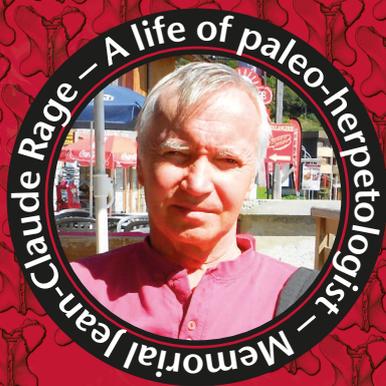
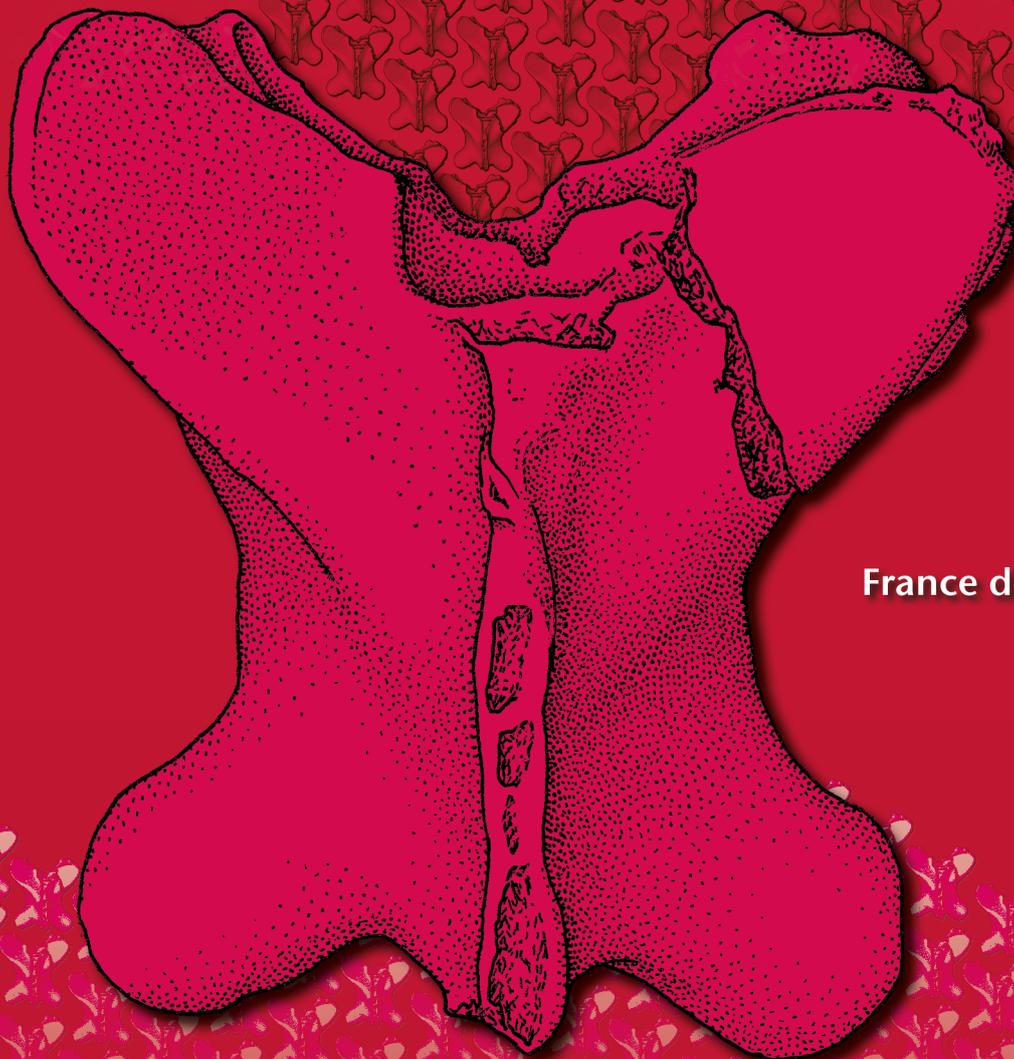


geodiversitas

2020 • 42 • 22



Amphibians and reptiles from the Neogene of Afghanistan



France de LAPPARENT de BROIN,
Salvador BAILON,
Marc Louis AUGÉ &
Jean-Claude RAGE†

DIRECTEUR DE LA PUBLICATION / *PUBLICATION DIRECTOR* : Bruno David,
Président du Muséum national d'Histoire naturelle

RÉDACTEUR EN CHEF / *EDITOR-IN-CHIEF*: Didier Merle

ASSISTANT DE RÉDACTION / *ASSISTANT EDITOR*: Emmanuel Côté (geodiv@mnhn.fr)

MISE EN PAGE / *PAGE LAYOUT*: Emmanuel Côté

COMITÉ SCIENTIFIQUE / *SCIENTIFIC BOARD*:

Christine Argot (Muséum national d'Histoire naturelle, Paris)
Beatrix Azanza (Museo Nacional de Ciencias Naturales, Madrid)
Raymond L. Bernor (Howard University, Washington DC)
Alain Blicek (chercheur CNRS retraité, Haubourdin)
Henning Blom (Uppsala University)
Jean Broutin (Sorbonne Université, Paris, retraité)
Gaël Clément (Muséum national d'Histoire naturelle, Paris)
Ted Daeschler (Academy of Natural Sciences, Philadelphie)
Bruno David (Muséum national d'Histoire naturelle, Paris)
Gregory D. Edgecombe (The Natural History Museum, Londres)
Ursula Göhlich (Natural History Museum Vienna)
Jin Meng (American Museum of Natural History, New York)
Brigitte Meyer-Berthaud (CIRAD, Montpellier)
Zhu Min (Chinese Academy of Sciences, Pékin)
Isabelle Rouget (Muséum national d'Histoire naturelle, Paris)
Sevket Sen (Muséum national d'Histoire naturelle, Paris, retraité)
Stanislav Štámbek (Museum of Eastern Bohemia, Hradec Králové)
Paul Taylor (The Natural History Museum, Londres, retraité)

COUVERTURE / *COVER*:

Réalisée à partir des Figures de l'article/*Made from the Figures of the article.*

Geodiversitas est indexé dans / *Geodiversitas is indexed in:*

- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Physical, Chemical, and Earth Sciences®
- Scopus®

Geodiversitas est distribué en version électronique par / *Geodiversitas is distributed electronically by:*

- BioOne® (<http://www.bioone.org>)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Geodiversitas* sont référencés par /
Articles and nomenclatural novelties published in Geodiversitas are referenced by:

- ZooBank® (<http://zoobank.org>)

Geodiversitas est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Geodiversitas is a fast track journal published by the Museum Science Press, Paris

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish: Adansonia, Zoosystema, Anthropolozologica, European Journal of Taxonomy, Naturae, Cryptogamie* sous-sections *Algologie, Bryologie, Mycologie, Comptes Rendus Palevol*

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / <http://sciencepress.mnhn.fr>

© Publications scientifiques du Muséum national d'Histoire naturelle, Paris, 2020
ISSN (imprimé / *print*): 1280-9659/ ISSN (électronique / *electronic*): 1638-9395

Amphibians and reptiles from the Neogene of Afghanistan

France de LAPPARENT de BROIN

Centre de Recherches sur la Paléobiodiversité et les Paléoenvironnements,
CR2P (CNRS, MNHN, UPMC, Sorbonne Université),
Département Origines et Évolution, Muséum national d'Histoire naturelle,
case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
france.delapparent123@orange.fr

Salvador BAILON

Archéozoologie, Archéobotanique : Sociétés, pratiques et environnements –
Histoire naturelle de l'Homme préhistorique (CNRS, MNHN, Sorbonne Université),
Muséum national d'Histoire naturelle,
case postale 55, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
salvador.bailon@mnhn.fr

Marc Louis AUGÉ Jean-Claude RAGE†

Centre de Recherches sur la Paléobiodiversité et les Paléoenvironnements,
CR2P (CNRS, MNHN, UPMC, Sorbonne Université),
Département Origines et Évolution, Muséum national d'Histoire naturelle,
case postale 38, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
marc.louis.ed.auge@gmail.com

Submitted on 26 March 2019 | accepted on 20 September 2019 | published on 17 September 2020

[urn:lsid:zoobank.org:pub:07001ACA-EBDE-4256-BCB9-55E3159F81DC](https://doi.org/10.5252/geodiversitas2020v42a22)

Lapparent de Broin F. de, Bailon S., Augé M. L. & Rage† J.-C. 2020. — Amphibians and Reptiles from the Neogene of Afghanistan, in Steyer J.-S., Augé M. L. & Métails G. (eds), Memorial Jean-Claude Rage: A life of paleo-herpetologist. *Geodiversitas* 42 (22): 409-426. <https://doi.org/10.5252/geodiversitas2020v42a22>. <http://geodiversitas.com/42/22>

ABSTRACT

Amphibians and reptiles are described for the first time from the Cenozoic of Afghanistan. They originate from four Neogene localities. Sherullah 9 (late Miocene) yielded anuran amphibians (? Alytidae Fitzinger, 1843 (? Discoglossinae Günther, 1858), “Ranidae” Batsch, 1796 and another, indeterminate family), one chelonian, the terrestrial testudinine *Agrionemys* Khozatsky & Mlynarski, 1966, which is compared to a Maragheh fossil specimen, and the genus still being present in the Kabul area; one indeterminate lizard, snakes (Colubridae Oppel, 1811 s.l. and two distinct snakes that pertain to either the Colubridae s.l. or Elapidae Boie, 1827). The faunas of the three other localities are very poor. Molayan (late Miocene) produced only one lizard (*Varanus* sp. Merrem, 1820, Varanidae Gray, 1827). Pul-E Charkhi (early Pliocene) yielded indeterminate anurans, one indetermined lizard and colubrid snakes. Only an indeterminate anuran family is known at Hadji Rona (early Pliocene). Then, as known, the fauna is constituted of families which still have representatives living in Afghanistan.

KEY WORDS

Afghanistan,
Amphibia,
Anuran,
Reptilia,
turtles,
lizards,
snakes,
Miocene,
Pliocene.

RÉSUMÉ

Amphibiens et reptiles du Néogène d'Afghanistan.

Des amphibiens et reptiles sont décrits pour la première fois dans le Cénozoïque d'Afghanistan. Ils proviennent de quatre gisements. Sherullah 9 (Miocène supérieur) a fourni des amphibiens anoures (? Alytidae Fitzinger, 1843 (? Discoglossinae Günther, 1858), « Ranidae » Batsch, 1796 et une autre famille, indéterminée), la tortue terrestre testudinine *Agrionemys* Khozatsky & Młynarski, 1966, d'un genre présent actuellement dans la région de Kaboul, et comparé à un spécimen fossile de Maragheh (Iran) ; un lézard indéterminé, des serpents Colubridae Opperl, 1811 s.l. et deux serpents différents qui peuvent appartenir aux Colubridae s.l. ou aux Elapidae Boie, 1827. Les trois autres gisements sont très pauvres. Dans le Pliocène inférieur de Molayan seul un lézard (*Varanus* sp. Merrem, 1820, Varanidae Gray, 1827) a été trouvé. Pul-E Charkhi (Pliocène inférieur) a livré des anoures et un lézard indéterminé ainsi que des colubridés, aussi indéterminés. Hadji Rona (Pliocène inférieur) n'a fourni qu'un anoure appartenant à une famille indéterminée. Dans la mesure où elle est connue, la faune est ainsi constituée de familles toujours présentes en Afghanistan.

MOTS CLÉS

Afghanistan,
Amphibia,
Anoures,
Reptilia,
tortues,
lézards,
serpents,
Miocène,
Pliocène.

INTRODUCTION

The amphibian and reptile studied material originates from the French Paleontological Expeditions to Afghanistan between 1976 and 1979 (Heintz *et al.* 1978a, b). Emile Heintz supervised these expeditions with his colleagues, and they discovered several mammal localities, including Molayan. In Afghanistan, about 15 fossiliferous localities produced vertebrates of Neogene age (Brunet *et al.* 1981, 1984; Sen 1998). They range from the late Vallesian (late Miocene) to the late Ruscinian (early Pliocene). The localities are concentrated in the Kabul area (Brunet *et al.* 1981). Only four of them yielded amphibians and/or reptiles (Table 1): Sherullah 9 and Molayan (Khordkabal basin, late Miocene), Pul-E Charkhi (Kabul basin) and Hadji Rona (Sarobi basin) (early Pliocene). These fossiliferous sites rank among the rare localities that yielded amphibians and reptiles from the Cenozoic of Asia. Their map of localization is given in Brunet *et al.* (1981).

Sherullah 9 (late Miocene) produced the richest herpetofauna. This fauna is comparatively diverse. It includes 116 specimens of an undefined number of individuals of amphibians (only anurans, three families), turtles (one form), one lizard and snakes (as many as two or three families).

According to Brandy (1979), the age of Sherullah 9 is close to the Vallesian/Turolian transition. Brunet *et al.* (1981) suggested a late Vallesian age (MN10/11), which is consistent with Brandy's opinion. This locality corresponds to channel-fill deposits in grey marls that overlie azoic red beds (Brunet *et al.* 1981).

Molayan (late Miocene) yielded only a varanid lizard, as far as herpetofauna is concerned. Heintz & Brunet (1982), Brunet *et al.* (1984) and Sen (1998, 2001) definitely retain a middle Turolian age (MN12) for the Molayan locality.

Pul-E Charkhi furnished very fragmentary specimens of amphibian anurans and reptiles including a lizard and colubrid snakes. Brunet *et al.* (1984) assigned the Pul-E Charkhi fauna to early Ruscinian (Turolian-Ruscinian boundary), i.e. earliest Pliocene age (MN 13/14) (Sen 2001).

Hadji Rona is late Ruscinian, that is late early Pliocene in age (Brunet *et al.* 1984), (late MN15) (Sen 2001). It did not produced reptile remains and only two elements represent anuran amphibians.

