP-H 1-4 (1 and 2 ♀ ♀, 3 and 4 ♂ ♂); MNCN-H 21564 (♂).

B. bufo - DSTF 13, 14, 32, 33, 50, 51, 53, 56, 57, 104, 211; MNCN 15432, 19522, 19523.

B. calamita - MNCN 13258, 13646, 15447, 15449, 15450, 15451, 15454, 15464, 15469, 15470, 22335, 22338, 22339, 22343, 22344, 40953.

B. raddei - MNCN 21566.

B. mauritanicus - DSTF 269-271; MNCN 17358-60, 40889.

B. viridis - DSTF 35, 36, 58, 123, 258; MNCN 13254-56, 40454, 40958.