In each locality, the taxa are compared with extant taxa and fossils known from other localities in the world.

MATERIAL AND METHODS

The material has been preliminary studied by two of us (FLB and JCR), and it remained waiting for a completion and revision. Here, with the help of two of us (SB and MA) we publish the work after the death of our friend, respecting Jean-Claude Rage's text and figures on Anura and Squamata, just actualizing it. The AFG material is provisionally deposited in the Paleontology collection of the Muséum national d'Histoire naturelle, Paris. Beside the MNHN.RA anatomical collections, the REP material is an informal collection which is deposited in MNHN, collection de paléontologie.

INSTITUTIONAL ABBREVIATIONS

AFG	work catalog of Afghan fossil material;
MNHN	Muséum national d'Histoire naturelle, Paris;
.F	MNHN, collection de paléontologie;
.RA	MNHN, collection d'anatomie comparée du Laboratoire de zoologie, reptiles et amphibiens;
.REP	MNHN informal reptile comparative collection of Paleontology.

SYSTEMATICS

Class AMPHIBIA Linnaeus, 1758
Order ANURA Fischer von Waldheim, 1813
? Family ALYTIDAE Fitzinger, 1843
? Subfamily DISCOGLOSSINAE Günther, 1858

? Gen. et sp. indet.
(Figs 1A; 2AB)

LOCALITY AND AGE. — Sherullah 9, Khordkabal basin, Afghanistan, late Miocene, Late Vallesian-basal Turolian transition. MN10/11.

MATERIAL EXAMINED. — One fragmentary humerus (AFG 1650), 1 incomplete vertebra (AFG 1651). This material was mentioned by Roček & Rage (2000).

DESCRIPTION

The humerus is represented by a distal extremity which comprises the humeral ball, ulnar epicondyle and a short part of the diaphysis (Figs 1A; 2A). The condyle is large and spherical. The cubital fossa is poorly limited laterally. The well-developed ulnar crest extends laterally; it is not deflected dorsally. It was likely short anteroposteriorly. The ulnar epicondyle is large whereas the radial epicondyle is damaged. A small radial crest slightly deflected ventrally is present. Because of the large size of the condyle and ulnar epicondyle, the distal extremity is widened transversely; moreover, it appears to be somewhat flattened dorsoventrally. Such a morphology recalls that of Alytidae of the *Discoglossinae* subfamily.

The vertebra is a presacral one (Fig. 2B). The anterior part of the centrum is damaged and covered by matrix. The vertebra is apparently opisthocoelous but this cannot be definitely confirmed. If it is really opisthocoelous, then it probably belongs to the Alytidae. Its size is consistent with that of the humerus.

COMMENTS

The referral of these two specimens to the Alytidae is doubtful. It is based only on the overall morphology of an incomplete humerus and on a vertebra the main characteristic of which (opisthocoely) is not certain. The Alytidae is a primitive family whose earliest representative was recovered from the middle Jurassic of England (Evans *et al.* 1990). Today they are known in Europe, west Asia, and northernmost Africa (Frost *et al.* 2006). In the Cenozoic of Asia, apart from the possible alytid of Sherullah 9, the family was reported from the early Eocene of the Vastan Lignite Mine (Bajpai & Kapur 2008) and the middle Miocene lower Siwalik deposits (Parmar & Jigmet 2014), in India; from the Miocene of Turkey (Claessens 1995; Sanchiz 1998; Rückert-Ülkümen *et al.* 2002) and in the Miocene of Thailand (Rage & Ginsburg 1997). However, this latter identification cannot be confirmed (Roček & Rage 2000).

Superfamily RANOIDEA Batsch, 1796
Family “RANIDAE” Batsch, 1796

Gen. et sp. indet.
(Figs 1B-D; 2C-E)

LOCALITY AND AGE. — Sherullah 9, Khordkabal basin, Afghanistan, late Miocene, Late Vallesian-basal Turolian transition, MN10/11.

MATERIAL EXAMINED. — One coracoid (AFG 1652), 3 humeri (AFG 1653, 1654), 1 ilium (AFG 1655).

DESCRIPTION

The coracoid is represented by its ventro-medial part (*pars epicoracoidalis*; Špinar, 1972) and its “neck” (*corpus coracoidalis*); the lateral extremity (*intumescencia glenoidalis*) is broken off (Figs 1C; 2E). The ventro-medial part expands as a broad plate (wider than in Bufonidae Gray, 1825, Alytidae and Rhacophoridae Hoffman, 1932); unfortunately, its anterior and posterior extremities are lacking. The neck is cylindrical.

The diaphysis of the humeri is straight. The condyle is spherical, relatively small, and located in the prolongation of the diapophysial axis (in Alytidae, Bufonidae and Rhacophoridae, the condyle is radially shifted). The cubital fossa is small, crescentic, and well-limited laterally. The epicondyles are dissymmetrical, the radial one being reduced. A small radial crest is present. The ulnar crest extends laterally in two humeri (Figs 1B; 2C) which probably represent male individuals; in the third one, the crest is small (female individual).

The ilium is incomplete, most of the acetabular area is broken away. A high dorsal crest is present on the ilial shaft (higher than in *Discoglossinae* and in most of the *Rhacophoridae*) (Figs 1D; 2D). A thickening of the posterior border of the crest forms the *tuber superius*. This *tuber* slopes steeply into the acetabular part (more steeply than in alytid *Discoglossinae* and *Rhacophoridae*).

COMMENTS

The family “Ranidae” is in quotes to indicate its non-monophyly, until a consensus on its definition is reached (i.e. Frost *et al.* 2006; Cannatella 2007 or Che *et al.* 2007). In this work, *Rhacophoridae* is considered as a family of the *Ranoidea*.

The morphology of these bones argues for referral to the “Ranidae”. More specifically, the morphologies of the ventro-medial part of the coracoid and that of the *tuber superius* of the ilium clearly point to this family. But, the poor preservation of the specimens prevents identification within the family.

Today, the “Ranidae” are cosmopolitan; they are absent only in South America and most of Australia. The earliest representatives of the family were recovered from the late Eocene in Europe (Rage 1984). In Asia, the earliest ranids were briefly reported from the middle Oligocene of Kazakhstan (Čkhikvadze 1985), but without a description or figure it is not possible to evaluate the reliability of this identification. In Asia, “Ranidae” have been found in the Early Eocene of the Vastan Lignite Mine (Folie *et al.* 2013), in the Miocene of Anatolia, China, and Thailand, and in the Pliocene of Anatolia, Azerbaydzhan, India, and China (Roček & Rage 2000; Rage *et al.* 2001). Finally, Syromyatnikova (2016) mentioned in the late earliest-early middle Miocene (MN5) of Tagay, the earliest record of the lineages of green and brown frogs (respectively *Pelophylax* Fitzinger, 1843: *Pelophylax* sp., and *Rana* Linnaeus, 1758: *Rana* sp.) in Asia.

ANURA indet. sp. A

LOCALITY AND AGE. — Sherullah 9, Khordkabal basin, Afghanistan, late Miocene, late Vallesian-basal Turolian transition, MN10/11.

MATERIAL EXAMINED. — Five fragments of toothed maxillae (AFG 1656), 1 fragment of angulosplenial (AFG 1657), 1 fragment of atlas (AFG 1658), 5 amphicoelous presacral vertebrae (AFG 1659), 7 non-amphicoelous presacral vertebrae (AFG 1660), 5 opisthocoelous sacral vertebrae (AFG 1661), 2 procoelous sacral vertebrae (AFG 1662), 5 fragments of urostyles (AFG 1663), 34 ilia (AFG 1664), 3 fragmentary humeri (AFG 1665), 3 fragments of radio-ulna (AFG 1666), 1 fragment of femur (AFG 1667).

DESCRIPTION AND COMMENTS

Only the maxillae, vertebrae and ilia deserve comments. The other remains provide no information. The presence of teeth on the maxillae allows to rule out Bufonidae, where these bones are toothless. The vertebrae are only represented by their centra. Five centra of presacral vertebrae are amphicoelous, deeply biconcave, whereas seven are non-amphicoelous (it is not possible to determine their condition, procoelous or opisthocelous). Vertebrae of Alytidae are opisthocelous. In “Ranidae”, the last presacral vertebra is amphicoelous whereas the seven others are procoelous. Consequently, within the set of presacral vertebrae from Sherullah 9, the ratio amphicoelous/non-amphicoelous vertebrae is somewhat surprising. In a few anuran groups, all presacral vertebrae are amphicoelous: in the living Leiopelmatidae Mivart, 1869 (New Zealand) and Ascaphidae Fejérváry, 1923 (Western North America) the centra are clearly amphicoelous; in the Megophryidae Bonaparte, 1850 (southern Asia) and various Myobatrachidae Schlegel, 1850 (Australia) the intervertebral cartilages remain free in adults, therefore the vertebrae are amphicoelous but they are not deeply biconcave. Among extinct forms, *Notobatrachus* Reig, 1956 and likely *Vieraella* Reig, 1961 (both from the Jurassic of South America), as well as the Gobiataidae

Roček & Nessov 1993 (Cretaceous of Central Asia) are amphicoelous (Báez & Basso 1996; Roček & Nessov 1993). But, comparisons between “amphicoelous taxa” and amphicoelous vertebrae from Sherullah 9 cannot be made because the latter specimens are known only by their centra. Based on the available specimens from Sherullah 9 a family assignment is not possible.

Sacral vertebrae, as presacral ones, are represented by centra. The posterior face of all centra is bicondylar. But, in five sacral vertebrae the anterior face is convex (opisthocelous) while it is concave (procoelous) in two specimens. The opisthocelous sacral vertebrae may belong to Alytidae or “Ranidae”. But procoelous sacral vertebrae represent another family that cannot be identified.

All ilia have a dorsal crest. This morphological feature is present in Discoglossinae (Alytidae), Pipidae Gray, 1825, “Ranidae”, Rhacophoridae and various Leptodactylidae Werner, 1896 and Hylidae Rafinesque, 1815. The morphology of the *tuber superius* and dorsal crest of the fossil leads to rule out Pipidae, Rhacophoridae, Leptodactylidae and Hylidae, but the poor preservation of these bones does not permit to refer them to either the Discoglossinae (Alytidae) or “Ranidae”.

ANURA indet. sp. B

LOCALITY AND AGE. — Pul-E Charkhi, Kabul basin, Afghanistan, earliest Pliocene, early Ruscinian, MN 13/14.

MATERIAL EXAMINED. — One fragment of tibio-fibula (AFG 1674).

COMMENTS

Generally, tibio-fibula provide poorly information for identification within anurans. The fragment from Pul-E Charkhi only shows that a frog was present. In any case, it forms the first evidence of frog occurrence in this locality during the early Pliocene.

ANURA indet. sp. C

(Figs 1E; 2F)

LOCALITY AND AGE. — Hadji Rona, Sarobi basin, Afghanistan, late early Pliocene, late Ruscinian, MN15.

MATERIAL EXAMINED. — One fragment of maxilla (AFG 1679), 1 incomplete sacral vertebra (AFG 1680).

DESCRIPTION AND COMMENTS

The fragment of maxilla bears teeth typical of most of the anurans (thus, among the current Asian anurans, Bufonidae members are edentulous), but it does not provide precise information. The sacral vertebra shows two posterior condyles (Figs 1E; 2F). The anterior face of the centrum is concave therefore this vertebra cannot be referred to the Alytidae or “Ranidae”. Its sacral expansions are broken off, but their bases demonstrate that they were not widely extended anteroposteriorly. It is not possible to determine whether they were cylindrical or moderately extended. Therefore, an assignment at a family level cannot be suggested. Similarly, it is not possible to state whether this vertebra belongs to the Anura indeterminata A from Sherullah 9 that is represented by procoelous sacral vertebrae.

Class REPTILIA Laurenti, 1768

Order TESTUDINES Linnaeus, 1758

Infraorder CRYPTODIRA Cope, 1868

Family TESTUDINIDAE Batsch, 1788

subfamily TESTUDININAE Batsch, 1788

Genus *Agrionemys* Khozatsky & Mlynarski, 1966

Agrionemys sp.

(Fig. 3)

LOCALITY AND AGE. — Sherullah 9, Khordkabal basin, Afghanistan, late Miocene, late Vallesian-basal Turolian transition. MN10/11.

MATERIAL EXAMINED. — AFG 130, left epiplastron (Fig. 3F); AFG 131, peripheral plate, fragment without distal border (Fig. 3J); AFG 132, pygal plate fragment (Fig. 3A); AFG 133, peripheral plate, fragment with free border; AFG 134, peripheral plate, fragment (Fig. 3K); AFG 135, neural 5 (Fig. 3C); AFG 136 [+ 138 (10)], fragmentary right xiphiplastron (Fig. 3G, H2); AFG 137, plate fragment; AFG 138 including 10 specimens: 138(1) and 138(2), peripheral plate fragments with preserved distal border; 138(3), peripheral plate fragment without the border; 138(4) (5) (6) (7) (8), plate fragments; 138(9), fragmentary left epiplastron (Fig. 3D); 138(11) fragment of a xiphiplastral anal part (Fig. 3I, H1).

DESCRIPTION

The specimens belonged to several individuals of moderate size (shells *c.* 17-19 cm long). The fragmentary right xiphiplastron AFG 136 (+ 138[10])(Fig. 3G, H2) (4.4 cm long) belonged to a plastron of the size of an extant *Agrionemys horsfieldii* (Gray, 1844) (specimen REP 59) from Molayan, Khordkabal basin of Afghanistan [“Kabul, Afghanistan”, being the type locality of the living species (Iverson 1992)], which is 15.7 cm long, and it was barely smaller than the

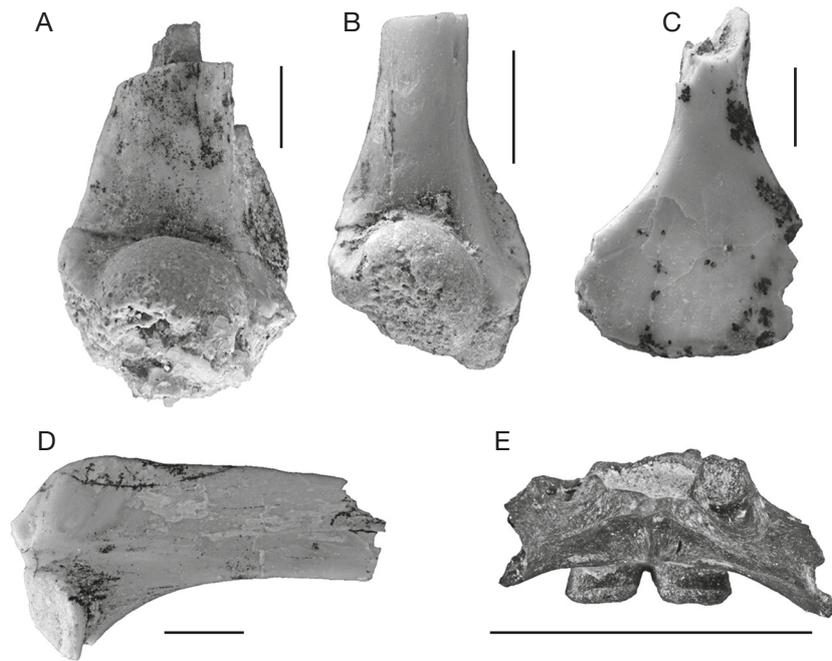


FIG. 1. — Anura. Sherullah, late Miocene, photos, **A-D**: **A**, ? *Discoglossinae* (? *Alytidae*), right humerus AFG 1650, ventral view; **B-D**, “*Ranidae*”, **B**, right humerus AFG 1653, ventral view; **C**, right coracoid AFG 1652, inner face; **D**, right ilium AFG 1655, lateral view; Hadji Rona, early Pliocene; **E**, Anura indet. sp. C, sacral vertebra AFG 1680, dorsal view. Scale bars: 2 mm.

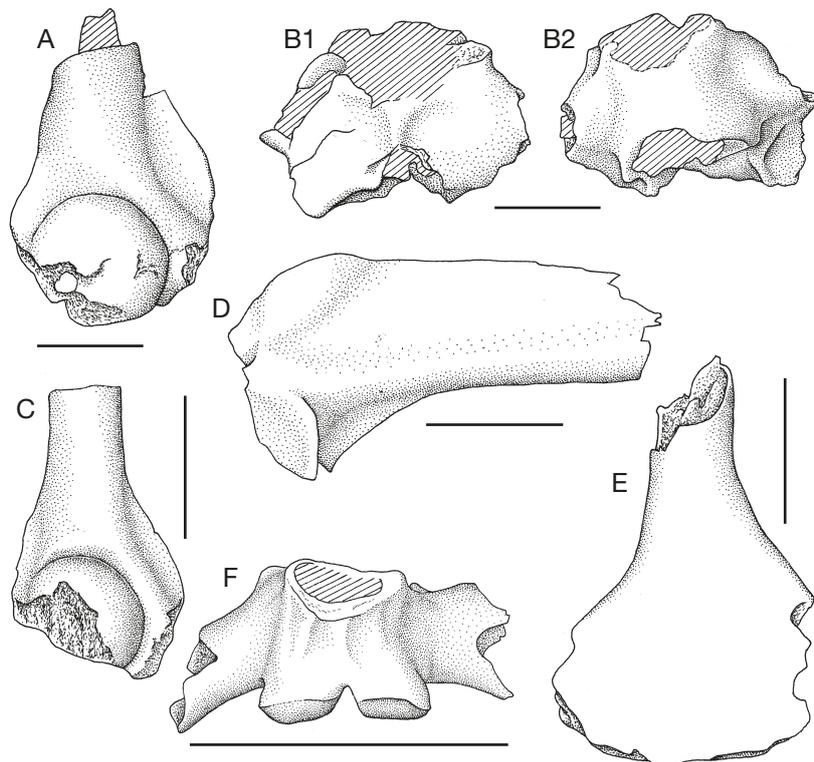


FIG. 2. — Anura. Sherullah, late Miocene, drawings, **A-F**: **A, B**, ? *Discoglossinae* (? *Alytidae*); **A**, right humerus AFG 1650, ventral view; **B**, presacral vertebra AFG 1651, dorsal (**B1**) and ventral (**B2**) views; **C-E**, “*Ranidae*”; **C**, right humerus AFG 1653, ventral view; **D**, right ilium AFG 1655, lateral view; **E**, right coracoid AFG 1652, inner face. Hadji Rona, early Pliocene, **F**, Anura indet. sp. C, sacral vertebra AFG 1680, ventral view. Scale bars: 3 mm.

plastron of the epiplastron AFG 130 (Fig. 3F) (3.2 cm wide). The left epiplastral fragment AFG 138(9) (Fig. 3D) is barely larger than AFG 130. The fragment of xiphiplastral anal part

AFG 138 (11) seems to have belonged to an individual as large as the fragment AFG 136 (138[10]) (Fig. 3H). The neural 5 (Fig. 3C) corresponds to a dorsal shell of an *A.*

kazachstanica Čkhikvadze, 1988 specimen (MNHN.RA) of 17.3 cm long, also corresponding to the plastral length of REP 59 and xiphiplastron AFG 136. It was from a slightly smaller individual than the pygal AFG 132 (this maybe of a carapace long of 18.5-19 cm).

The texture of the bones is typical for testudinines: the external surface is apparently relatively smooth with minute points and small granulations. The morphology of the best preserved scute sulci is also typical for testudinines: a fine acute groove limited on each border by a crest, which is especially clear on AFG 130 (Fig. 3F2) for the gularo-humeral sulcus.

Most of the fragments do not provide any particular information within testudinines; their identification is inferred from their conjunction, the best preserved ones being figured, conforming to the genus *Agrionemys*.

The neural is a neural 5, short, wider than long, hexagonal. It has short sides in front and anterior borders wider than posterior borders. It is anteriorly transversally crossed by the sulcus between vertebrals 3 and 4, at the level of its smaller anterolateral sides. The preserved peripherals are all broken. The plates are massive, thick for their length. Two of them are figured (AFG 131, Fig. 3J and AFG 134, Fig. 3K). They are slightly dorsally incurved, being posterior peripherals, probably the 9th and 10th. The fragmentary pygal (AFG 132, Fig. 3A) is long, thick, slightly convex (Fig. 3A3) from right to left and concave interiorly, apparently being from a male (Fig. 3A2, B). The unique supracaudal inner overlap is very long, nearly reaching the suprapygal-pygal suture, as in *Agrionemys* living specimens and in a Maragheh fossil specimen (Iran, Turolian) (Maragha in Lapparent de Broin *et al.* 2006b, c). In the Fig. 3B, the fossil Afghan partial plate is superposed on the fossil Maragheh pygal

The left epiplastron AFG 130 (Fig. 3F) is slightly broken, missing a small posterolateral angle at the suture with the hypoplastron. Its posterolateral external surface part is smooth due to a worn surface, then artificially limited by a line nearly parallel to the gularohumeral sulcus. The specimen is relatively wide for its full length. Its anterior border is transversal, with a wide gular border which is barely protruded anteriorly to the humerals. The oblique inclination of the specimen lateral border indicates the anterior lobe was trapezoid. The lateral borders are moderately converging, as in the drawing of the Fig. 3E (drawn on the specimen REP57 of extant *A. horsfieldii* from Khordkabal basin) and not rounded. The dorsal epiplastral lip is wide, slightly shorter than wide anteriorly, dorsally convex and thick (Fig. 3F1, F3, F4), and it rather abruptly overhangs the posterior epiplastral surface, with a very minute gular pocket, anterior to the entoplastral suture (Fig. 3F1, F3): the wider than long posterior lip border is convex and ends in front of the entoplastron. Ventrally, the gular scute is as long as wide and it was barely prolonged on the entoplastron. The gular is not anteriorly protruding and its surface does not protrude in relation to the humeral. The gularohumeral sulcus is straight, not being anteriorly slightly incurved, as it is sometimes the case on one side in *Chersine* and in living *Agrionemys*. On the whole, the anterior lobe of AFG 130 was not wide on each side of the wide

entoplastron and not much anteriorly narrowed. The other left (fragmentary) epiplastron AFG 138(9) (Fig. 3E) is a fragment at the boundary of the gular and the humeral, at the lateral beginning of the dorsal epiplastral lip: it is thick, and the lateral beginning of the dorsal lip shows it was well elevated anterior to the entoplastron (Fig. 3D3) and perhaps the gular was more anteriorly protruding than in AFG 130; the anterior lobe borders were more anteriorly converging than in AFG 130. The xiphiplastron AFG 136 (Fig. 3G) is preserved by the lateral part only. It is anteriorly limited by the hypoxiphiplastral suture which was not transformed in a hinge. It is referred to testudinines by the strong dorsal elevation of the bone below the dorsal overlap of the femoral, much raising from the external border towards the inner scute limit (Fig. 3G2), and from the posterior extremity up to the hypoxiphiplastral suture (Fig. 3G3); this elevation had to follow on the hypoplastron to end in the inguinal notch without a hinge. The xiphiplastral posterior anal extremity is angular (95°). Associating the two xiphiplastral extremities (that of AFG 136 and that of AFG 138[11]), which are convenient for a same individual size, the anal notch was a wide and short triangle: this is shown when superposing (Fig. 3H) these two specimens on the xiphiplastra of the extant *Agrionemys horsfieldii* (specimen REP 57) of Khordkabal basin. The xiphiplastral had to be approximately anteriorly as wide (at hypoxiphiplastral suture) as long (medially), with lateral borders much converging to the anal notch, as in living *Agrionemys*. As in *Agrionemys*, the anal scute ventral overlap was less long than the femoral overlap part on the xiphiplastron.

COMMENTS

The specimens clearly show that the turtle from Sherullah 9 belonged to the group of Palaearctic terrestrial testudinids, the Testudininae, integrated in the past in the waste basket genus “*Testudo* Linnaeus, 1758 s.l.” (as in Broin 1977). The group includes the living – *Testudo* (s.s.), type-species *T. graeca* Linnaeus, 1758, – *Chersine* Merrem, 1820, type species *Testudo hermanni* Gmelin, 1789 [or *Eurotestudo* Lapparent de Broin, Bour, Parham & Perälä, 2006 (see Bour & Ohler 2008)] and *Agrionemys*, type species *Testudo horsfieldii* Gray, 1844 (see Lapparent de Broin *et al.* 2006a, b, c) (among which genus are notably the species *A. horsfieldii* and *A. kazachstanica*) (Iverson 1992). Western fossil species were included in *Testudo* (s.l.) among which those attributed to the fossil genus *Paleotestudo* Lapparent de Broin, 2000. This has for type species *Testudo canetotiana* Lartet, 1851 from the middle Miocene of Sansan (France). Sherullah 9 material is here particularly compared with living specimens (REP and MNHN.RA coll.). It is also compared with fossil material from Maragheh (Iran, MNHN.F.MAR2424, MAR2425, 1905-10 coll.), late Miocene, early Turolian. This is approximately of the same age as Molayan (Sen 1998). Maragheh material has been attributed without comments to *Agrionemys* cf. *bessarabica* Riabinin, 1918 in Lapparent de Broin *et al.* (2006b, c) and it is confirmed here as being at least an *Agrionemys* sp. Sherullah 9 material was already mentioned as belonging to *Agrionemys* in Lapparent de Broin *et al.* (2006b, c) (without description).

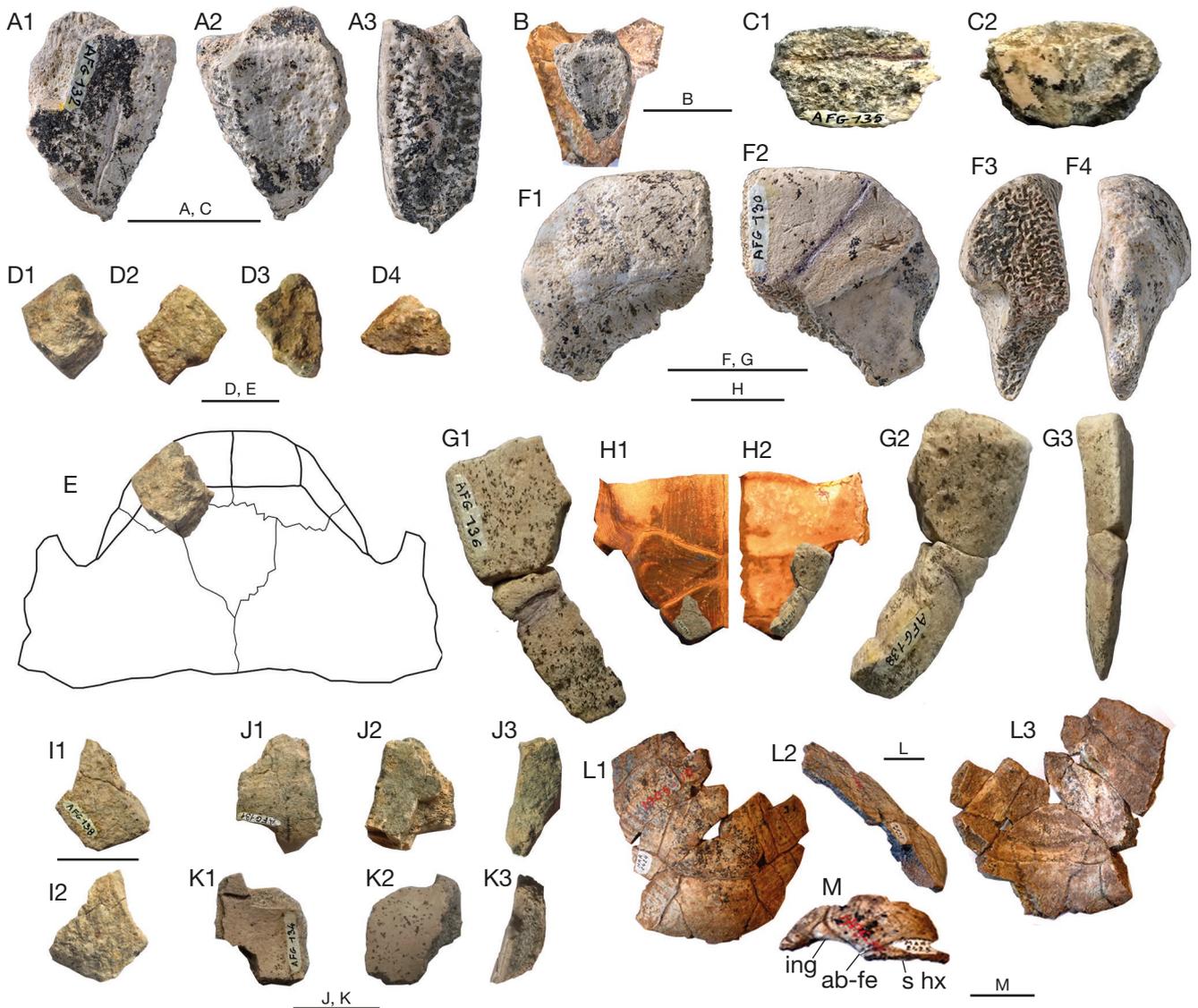


Fig. 3. — Testudines, Sherullah, late Miocene, *Agrionemys* sp. : **A**, pygal AFG 132, dorsal, ventral and right lateral views; **B**, pygal AFG 132 superposed on pygal of *Agrionemys* sp of Maragheh (Iran) in ventral view; **C**, AFG 135, neural 5, dorsal and ventral views; **D**, AFG 138 (9), left epiplastron, dorsal, ventral, medial and posterior views; **E**, AFG 138 (9), left epiplastron superposed on a drawing of an anterior lobe of *Agrionemys horsfieldii* from Khordkabal basin REP 57 (without scutes), dorsal view; **F**, AFG 130, left epiplastron, dorsal, ventral, medial (symphyseal) and left (external) views; **G**, AFG 136, right fragmentary xiphiplastron, ventral, dorsal and lateral views; **H**, *Agrionemys horsfieldii*, REP 57, half posterior lobe parts of specimens from Khordkabal basin (with scutes) with superposition of fragmentary xiphiplastral AFG 138 (11) and AFG 136, respectively ventral and dorsal view (not to scale); **I**, AFG 138 (11), right anal xiphiplastral extremity, ventral and dorsal views; **J**, AFG 131, fragmentary posterior peripheral, dorsal, ventral and distal views; **K**, AFG 134, fragmentary posterior peripheral, dorsal, ventral and distal view. *Agrionemys* sp., Maragheh (Iran), late Miocene, fragmentary shell; **L**, MNHN.F.MAR2424, pygal-suprapygal area, dorsal proximal and ventral views; **M**, MNHN.F.MAR2425, fragmentary right hypoplasra, oblique-posterior view on inguinal notch. Abbreviations: **ab-fe**, abdominofemoral sulcus; **ing**, inguinal scute; **shx**, hypoxiphiplastral suture. Scale bars: 20 mm.

During the late Miocene, the testudinines are well diversified in the Eurasian area in the three genera *Testudo*, *Chersine* and *Agrionemys* (see Lapparent de Broin *et al.* 2006a, b, c). *Testudo* is distinguished from both others by the derived presence of a hinge between the xiphiplastron and the hypoplasra, in males as in females, with a longer posterior lobe only composed of the xiphiplastron, being narrower with less converging lateral borders. Here, the xiphiplastron AFG 136 is clearly not hinged as in *Agrionemys* and *Chersine*. *Agrionemys* has a rather wide posterior lobe at inguinal notches, as *Chersine*, eventually wider according to the species and subspecies and sex, and this conforms to Sherullah 9 partial xiphiplastron

(Fig. 3H); in conjunction with the wide posterior lobe at its base, the shape of the carapace of living *Agrionemys* is wide. It may be wider for its length according to the species or subspecies and sex but, on the whole, it is wider than in *Testudo*. This cannot be confirmed for Sherullah 9, the carapace plates being too poorly preserved, but the xiphiplastron are congruent for this greater width. Furthermore, *Agrionemys* has a short dorsal gular lip anterior to the entoplasra and the gular pocket is always slight, as in Sherullah 9 specimens. Although also anterior to the entoplasra, the epiplastral gular lip is variably long and deep in *Chersine* (such a variability being known in Plio-Pleistocene *Ch. hermanni* spp.-subsp.

group, in Lapparent de Broin *et al.* 2006a, b, c). In *Testudo*, the pocket is most often larger and overlapped by a long dorsal epiplastral lip, often extending over the entoplastron. The discriminant character of *Chersine* is a derived secondary division of the supracaudal scute, either only dorsally or only ventrally (in fossil species and subspecies) or both dorsally and ventrally in living representatives. The pygal from Sherullah 9 AFG 132 does not share this character: there is only one supracaudal as in *Testudo* and *Agrionemys* (Lapparent de Broin *et al.* 2006a, b, c).

Conforming to *Agrionemys*: the neural 5 AFG 135 conforms to that observed in extant compared *Agrionemys* spp. specimens. It is either shorter for its width and/or more hexagono-trapezoid and less rectangular or quadratic than in *Testudo* and *Chersine* observed specimens. However, the sulcus V3-V4 position is variable and here it is anterior to the middle length. The pygal is relatively long, according to males of *Agrionemys* (but also in males of *Chersine*) but it is much thicker than in living specimens. The single supracaudal ventral overlap of AFG 132 is long as in *Agrionemys* male specimens (Fig. 3B: AFG 132 pygal superposed on Maragheh pygal). The lateral borders of the plastral lobes are more or less convex in *Agrionemys*, including the straighter condition of Sherullah 9. In the living species, the anterior lobe is always wide at its base (in relation to the wide carapace) but it may be more or less anteriorly narrowed and protruding at gular lip: there is a bony shape variability which is not yet clearly defined in its relation to sex, individual and speciation. The epiplastron AFG 130 indicates an anterior lobe with moderately converging lateral borders anteriorly, and it is anteriorly straight with wide gulars but without a protruding lip in relation to *Agrionemys* specimens. However, AFG 138(9) gulars might have been slightly protruding in relation to humerals at least as in some living specimens (Fig. 3E). The lateral posterior lobe borders of AFG 136 are barely rounded with a small femoroanal indentation as in the specimen of *A. horsfieldii* of Khordkabal basin REP 57. AFG 136 is superposed on extant REP 57 in Fig. 3H, this being presented with its scutes: the scutes are visible lateroposteriorly exceeding the bone, in black. Sherullah 9 AFG 136 and 138(11) share with *A. horsfieldii* a short and straight anal notch. Other characters which can allow *Agrionemys* and *Chersine* to be distinct from *Testudo*, such as femur trochanter junction (Lapparent de Broin & Antunes 2000) are not represented here. Similarly discriminant, but not fully preserved here, is the carapace shape which is rounded and wide in living *Agrionemys*, and which is particularly short for its length in known *A. horsfieldii* specimens (type species of the genus). Also discriminant is the fact the *Agrionemys* shell is much higher than in *Chersine* and *Testudo*, with a higher bridge and a more elevated anterior lobe extremity. However, the shell is lower in *A. horsfieldii* than in *A. kazachstanica* (Lapparent de Broin *et al.* 2006a: fig. 11c).

Testudo and *Chersine* lineages have a more western distribution (around Mediterranean countries; *Chersine* being only European) compared to living *Agrionemys* which ranges from Georgia to western Xinjiang (eastern China) and is mostly present in eastern Asia (Iverson 1992; Rhodin *et al.* 2017).

The three lineages have been separated for a long time. *Testudo* (s.s.) is diversified since the late Miocene, being present in the Vallesian of Greece at the locality “Ravin de la Pluie” [MN10] (Garcia *et al.* 2011) and the Tortonian of Greece (Gaudry 1862, 1862-1867; Georgalis & Kear 2013; Garcia *et al.* 2016) at Nikiti [MN 11] and Pikermi, Turolian [MN 12-13]) and seemingly at the same time in Northern Africa (Djebel Semène, Late Vallesian, Tunisia) (Gmira *et al.* 2013). This wide area indicates a much older diversification. *Chersine* is present with the double supracaudal (yet not dorsally and ventrally stabilised as in living specimens) in the Pliocene (Ruscian, MN 15) of Perpignan (*Ch. Pyrenaica* (Dépéret & Donnezan, 1890)), and of Poland. *Chersine* lineage is considered as dating back to the middle part of the Miocene at Langhian-Serravallian epochs, being considered as firstly represented by the species *Paleotestudo canetotiana* from Sansan (middle Miocene, early Astaracian, MN6) (Broin 1977; Lapparent de Broin 2000, 2001). The lineage of *Paleotestudo* is here considered *sensu* Lapparent de Broin *et al.* 2006a, b, c, being grounded on this oldest *Paleotestudo* species (*P. canetotiana*), which is not considered as a synonym of *T. antiqua* Bronn, 1831 *sensu* Corsini *et al.* 2014 and of *T. catalaunica* Bataller, 1926 *sensu* Pérez-García *et al.* 2016 (MN 7-8, late Astaracian). Notably, the contour of the anterior lobe and the shape of the epiplastral gular lip of these species are different, and whatever the individual considered variability. However, these species are all considered as part of the same larger lineage leading to *Chersine* (Lapparent de Broin *et al.* 2006a, b, c; Luján *et al.* 2016; Pérez-García 2017), being distinguished from the lineage of *Agrionemys*.

The first known representative of *Agrionemys* lineage seems to be *Testudo bessarabica* (Lapparent de Broin 2000, 2001; Lapparent de Broin *et al.* 2006a, b, c; Macarovici 1930; Riabinin 1918) from the late Miocene (Turolian, MN 12) of Taraklia and Ciobirciu (Bessarabia, Moldavia). This species is the type species of *Protestudo* Čkhikvadze, 1970, for us a potential junior synonym of *Agrionemys*. It was recombined as *Agrionemys bessarabica* by Lapparent de Broin *et al.* (2006b). It has the same high shell due to a high bridge and wide and short xiphiplastron, in a posterior lobe with posteriorly well converging, straight or slightly convex, lateral borders. The narrow anterior lobe has much converging borders and much protruded gulars. As *Agrionemys*, it has a long ventral gular overlap on the entoplastron, however longer with regard to Sherullah specimen AFG 130. *Agrionemys bessarabica* differs from living *Agrionemys* by the more posterior humeropectoral sulcus which is just posterior or clearly posterior to the entoplastron and not at all overlapping it: this is missing in Sherullah 9, but this is a character also known in some *Chersine* and *Testudo* specimens (Gmira 1995; Gmira *et al.* 2013; Lapparent de Broin *et al.* 2006b) and that is then potentially specific rather than generic. *Agrionemys bessarabica* much differs by the gular lip which is anteriorly more narrowly protruding with converging lateral borders, as seen in the four ventrally figured specimens of Riabinin (1918: figs 3-4). This is different from Sherullah 9 AFG 130 specimen (Fig. 3E) which is devoid of gular protrusion as in some *Agrionemys horsfieldii*

and *A. kazachtanica* living specimens. While, several other preserved living *A. horsfieldii* specimens from Khordkabal basin present more protruding gulars (REP coll.); they are then closer to *A. bessarabica* although the protrusion is less long, less anteriorly narrow and externally rounder. The entoplastron seems considerably larger than in *Chersine* and *Testudo*, at least it is longer in *A. horsfieldii* and in *A. bessarabica* known specimens. The entoplastron is visible in four of the five figured specimens of *A. bessarabica* (Riabinin 1918: figs 3-4), appearing as more important in the anterior lobe, which is narrower on each side of this entoplastral bone (as in Sherullah 9 AFG 130), but anteriorly pointed: in Sherullah 9 AFG 130, the widely curved posteromedial border of the epiplastron (sutured with the entoplastron) in relation to its lateral width and the symmetrical juxtaposition Fig. 3F1, F2, seems also to indicate the presence of a wide entoplastron. *Agrionemys bessarabica* is different from both *A. horsfieldii* spp. and Sherullah 9 species by the deeper anal notch.

Agrionemys sp. (or previously cf. *bessarabica*) is considered as present at Maragheh, Iran (late Miocene, early Turolian), by the specimen MNHN.F.MAR2424, MAR2425 (coll. Mecquenem-Morgan 1905-10) (Lapparent de Broin *et al.* 2006c). In this country, as in Afghanistan, lives *A. horsfieldii* and not *Chersine*. The fossil is preserved by a part of posterior carapace of a male with the curved suprapygal-pygala area (Fig. 3L), and a fragment of hypoplastron; this specimen shows the inguinal notch bears a triangular medial inguinal scute which is well separated from the sulcus abdominofemoral, itself well separated from the hypoxiphiplastral suture (Fig. 3M). As *Chersine*, *A. bessarabica* and living *Agrionemys*, the Maragheh specimen differs from *Testudo* by the primitive absence of hypoxiphiplastral hinge, the suture being well separated from the abdominofemoral sulcus. It also conforms to *A. bessarabica* and living *Agrionemys* males by the obliquely much elevated, curved and protruding posterior border of the carapace (Fig. 3L2). This border was elevated above the plastral ventral level due to high bridge, at the difference with *Chersine*. Maragheh specimen is notably different from *Chersine*, as Sherullah 9 specimen and *Agrionemys*, by the absence of supracaudal division. Sherullah 9 and Maragheh male specimens share the long arched pygal with a long ventral supracaudal overlap (Fig. 3B), while the pygal is shorter for its length in observed living *Agrionemys* female specimens. In Sherullah 9 species, the epiplastral gular dorsal lip overhangs the dorsal epiplastral surface vertically (Fig. 3D3) or nearly (Fig. 3F3, F4) and it does not overlap the entoplastron, as in living *Agrionemys* and *Ch. hermanni* (which is a primitive character), and there is no gular pocket (also a primitive character): this feature is unknown in the not prepared *A. bessarabica* Riabinin's specimens; it is not preserved in the Maragheh form.

In fine, as seen above, the size of the species from Sherullah 9 is similar to that of extant individuals of *Agrionemys*. It agrees by the conjunction of the following characters: neural 5 shape and length, male pygal shape and proportions with long ventral unique supracaudal overlap, dorsal epiplastral lip anterior to entoplastron and weak to absent gular pocket,

suitable xiphiplastral shape and proportions, and short and straight anal notch. The species from Sherullah 9 is different from the living *Agrionemys* compared species and from *A. bessarabica*, at least by its ventrally shortest gular part on the entoplastron. However, it is morphologically closer to various *Agrionemys* extant specimens than to *A. bessarabica* by the character of wider and few projected gulars. It is similar to *A. bessarabica* and part of extant specimens by the xiphiplastral general morphology (those specimens with straighter lateral borders) and similar to *A. bessarabica* by the narrower anterior lobe on each side of the entoplastron. As living *Agrionemys*, Sherullah 9 species had a shorter anal notch than in *A. bessarabica*.

The presence of *Agrionemys* in Moldavia and Afghanistan is perhaps not its only fossil witness in Europe. The question is raised for *Testudo brevitesta* Vlachos & Tsoukala, 2015, from the Pliocene of Milia (Greece): beside the absence of indication of a hypoxiphiplastral hinge (the hypoplastron being broken anterior to the posterior lobe and not at a hinge), Vlachos & Tsoukala 2015 figure a wide shell in a "rounded at angles-rectangular" shape (as in some living *Testudo* and overall some *Agrionemys* specimens), a wide anterior lobe with rounded converging borders with narrow anteriorly rounded and few protruding gulars, an elevated anterior lobe extremity, an epiplastral dorsal gular lip anterior to the entoplastron which is very large. These characters are found in specimens of *Agrionemys*, particularly the large entoplastron, and they particularly agree with the shell of some MNHN.RA *Agrionemys* female specimens, those which are less short for their width than others. The more curved gular lip differs. The rounded posterior peripheral half collar presented as characteristic of the species is of a female: it is similar to living compared female specimens of *A. horsfieldii*, although the Greek pygal is slightly more expanded medioposteriorly: this, really, can correspond to a specific difference. It is clearly different from the living *Agrionemys* species by the humeropectoral sulcus position which is primitively posterior to the entoplastron as in one of the four *A. bessarabica* ventrally figured specimen (being at its contact in the others). A larger entoplastron in the anterior lobe is also seen in other testudinines such as "*Ergilemys*" *bruneti* Broin, 1977 and *Centrochelys sulcata* (Miller, 1779) (see figures in Broin 1977; Lapparent de Broin 2003). This is a homoplastic character, because observed in these different lineages but noting the width of the anterior lobe on each side of the entoplastron varies, according to each form. Nevertheless, no described *Testudo* species share together so many characters with *Testudo brevitesta*. It is interesting to notice here this possible European expansion of the genus *Agrionemys* before present times, tending to do a link with the more western living *Agrionemys* population (which is known in Georgia), but more material is necessary.

In Afghanistan, Sherullah 9 indetermined species is the first fossil representative of the *Agrionemys* lineage of the country and, also, the first described fossil turtle of the country. It belongs to the oldest representatives of the genus at late Miocene, early Turolian.



FIG. 4. — *Varanidae*, Molayan, *Varanus* sp., trunk vertebra MOL 4126, photos: **A** anterior view; **B**, dorsal view; **C**, lateral view; **D**, ventral view. Right humerus fragment in dorsal and ventral view, respectively. Scale bar: 5 mm.

Order SQUAMATA Oppel, 1811
 Superfamily VARANOIDEA Camp, 1923
 Family VARANIDAE Gray, 1827
 Genus *Varanus* Merrem, 1820

Varanus sp.
 (Figs 4-6)

LOCALITY AND AGE. — Molayan, Khordkabal basin, late Miocene, middle Turolian in age, MN12.

MATERIAL EXAMINED. — Three trunk vertebrae (MOL 1853, MOL 1895, MOL 4126). 1 incomplete humerus, MOL 1854.

DESCRIPTION

Trunk vertebrae (Figs 4A, B; 5)

They show the morphology that is characteristic of *Varanus*. The neural arch slopes anteriorly. In the anterior half of the vertebra it forms a marked triangular depression on either side of the neural spine. The *pars tectiformis* that roofs the

anteriormost part of the neural canal is a typical feature of *Varanus*, but it is broken off in all specimens from Molayan. The condyle and cotyle are elliptical in outline. Their axis is markedly oblique: the condyle faces posterodorsally whereas the axis of the cotyle is directed anteroventrally (i.e., the cotyle is largely exposed in ventral aspect). The centrum is constricted anterior to the condyle (i.e., precondylar constriction). Apart from these features which are common to all *Varanus* species and it is worth mentioning that the vertebrae from Molayan are depressed, the cotyle and condyle are strongly depressed, and the ventral face of the centrum is hardly convex.

Humerus MOL 1854 (Fig. 4C).

Distal end of a right humerus, the ulnar and radial condyles are lacking. It is tentatively referred to *Varanus* sp. based on size and varanid features. The diaphysis appears medio-distally enlarged. Laterally, the ectepicondyle is broken but it seems prolonged proximally by a small ascending crest

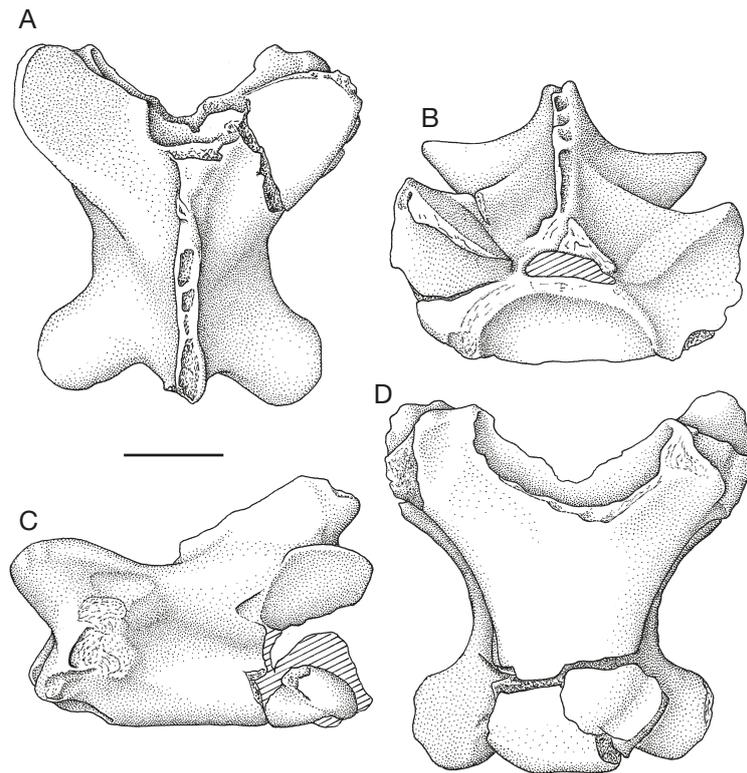


FIG. 5. — *Varanidae*, Molayan, late Miocene, *Varanus* sp., trunk vertebra MOL 4126, drawings: **A**, anterior view; **B**, dorsal view; **C**, lateral view; **D**, ventral view. Scale bar: 5 mm.

(ectepicondylar crest). The entepicondyle is projected medially. In ventral view, a large triangular, shallow depression is present, just proximal to the condyles and a small foramen opens on the proximal rim of the depression.

The possible presence of an ectepicondylar crest is consistent with referral of this humerus to varanids, as well as the enlarged diaphysis (Lécuru 1969). In addition, the large, shallow, triangular depression above the condyles, pierced by a small foramen that opens on the proximal rim of the depression are characteristic of varanid lizards. According to Lécuru (1969) and Smith (2009) this foramen is observed in nearly all limbed squamates, but it is quite reduced or even absent in *Varanus*. Georgalis *et al.* (2018) described an humerus from the late Miocene of Ravin de la Pluie (Greece). The authors state that Miocene European *Varanus* had short and robust limbs. Unfortunately, the humerus studied here is too fragmentary to allow thorough comparisons with the material from Greece. However, the diaphysis, as preserved, seems robustly built like the humerus described by Georgalis *et al.* (2018).

COMMENTS

The referral of these specimens to the genus *Varanus* appears to be unquestionable (at least for the vertebrae) but assignment at species level would require comparisons with all living species, which is not possible. Here, preliminary comparisons are made only with extinct species the vertebrae of which are known.

The oldest fossils attributed to *Varanus* consist of vertebrae from the late Eocene (Priabonian) and the early Oligocene of Egypt (Holmes *et al.* 2010; Smith *et al.* 2008; Augé & Guével 2018).

Earliest Miocene *Varanus* material come from the early Miocene (Orleanian, i.e. Burdigalian) of Africa and Europe (Clos 1995; Hoffstetter 1969, Ivanov *et al.* 2018).

Many varanid vertebrae have been described and several species have also been named but now serious doubts are raised about the possibility of alpha taxonomy based on isolated vertebrae. *Varanus rusingensis* Clos, 1995 from the Orleanian of Kenya (Clos 1995), *V. hofmanni* Roger, 1898, from the early (Orleanian), middle (Astaracian) and perhaps late (Vallesian) of western Europe (Estes 1983), *V. mokrensis* Ivanov, Ivanov, Ruta, Klembara & Böhme, 2018, from the early Miocene (Orleanian, MN4) of Czech Republic, *V. pronini* Zerova & Čkhikvadze, 1986 (from middle Miocene of Kazakhstan), *V. tyrsiensis* Zerova & Čkhikvadze, 1983 in Lungu, Zerova & Čkhikvadze, 1983, and *V. lungui* Zerova & Čkhikvadze, 1983 from the late Miocene (Sarmatian) of Moldova (Zerova & Čkhikvadze 1983, 1986), *V. semjonovi* Zerova & Čkhikvadze, 1986 from the late Miocene (Meotian) of Ukraine, *V. amnhophilis* Conrad, Balcarcel & Mehling, 2012 from the late Miocene (Turolian) of Samos, Greece, *V. marathonsensis* Weithofer, 1888 from the middle (Gaudry 1862-1867; Villa *et al.* 2018) to late Miocene, early Pliocene (Ruscianian), and from the early Pliocene (Ruscianian) of Anatolia (Rage & Sen 1976), and *V. bolokayi* Fejérváry,

1935 from the Pleistocene of Indonesia. Fossils from the middle Pleistocene of Greece represent the last occurrence of varanid lizards in Europe (Georgalis *et al.* 2017).

In addition, in Asia, rare vertebrae belonging to *Varanus* have been recovered from the Siwalik beds; one of these vertebrae, of presumed Pliocene age, was referred to the extinct species *V. sivalensis* Falconer, 1868 that is based on a humerus. The assignment of this vertebra to *V. sivalensis* is not justified. Another vertebra, from the late Miocene of Siwalik deposits has been referred to as *Varanus* sp. (Rage *et al.* 2001). In addition, Čerňanský *et al.* (2018) described vertebrae of *Varanus* sp. from the late Miocene of Solnechnodolsk (Russia).

Iberoveranus catalaunicus (Hoffstetter, 1969) comes from the early Miocene (MN3/MN4) of Spain; it has been synonymized with *Varanus* and the species *V. catalaunicus* is now regarded as a nomen dubium (Delfino *et al.* 2013). (See a revision of the fossil record of the genus *Varanus* in Molnar (2004)).

Ivanov *et al.* (2018) retained only four valid species (*V. rusingensis*, *V. hofmanni*, *V. amnhophilis* and *V. marathonsensis*) in addition to the new species *V. mokrensis* and Villa *et al.* (2018) suggest that *V. amnhophilis* is a synonym of *V. marathonsensis*. Many nominal fossil varanid species are based on insufficient material (isolated vertebrae) and are regarded as *nomina dubia* by several authors and the status of these taxa awaits a thorough revision.

As recognized by previous authors, isolated vertebrae are poorly diagnostic, at least at the species rank, their identification is hindered by poor knowledge of their variability (intra or inter specific). (See discussion in Georgalis *et al.* 2018 about the problematic status of vertebral based varanid taxa).

The strongly depressed condyle and cotyle represent the main distinctive feature of the vertebrae from Molayan. cursory comparison shows that the Afghan fossil is clearly distinguished from the purported *Varanus* species listed above, except *V. tyrsiensis* and *V. semjonovi*. Comparisons between the cotyle/condyle of the vertebrae from Molayan and those of *V. tyrsiensis* cannot be made. However, the vertebrae of the latter species appear to be less depressed than the specimens from Molayan. The cotyle and condyle of *V. semjonovi* are similar to those of the Molayan specimens; nevertheless, the latter vertebrae differ from those of *V. semjonovi* in being more depressed and in having a deeper interzygapophyseal constriction. Finally, the fossil from Molayan differs from all extinct species. Nevertheless, the possibility that this *Varanus* pertains to an extant species cannot be definitely excluded.

Order SQUAMATA Opper, 1811

Gen. et sp. indet. A

LOCALITY AND AGE. — Sherullah 9, Khordkabal basin, Afghanistan, late Miocene, late Vallesian-basal Turolian transition, MN10/11.

MATERIAL EXAMINED. — One fragment of bone with teeth (AFG 1668), 1 incomplete vertebra (AFG 1669).

COMMENTS

A small fragment of bone bears two teeth. The implantation of the teeth is clearly, although not deeply, pleurodont. The second specimen is a fragmentary vertebra which provides no information.

These specimens demonstrate that lizards are present, but their fragmentary nature excludes all other statement. To be fair, agamid and anguimorph lizards have, respectively, acrodont and subpleurodont dentition (*sensu* Hoffstetter 1954) but members of these taxa often exhibit pleurodont teeth on the anterior part of the jaw (Augé 1997, 2005).

Gen. et sp. indet. B

LOCALITY AND AGE. — Pul-E Charkhi, Kabul basin, Afghanistan, earliest Pliocene, early Ruscinian, MN 13/14.

MATERIAL EXAMINED. — Two fragments of bones with teeth (AFG 1675, AFG 1676), 1 fragmentary vertebra (AFG 1677).

COMMENTS

The two fragments of bones bear a few teeth. The teeth are pleurodont on both bones, but they are thick on one specimen whereas they are slender on the other fragment. Therefore, two distinct lizards are probably present, yet further identification would be unwise given the poor preservation of the jaws (see above). The fragment of vertebra is not diagnostic within lacertilians.

Suborder SERPENTES Linnaeus, 1758

Family COLUBRIDAE Opper, 1811

(*sensu* Lawson *et al.* 2005)

COLUBRIDAE s.l.

COLUBRIDAE gen. et sp. indet. A

LOCALITY AND AGE. — Sherullah 9, Khordkabal basin, Afghanistan, late Miocene, late Vallesian-basal Turolian transition, MN10/11.

MATERIAL EXAMINED. — Two incomplete vertebrae (AFG 1670).

DESCRIPTION AND COMMENTS

The neural arch and zygapophyses of the two specimens are damaged. The centrum is narrow with a convex ventral surface. The subcentral ridges are not prominent, they slightly diverge anteriorly. The haemal keel is thin, blunt, and not very prominent. The centrum is similar to that of snakes belonging to the “colubrine type” (*sensu* Szyndlar 1991a).

Today, the Colubridae represent about three-fourth of the snake species. The earliest colubrid was recovered from the late (latest: Benammi *et al.* 2001) Eocene of Thailand (Rage *et al.* 1992). Since the early Miocene, colubrids have been the dominant constituents of snake faunas (Rage 1987).

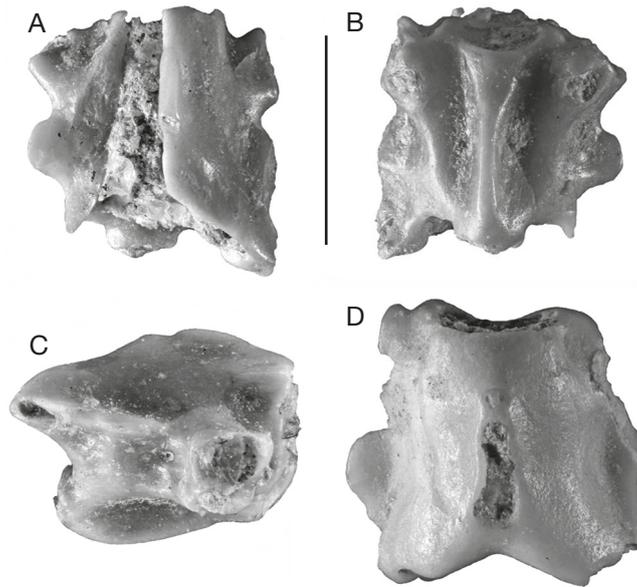


FIG. 6. — Xenodermidae (*Xenodermus*) or Elapidae (*Bungarus*), Sherullah, late Miocene, photos: **A, B, C**, trunk vertebra AFG 1672, dorsal, ventral and right lateral views; **D**, trunk vertebra AFG 1673, dorsal view. Scale bar: 2 mm.

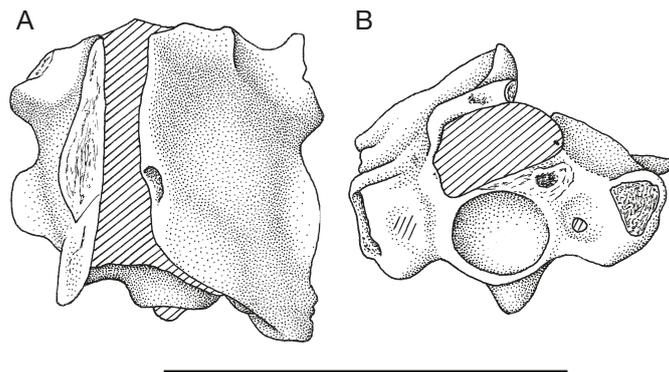


FIG. 7. — Xenodermidae (*Xenodermus*) or Elapidae (*Bungarus*), Sherullah, late Miocene, trunk vertebra, AFG 1672, drawings: **A, B**, dorsal and anterior views. Scale bar: 3 mm.

COLUBRIDAE gen. et sp. indet. B

LOCALITY AND AGE. — Pul-E Charkhi, Kabul basin, Afghanistan, earliest Pliocene, early Ruscinian, MN 13/14.

MATERIAL EXAMINED. — Three fragmentary vertebrae (AFG 1678).

COMMENTS

The vertebrae are represented by centra. On one of them, the haemal keel is well-preserved; its elongate, spatulate shape suggests that this fragment of vertebra belongs to a colubrid snake. The two other fragments apparently belong to the same taxon.

Family COLUBRIDAE Oppel, 1811
or ELAPIDAE Boie, 1827

COLUBRIDAE of the “natricine type” or ELAPIDAE of the *Naja* Laurenti, 1768 group

Gen. et sp. indet.

LOCALITY AND AGE. — Sherullah 9, Khordkabal basin, Afghanistan, late Miocene, late Vallesian-basal Turolian transition, MN10/11.

MATERIAL EXAMINED. — Eight vertebrae (AFG 1671).

DESCRIPTION

The vertebrae are mainly characterized by the morphology of their centrum. The ventral face is clearly delimited laterally by prominent subcentral ridges. The ridges slightly diverge anteriorly; consequently, the centrum is narrow. A hypapophysis was present (broken off on all specimens). A deep keel

TABLE 1. — List of amphibians and reptiles from the Neogene of Afghanistan.

Localities	Sherullah	Molayan	Pul-E Charkhi	Hadji Rona
Taxa	(Vallesian-Turolian boundary)	(Middle Turolian)	(Lower Ruscinian)	(Upper Ruscinian)
? Discoglossinae (Alytidae)	x	—	—	—
Ranidae	x	—	—	—
Non-alytid, non-ranid anuran(s)	x	—	—	x
Anuran(s) indeterminate	—	—	x	—
<i>Agrionemys</i> sp.	x	—	—	—
<i>Varanus</i> sp.	—	x	—	—
Lacertilan(s) indeterminate	x	—	x	—
Colubridae s.l. indeterminate	x	—	x	—
“Natricine” or elapid of the <i>Naja</i> group	x	—	—	—
<i>Xenodermus</i> or <i>Bungarus</i>	x	—	—	—

prolongs it anteriorly. The ventral surface is flat or slightly concave between the keel and subcentral ridges. The cotyle and condyle are comparatively large.

COMMENTS

Narrow centra, with a hypapophysis and well-delimited, flat or concave ventral face characterize “natricine” Colubridae (*sensu* Szyndlar 1991b) and Elapidae of the *Naja* group. In the specimens from Sherullah 9, no character permits assignment within this morphological assemblage. Therefore, this snake may be regarded as either a Colubridae or an Elapidae.

Family XENODERMIDAE Gray, 1849
or ELAPIDAE Boie, 1827
Genus *Xenodermus* Reinhardt, 1836
or *Bungarus* Daudin, 1803

Sp. indet.
(Figs 6; 7)

LOCALITY AND AGE. — Sherullah 9, Khordkabal basin, Afghanistan, late Miocene, late Vallesian-basal Turolian transition, MN10/11.

MATERIAL EXAMINED. — Two incomplete vertebrae (AFG 1672, AFG 1673)

DESCRIPTION

These vertebrae are poorly preserved (Figs 6; 7). They show a well-marked abrasion with rounded and polished surfaces affecting all vertebral structures: zygapophysis, neural spine and hypapophysis, most likely as a consequence of a water transport. These vertebrae display the bases of lateral laminae. These laminae originate from the interzygapophyseal ridges and anterolateral borders of the postzygapophyses. They extended horizontally; unfortunately, their shape and extent are unknown. The laminae do not contact the prezygapophyses. The vertebrae are rather depressed. The centrum seems to have a very worn hypapophysis.

COMMENTS

Such lateral laminae are present in rare snakes; among colubroids they occur only in a few colubrid genera (e.g. in the

African genus *Mehelya* and some American dipsadids (Bogert 1964; Hoffstetter & Gasc 1969; Sánchez-Martinez 2011) and in certain species of the elapid *Bungarus* (Hoffstetter 1939; Slowinski 1994). Within Asian colubrids, only *Xenodermus* (now in Xenodermatidae a basal caenophidian Family placed outside Colubridae [e.g. Vidal *et al.* 2007; Zaher *et al.* 2009; Pyron *et al.* 2011]) has vertebrae similar to those from Sherullah (Bogert 1964). On the basis of the two available specimens, referral to either *Xenodermus* or *Bungarus* is difficult. However, the Sherullah vertebrae are depressed and the posterior median notch of the neural arch is well pronounced, which is more reminiscent of *Bungarus*. As a result, this snake might be referred to either *Xenodermus* (Colubridae s.l.) or *Bungarus* (Elapidae).

A *Xenodermus*-like snake was reported from the early (or middle?) Miocene of Thailand (Rage & Ginsburg 1997), however, this material was not accompanied by any kind of figure. An indeterminate species of *Bungarus* was reported from the late Miocene of Pakistan by Head (2005); furthermore, a vertebra from the late Pleistocene-Holocene of Kurnool Cave, India, attributed to *Serpentes* indeterminate by Patnaik *et al.* (2008) is clearly a *Bungarus* vertebra. Today, both genera are restricted to Asia (*Xenodermus* in southeastern Asia, *Bungarus* in Southern Asia).

CONCLUSION

The four studied faunas (anuran, turtle, lizard and snake) document the first report of extinct amphibians and reptiles from Afghanistan. As such, despite the fact that the fossil material is rather fragmentary, its importance resides in its unique geographic origin.

Faunas of amphibians and reptiles from the Miocene and Pliocene times are generally rich and diverse. Astonishingly, among the explored area of Afghanistan only four localities yielded herpetofaunas and they are rather poor (Sherullah 9) or exceedingly poor. The herpetofauna from the late Miocene of Sherullah 9 is not rich but it is comparatively diverse (Table 1). It produced eight taxa, but only three taxa are present at Pul-E Charkhi (earliest Pliocene), whereas Molayan (late Miocene) and Hadji Rona (early Pliocene) each produced one taxon.

Varanus is known only in Molayan and *Agrionemys* only in Sherullah 9 (Table 1). These faunas do not provide stratigraphic information. None of the taxa has been identified at species level. Fossils are identified at least at genus level only in the late Miocene, representing extant genera.

The fauna has principally an Asiatic character. The snake that we here referred to either *Xenodermus* or *Bungarus* (from Sherullah 9) is (in any case) typically Asiatic. *Agrionemys* sp. (Sherullah 9) is known as extant from eastern Asia to only easternmost Europe. Its lineage is particularly interesting by its presence in the Miocene of Maragheh (Iran) and possibly in Moldavia at the same approximate age as Molayan. These records are the oldest of the lineage of the genus *Agrionemys*. The presence of the lizard *Varanus* in Molayan is notably interesting, being still present in Afghanistan with two species, *V. griseus* Daudin, 1803 and *V. bengalensis* Daudin, 1802, so that it seems plausible that *Varanus* is present in Afghanistan since the late Miocene. But it cannot be confirmed whether the fossil material pertains to an extinct lineage or some extant form. The genus *Varanus* represents an old lineage present in Africa, Eurasia and Australia. Its geographical origins are still discussed, knowing that the oldest fossils attributed to *Varanus* consist of vertebrae from the late Eocene (Priabonian) and the early Oligocene of Egypt (Holmes *et al.* 2010; Smith *et al.* 2008; Augé & Guével 2018). As far as the palaeoenvironment is concerned, anurans and the turtle *Agrionemys* provide some information. Anurans require at least temporary bodies of water: the presence of frogs depends on the existence of local bodies of water, which is possible in desertic areas. The living turtle *Agrionemys* (steppe tortoise) is a terrestrial and opportunist animal for feeding, living nowadays in continental desertic or semidesertic environment, cold in winter and hot in summer (Bonin *et al.* 2006). As desertic other turtles, *Agrionemys* hibernates or estivates in burrows during excessive conditions and drink in temporary ponds when possible. Therefore, although not sharing the same ecological niche during their life, the presence in the field locality of anurans with this turtle is compatible. Lizards and snakes had to endure similar conditions.

Acknowledgements

We are particularly grateful to the members of the French Expedition in Afghanistan and particularly to Emile Heintz (MNHN, paleontology) who provided the material, to Sevet Sen (MNHN, paleontology) for his kind and substantial help and first revision of the work, to Nour-Edine Jalil (MNHN.F, curator of reptiles) and to Laure Pierre-Huyet and Jérôme Courtois (MNHN.RA, curators) who provided fossil and extant material, and to Cécile Callou (MNHN, Collections Department) for access to the picture station of the Zoology – Comparative Anatomy Collections Management Unit, and to Vlad Codrea (Cluj University, Romania) for kind information. Clichés are from Salvador Bailon (MNHN, Archéozoologie, Archéobotanique, Sociétés, pratiques et environnements), Denis Serrette, Lilian Cazes and France de Lapparent de Broin (MNHN, Paleontology).

Drawings of anurans and snakes are from Jean-Claude Rage. The French Paleontological Expeditions to Afghanistan between 1976 and 1979 were financially supported by the MNHN and CNRS. Drs Georgalis and Čerňanský are thanked for their help to improve a first version of the manuscript. The MNHN gives access to the collections in the framework of the RECOLNAT national Research Infrastructure.

REFERENCES

- AUGÉ M. L. 1997. — A consideration of the phylogenetic significance of Acrodonty. *Herpetological Journal* 7: 111-113.
- AUGÉ M. L. 2005. — *Évolution des lézards du Paléogène en Europe*. Muséum national d'Histoire naturelle, Paris, 369 p. (*Mémoires du Muséum national d'Histoire naturelle*; 192).
- AUGÉ M. L. & GUÉVEL B. 2018. — New varanid remains from the Miocene (MN4-MN5) of France: inferring fossil lizard phylogeny from subsets of large morphological data sets. *Journal of Vertebrate Paleontology* 38 (1): e1410483. <https://doi.org/10.1080/02724634.2017.1410483>
- BÁEZ A. M. & BASSO N. G. 1996. — The earliest known frogs of the Jurassic of South America: Review and cladistic appraisal of their relationships. *Münchener Geowissenschaftliche Abhandlungen* A 30: 131-158.
- BAJPAI S. & KAPUR V. V. 2008. — Earliest Cenozoic frogs from the Indian Subcontinent: implications for out-of-India hypothesis. *Journal of the Palaeontological Society of India* 53 (1): 65-71. <http://repository.ias.ac.in/93927/>
- BENAMMI M., CHAIMANEE Y., JAEGER J. J., SUTEETHORN V. & DUCROCQ S. 2001. — Eocene Krabi Basin (Southern Thailand): Paleontology and magnetostratigraphy. *Geological Society of America Bulletin* 113: 265-273. [https://doi.org/10.1130/0016-7606\(2001\)113<265:EKBS>2.0.CO;2](https://doi.org/10.1130/0016-7606(2001)113<265:EKBS>2.0.CO;2)
- BOGERT C. M. 1964. — Snakes of the genera *Diaphorolepis* and *Synophis* and the colubrid subfamily Xenodermiinae (Reptilia, Colubridae). *Senckenbergiana Biologica* 45: 509-531.
- BONIN F., DEVAUX B. & DUPRÉ A. 2006. — *Toutes les tortues du monde*. Delachaux et Nestlé, Paris, 416 p.
- BOUR R. & OHLER A.-M. 2008. — *Chersine* Merrem, 1820 and *Chersina* Gray, 1831: a nomenclatural survey. *Zootaxa* 1752: 66-68. <https://doi.org/10.11646/zootaxa.1752.1.4>
- BRANDY L. D. 1979. — Données sur les successions des faunes de rongeurs du Néogène de l'Afghanistan. *Comptes Rendus de l'Académie des Sciences, Paris, série D*, 289: 269-270. <https://gallica.bnf.fr/ark:/12148/bpt6k5497434s/f295.item>
- BROIN F. DE 1977. — *Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé et du Tertiaire de France*. Muséum national d'Histoire naturelle, Paris, 115 p. (*Mémoires du Muséum national d'Histoire naturelle, Sér. C – Sciences de la Terre*; 38).
- BRUNET M., HEINTZ E. & SEN S. 1981. — Datations paléontologiques et séquence biochronologique dans le Néogène continental d'Afghanistan. *Comptes Rendus de l'Académie des Sciences de Paris, Série 3*, 293: 305-308. <https://gallica.bnf.fr/ark:/12148/bpt6k63270561/f317.item>
- BRUNET M., HEINTZ E. & BATTAIL B. 1984. — Molayan (Afghanistan) and the Khaur Siwaliks of Pakistan: an example of biogeographic isolation of late Miocene mammalian faunas. *Geologieen Mijnbouw* 63: 31-38.
- CANNATELLA D. C. 2007. — An integrative phylogeny of Amphibia, in NARINS P. & POPPER A. (eds), *Hearing and Sound Communication in Amphibians*. Springer Verlag, New York: 12-43. https://doi.org/10.1007/978-0-387-47796-1_2
- ČERŇANSKÝ A., SYROMYATNIKOVA E. V. & JABLONSKI D. 2018. — The first record of amphisbaenian and anguimorph lizards (Reptilia, Squamata) from the upper Miocene Solnechnodolsk locality in Russia. *Historical Biology* 32 (7): 869-879. <https://doi.org/10.1080/08912963.2018.1539973>

- CHE J., PANG J., ZHAO H., WU G., ZHAO E. & ZHANG Y. 2007. — Phylogeny of Raninar (Anura: Ranidae) inferred from mitochondrial and nuclear sequences. *Molecular Phylogenetics and Evolution* 43: 1-13. <https://doi.org/10.1016/j.ympev.2006.11.032>
- ČCHKHIKVADZE V. M. 1970. — [On the origin of extant palaeartic terrestrial turtles]. *Bulletin of the Academy of Sciences of the Georgian SSR* 57: 245-247 (in Russian).
- ČCHKHIKVADZE V. M. 1985. — [Preliminary results of the study of Tertiary amphibians and squamates from Zaisan Basin], in DAREVSKIY S. (ed.), *Voprosy Gerpetologii, 6th All-Union Herpetological conference*. Nauka, Leningrad: 234-235 (in Russian).
- CLAESSENS L. 1995. — *Miocene Reptilian and Amphibian Faunas of Anatolia, with Special Emphasis on the Anura*. Master Thesis, Institute of Earth Sciences, Utrecht University.
- CLOS L. M. 1995. — A new species of *Varanus* (Reptilia: Sauria) from the Miocene of Kenya. *Journal of Vertebrate Paleontology* 15: 254-267. <https://doi.org/10.1080/02724634.1995.10011228>
- CONRAD J. L., BALCARCEL A. M. & MEHLING C. M. 2012. — Earliest example of a Giant Monitor Lizard (*Varanus*, Varanidae, Squamata). *PLOS One* 7 (8): e41767. <https://doi.org/10.1371/journal.pone.0041767>
- CORSINI J. A., BÖHME M. & JOYCE W. G. 2014. — Reappraisal of *Testudo antiqua* (Testudines, Testudinidae) from the Miocene of Hohenhöwen, Germany. *Journal of Paleontology* 88: 948-966. <https://doi.org/10.1666/13-036>
- DAUDIN F. M. 1802. — *Histoire naturelle, générale et particulière des reptiles, ouvrage faisant suite à l'histoire naturelle, générale et particulière composée par Leclerc de Buffon et redirigée par C. S. Sonnini*. Vol. 3. F. Dufart, Paris, 452 p. <https://www.biodiversitylibrary.org/page/39967123>
- DAUDIN F. M. 1803. — *Histoire naturelle, générale et particulière des reptiles, ouvrage faisant suite à l'histoire naturelle, générale et particulière composée par Leclerc de Buffon et redirigée par C. S. Sonnini*. Vol. 8. F. Dufart, Paris, 439 p. <https://www.biodiversitylibrary.org/page/39965291>
- DELFINO M., RAGE J.-C., BOLET A. & ALBA D. M. 2013. — Early Miocene dispersal of the lizard *Varanus* into Europe: Reassessment of vertebral material from Spain. *Acta Palaeontologica Polonica* 58 (4): 731-735. <https://doi.org/10.4202/app.2012.0025>
- ESTES R. 1983. — Sauriaterrestria, Amphisbaenia, in WELLNHOFER P. (ed.), *Handbuch der Paläoherpetologie*. Volume 10A. Gustav Fischer, Stuttgart, xxii + 249 p.
- EVANS S. E., MILNER A. R. & MUSSETT F. 1990. — A discoglossid frog (Amphibia: Anura) from the middle Jurassic of England. *Palaeontology* 33: 299-311.
- FALCONER H. 1868. — *Palaeontological Memoirs and Notes of the late Hugh Falconer*. 2 Vols. AM, MD, London, R. Hardwicke. <https://www.biodiversitylibrary.org/bibliography/49217>
- FEJÉRVÁRY G. 1935. — Further contributions to a monograph of the Megalanidae and fossil Varanidae – with notes on recent varanians. *Annales Musei Historico-Naturalis Hungarici* 29: 1-130.
- FOLIE A., RANA R. S., ROSE K. D., SAHNI A., KUMAR K., SINGH L. & SMITH T. 2013. — Early Eocene frogs from Vastan Lignite Mine, Gujarat, India. *Acta Palaeontologica Polonica* 58 (3): 511-524. <https://doi.org/10.4202/app.2011.0063>
- FROST D. R., GRANT T., FAIVOVICH J., BAIN R. H., HAAS A., HADDAD C. F. B., DE SÁ R. O., CHANNING A., WILKINSON M., DONNELLAN S. C., RAXWORTHY C. J., CAMPBELL J. A., BLOTTO B. L., MOLER P., DREWES R. C., NUSSBAUM R. A., LYNCH J. D., GREEN D. M. & WHEELER W. C. 2006. — The amphibian tree of life. *Bulletin of the American Museum of Natural History* 297: 1-370. <https://doi.org/d7tmxr>
- GARCIA G., KOSTOPOULOS D. S., VALENTIN X., KOUFOS G. D. 2016. — Testudines, in KOUFOS G. D. & KOSTOPOULOS D. S. (eds), *Palaeontology of the Upper Miocene Vertebrate Localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece)*. *Geobios* 49: 23-27. <https://doi.org/10.1016/j.geobios.2016.01.003>
- GARCIA G., LAPPARENT DE BROIN F. DE, BONIS L. DE, KOUFOS G. D., VALENTIN X., KOSTOPOULOS D. S. & MERCERON G. 2011. — A new terrestrial Testudinidae from the Late Miocene hominoid locality “Ravin de la pluie” (Axios valley, Macedonia, Greece). 9th European Association of Vertebrate Palaeontologists Annual Meeting, 14-19 June 2011, Heraklion Crete, Greece, Abstract, 1 p.
- GAUDRY A. 1862. — Note sur les débris d’oiseaux et de reptiles trouvés à Pikermi, Grèce, suivie de quelques remarques de paléontologie générale. *Bulletin de la Société géologique de France* 19: 629-640.
- GAUDRY A. 1862-1867. — *Animaux fossiles et géologie de l’Attique*. Paris, F. Savy, 474 p. <https://gallica.bnf.fr/ark:/12148/bpt6k9609613r>
- GEORGALIS G. L. & KEAR B. P. 2013. — The fossil turtles of Greece: An overview of taxonomy and distribution. *Geobios* 46: 299-311. <https://doi.org/10.1016/j.geobios.2013.05.001>
- GEORGALIS G. L., RAGE J.-C., BONIS L. DE & KOUFOS G. 2018. — Lizards and snakes from the late Miocene hominoid locality of Ravin de la Pluie (Axios Valley, Greece). *Swiss Journal of Geosciences* 111: 169-181. <https://doi.org/10.1007/s00015-017-0291-2>
- GEORGALIS G. L., VILLA A. & DELFINO M. 2017. — The last European varanid: demise and extinction of monitor lizards (Squamata, Varanidae) from Europe. *Journal of Vertebrate Paleontology* 37 (2): e1301946. <https://doi.org/10.1080/02724634.2017.1301946>
- GMIRA S. 1995. — *Étude des Chéloniens fossiles du Maroc*. Anatomie. Systématique. Phylogénie. Muséum national d’Histoire naturelle, Paris, 174 p. (Cahiers de Paléontologie ; 25).
- GMIRA S., LAPPARENT DE BROIN F. DE, GERAADS D., LEFÈVRE D., MOHIB A. & RAYNAL J.-P. 2013. — Les Tortues du Pliocène d’Ahl al Oughlam (Casablanca, Maroc) et de localités avoisinantes. *Geodiversitas* 35 (3): 691-733. <https://doi.org/10.5252/g2013n3a9>
- HEAD J. J. 2005. — Snakes of the Siwalik Group (Miocene of Pakistan): Systematics and Relationship to Environmental Change. *Palaeontologia Electronica* 8 (1-18A), 33 p.
- HEINTZ E. & BRUNET M. 1982. — Une barrière géographique entre le sous-continent Indien et l’Eurasie occidentale pour les faunes continentales du Miocène supérieur. *Comptes Rendus de l’Académie des Sciences, Paris, Série 3*, 294: 301-304. <https://gallica.bnf.fr/ark:/12148/bpt6k56794098/f307.item>
- HEINTZ E., GINSBURG L. & CARBONNEL J.-P. 1978a. — Découverte du premier grand gisement à Mammifères fossiles d’Afghanistan. *Comptes Rendus de l’Académie des Sciences, Paris, Série D*, 286: 945-947. <https://gallica.bnf.fr/ark:/12148/bpt6k5677707/f307.item>
- HEINTZ E., GINSBURG L. & HARTENBERGER J.-L. 1978b. — Mammifères fossiles en Afghanistan: état des connaissances et résultats d’une prospection. *Bulletin du Muséum national d’Histoire naturelle, Sciences de la Terre* 69: 101-119. <https://www.biodiversitylibrary.org/page/55501023>
- HOFFSTETTER R. 1939. — Contribution à l’étude des Elapidae actuels et fossiles et de l’ostéologie des ophidiens. *Bulletin du Muséum d’Histoire naturelle de Lyon* 15: 1-82.
- HOFFSTETTER R. 1954. — Sur la position systématique de *Necrosaurus*: Saurien de l’Éocène européen. *Comptes Rendus de la Société géologique de France* 16: 422-424.
- HOFFSTETTER R. 1969. — Présence de Varanidae (Reptilia, Sauria) dans le Miocène de Catalogne. Considérations sur l’histoire de la famille. *Bulletin du Muséum national d’Histoire naturelle* 40: 1051-1064. <https://www.biodiversitylibrary.org/page/55344240>
- HOFFSTETTER R. & GASC J.-P. 1969. — Vertebrae and ribs of modern reptiles, in GANS C., BELLAIRS A. D’A. & PARSONS T. S. (eds), *Biology of the Reptilia*. Vol. 1. Morphology. Academic Press, London and New York: 201-310.
- HOLMES R. B., MURRAY A. M., YOUSRY S., ATTIA Y. S., SIMONS E. L. & CHATRATH P. 2010. — Oldest known *Varanus* (Squamata: Varanidae) from the upper Eocene and lower Oligocene of Egypt: Support for an African origin of the genus. *Palaeontology* 53 (5): 1099-1110. <https://doi.org/10.1111/j.1475-4983.2010.00994.x>

- IVANOV M., RUTA M., KLEMBARA J. & BÖHME M. 2018. — A new species of *Varanus* (Anguimorpha: Varanidae) from the early Miocene of the Czech Republic, and its relationships and palaeoecology. *Journal of Systematic Palaeontology* 16: 767-797. <https://doi.org/10.1080/14772019.2017.1355338>
- IVERSON J. B. 1992. — *A Revised Checklist with Distribution Maps of the Turtles of the World*. Privately Print, Richmond, Indiana, 363 p.
- KHOZATSKY L. I. & MEYNSKI M. 1966. — *Agrionemys* – nouveau genre de tortues terrestres (Testudinidae). *Bulletin de l'Académie polonaise des Sciences, II, Série des sciences biologiques*, 14: 123-125.
- LAPPARENT DE BROIN F. DE 2000. — Les Chéloniens de Sansan, in GINSBURG L. (ed.), *La faune miocène de Sansan et son environnement*. Chap. 1. Muséum national d'Histoire naturelle, Paris: 219-261 (*Mémoires du Muséum national d'Histoire naturelle*; 183).
- LAPPARENT DE BROIN F. DE 2001. — The European turtle fauna from the Triassic to the Present: a short review. *Dumerilia* 4 (3): 155-216.
- LAPPARENT DE BROIN F. DE 2003. — The Miocene chelonians from the southern Namibia, in SENUT B. & PICKFORD M. (eds), *Faunas from the southern Namibia. Memoirs of the Geological Survey of Namibia* 19: 67-102.
- LAPPARENT DE BROIN F. DE & ANTUNES M. T. 2000. — Pleistocene Chelonians from Gruta da Figueira Brava (Arrábida, Portugal), in TELLES ANTUNES M. (ed.), *Colloquium: Last Neanderthals in Portugal. Odontologic and other evidence, January 18th 1999. Memórias da Academia das Ciências de Lisboa, Classe de Ciências* 38: 101-112.
- LAPPARENT DE BROIN F. DE, BOUR R., PARHAM J. F. & PERÄLÄ J. F. 2006a. — *Eurotestudo*, a new genus for the species *Testudo hermanni* Gmelin, 1789 (Chelonii, Testudinidae). *Comptes Rendus Palevol* 5: 803-811. <https://doi.org/10.1016/j.crpv.2006.03.002>
- LAPPARENT DE BROIN F. DE, BOUR R. & PERÄLÄ J. F. 2006b. — Morphological definition of *Eurotestudo* (Testudinidae, Chelonii): First part. *Annales de Paléontologie* 92 (3): 255-304. <https://doi.org/10.1016/j.annpal.2006.07.001>
- LAPPARENT DE BROIN F. DE, BOUR R. & PERÄLÄ J. F. 2006c. — Morphological definition of *Eurotestudo* (Testudinidae, Chelonii): Second part. *Annales de Paléontologie* 92 (4): 325-357. <https://doi.org/10.1016/j.annpal.2006.07.003>
- LAWSON R., SLOWINSKI J. B., CROTHER B. I. & BURBRINK T. T. 2005. — Phylogeny of the Colubroidea (Serpentes): new evidence from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* 37: 581-601. <https://doi.org/10.1016/j.ympev.2005.07.016>
- LÉCURU S. 1969. — Étude morphologique de l'humérus des Lacertiliens. *Annales des Sciences naturelles, Zoologie, Paris*, 12^e série 11: 515-558.
- LUJÁN A., DELFINO M., ROBLES J. M. & ALBA D. M. 2016. — The Miocene tortoise *Testudo catalaunica* Bataller, 1926, and a revised phylogeny of extinct species of genus *Testudo* (Testudines: Testudinidae). *Zoological Journal of the Linnean Society* 178 (2): 312-342. <https://doi.org/10.1111/zoj.12414>
- LUNGU A. N., ZEROVA G. A. & CHKHIKVADZE V. M. 1983. — Primary evidence on the Miocene *Varanus* of the North Black Sea littoral. *Bulletin of the Academy of Sciences of Georgian SSR* 110: 417-420 (in Russian, with English summary).
- MACAROVICI N. G. 1930. — Sur une *Testudo bessarabica* Riab. trouvée dans les couches méotiques de Cioburciu (Dép. Tighina-Roumanie). *Bulletin de la Section scientifique de l'Académie roumaine*, 13^e ann., 1-2: 26-30.
- MERREM B. 1820. — *Versuch eines systems der Amphibien*. Vol. 8. J.C. Krieger, Marbuch, 191 p.
- MILLER L. 1779. — *Icones animalium et plantarum*. Letterpress, London, 10 p. [published 1776-1782]. <https://doi.org/10.5962/bhl.title.112488>
- MOLNAR R. E. 2004. — The long and honorable History of Monitors and their Kins, in PIANKA E. R. & KING D. R. (eds), *Varanoid Lizards of the World*. Indiana University Press, Bloomington: 10-67.
- PARMAR V. & JIGMET T. 2014. — First Fossil Discoglossinae (Anura) from the Siwaliks of the Indian Subcontinent. *International Research Journal of Earth Sciences* 2 (8): 1-6.
- PATNAIK R., BADAM G. L. & MURTY M. L. K. 2008. — Additional vertebrate remains from one of the Late Pleistocene-Holocene Kurnool Caves (Muchchhla Chintamanu Gavi) of South India. *Quaternary International* 192: 43-51. <https://doi.org/10.1016/j.quaint.2007.06.018>
- PÉREZ-GARCÍA A. 2017. — Analysis of the Iberian Aragonian record of *Paleotestudo*, and refutation of the validity of the Spanish '*Testudo catalaunica*' and the French '*Paleotestudo canetotiana*'. *Spanish Journal of Palaeontology* 31 (2): 321-340. <https://doi.org/10.7203/sjp.31.2.17159>
- PÉREZ-GARCÍA A., ORTEGA F. & JIMÉNEZ FUENTES E. 2016. — Taxonomy, systematics and diversity of the European oldest testudinids. *Zoological Journal of the Linnean Society* 177 (3): 648-675. <https://doi.org/10.1111/zoj.12381>
- PYRON R. A., BURBRINK F. T., COLLI G. R., NIETO MONTES DE OCA A., VITT L. J., KUCZYNSKI C. A. & WIENS J. J. 2011. — The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. *Molecular Phylogenetics and Evolution* 58: 329-342. <https://doi.org/10.1016/j.ympev.2010.11.006>
- RAGE J.-C. 1984. — Are the Ranidae (Anura, Amphibia) known prior to the Oligocene? *Amphibia-Reptilia* 5: 281-288. <https://doi.org/10.1163/156853884X-005-03-09>
- RAGE J.-C. 1987. — Fossil History, in SEIGEL R. A., COLLINS J. T. & NOVAK S. S. (eds), *Snakes: Ecology, and Evolutionary Biology*. McGraw-Hill Inc., New York: 51-76.
- RAGE J.-C. & SEN S. 1976. — Les Amphibiens et les Reptiles du Pliocène supérieur de Çalta (Turquie). *Géologie méditerranéenne* 3: 127-134. <https://doi.org/10.3406/geolm.1976.969>
- RAGE J. C., BUFFETAUT É., BUFFETAUT-TONG H., CHAIMANEE Y., DUCROCQ S., JAEGER J.-J. & SUTEETHORN V. 1992. — A colubrid snake in the late Eocene of Thailand: The oldest known Colubridae (Reptilia, Serpentes). *Comptes Rendus de l'Académie des Sciences, Paris, série II*, 314: 1085-1089. <https://gallica.bnf.fr/ark:/12148/bpt6k54931689/f337.item>
- RAGE J.-C. & GINSBURG L. 1997. — Amphibians and Squamates from the early Miocene of Li Mae Long, Thailand: The richest and most diverse herpetofauna from the Cainozoic of Asia, in ROČEK Z. & HART S. (eds), *Herpetology '97, 3rd World Congress of Herpetology, Prague*: 167, 168.
- RAGE J. C., GUPTA S. S. & PRASAD G. V. R. 2001. — Amphibians and Squamates from the Neogene Siwalik beds of Jammu and Kashmir, India. *Paläontologische Zeitschrift* 75(2): 197-205. <https://doi.org/10.1007/BF02988013>
- RHODIN A. G. J., IVERSON J. B., VAN DIJK P. P., SAUMURE R. A., BUHLMANN K. A., PRITCHARD P. C. H. & MITTERMEIER R. A. 2017. — Turtles of the world. Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status. 8th ed. TTWG, Conservation Biology of Freshwater Turtles and Tortoises. *Chelonian Research Monographs* 7, 292 p. <https://doi.org/10.3854/crm.7.checklist.atlas.v8.2017>
- RIABININ A. N. 1918. — [On the turtles from Meotian deposits of Bessarabia]. *Trudy Geologicheskogo i Mineralogicheskogo Muzejajmenii Petra Velikago Imperatorskoj Akademii Nauk (St Petersburg) (1915)* 1: 1-16 (in Russian).
- ROČEK Z. & NESSOV L. A. 1993. — Cretaceous anurans from Central Asia. *Palaeontographica A* 226: 1-54.
- ROČEK Z. & RAGE J.-C. 2000. — Tertiary Anura of Europe, Africa, Asia, North America and Australia, in HEATWOLE H. & CARROLL R. L. (eds), *Amphibian Biology*. Vol. 4. Surrey Beatty, Chipping Norton: 1332-1387.
- RÜCKERT-ÜLKÜMEN N., BÖHME M., REICHENBACHER B., HEISSIG K., WITT W. & BASSLER B. 2002. — Die Fossilführung des kontinentalen Neogens (Ober-Miozän-Unter-Pliozän) von Develiköy (Manisa, Türkei). *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie* 42: 51-74. <https://www.biodiversitylibrary.org/page/29506901>
- SÁNCHEZ-MARTINEZ P. M. 2011. — *Anatomia comparada da tribu Nothopsini (Serpentes, Dipsadidae)*. Dissertação Mestre em Ciências,

- Instituto de Biociências da Universidad de São Paulo, 159 p. <https://doi.org/10.11606/D.41.2011.tde-13092011-113302>
- SANCHIZ B. 1998. — *Encyclopedia of Paleoherpétology*. Part 4. Salién-tia. Verlag Dr. Friedrich Pfeil, Munich, 276 p.
- SEN S. 1998. — The age of the Molayan mammal locality, Afghanistan. *Geobios* 31: 385-391. [https://doi.org/10.1016/S0016-6995\(98\)80021-1](https://doi.org/10.1016/S0016-6995(98)80021-1)
- SEN S. 2001. — Rodents and insectivores from the upper Miocene of Molayan, Afghanistan. *Palaeontology* 44 (5): 913-932. <https://doi.org/10.1111/1475-4983.00208>
- SLOWINSKI J. B. 1994. — A phylogenetic analysis of *Bungarus* (Elapidae) based on morphological characters. *Journal of Herpetology* 28: 440-446. <https://doi.org/10.2307/1564956>
- SMITH K. T. 2009. — A new lizard assemblage from the earliest Eocene (Zone WAO) of the Bighorn Basin, Wyoming, USA: Biogeography during the warmest interval of the Cenozoic. *Journal of Systematic Palaeontology* 7 (3): 299-358. <https://doi.org/10.1017/S1477201909002752>
- SMITH K. T., BHULLAR B. A. & HOLROYD P. A. 2008. — Earliest African Record of the *Varanus* stem clade (Squamata: Varanidae) from the Early Oligocene of Egypt. *Journal of Vertebrate Paleontology* 28 (3): 909-913. <https://doi.org/dhs5g4>
- ŠPINAR Z. V. 1972. — *Tertiary Frogs from Central Europe*. Academia, Prague, 286 p. <https://doi.org/10.1007/978-94-010-2932-2>
- SYROMYATNIKOVA E. V. 2016. — Anurans of the Tagay Locality (Baikal Lak, Russia; Miocene): Bombinatoridae, Hylidae, and Ranidae. *Russian Journal of Herpetology* 23 (2): 145-157. <https://doi.org/10.30906/1026-2296-2016-23-2-145-157>
- SZYNDLAR Z. 1991a. — A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. *Estudios Geológicos* 47: 103-126. <https://doi.org/10.3989/egcol.91471-2412>
- SZYNDLAR Z. 1991b. — A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. *Estudios Geológicos* 47: 237-266. <https://doi.org/10.3989/egcol.91473-4422>
- VIDAL N., DELMAS A. S., DAVID P., COULOUX A. & HEDGES S. B. 2007. — The phylogeny and classification of caenophidian snake inferred from seven nuclear protein-coding genes. *Comptes Rendus Biologies* 330: 182-187. <https://doi.org/10.1016/j.crv.2006.10.001>
- VILLA A., ABELLA J., ALBA D. M., ALMECJA S., BOLET A., KOUFOS G. D., KNOLL F., LUJAN A. H., MORALES J., ROBLES J. M., SANCHEZ I. M. & DELFINO M. 2018. — Revision of *Varanus marathonsis* (Squamata, Varanidae) based on historical and new material: morphology, systematics, and paleobiogeography of the European monitor lizards. *PLoS ONE* 13 (12): e0207719. <https://doi.org/10.1371/journal.pone.0207719>
- VLACHOS E. & TSOUKALA E. 2015. — The diverse fossil chelonians from Milia (Late Pliocene, Grevena, Greece) with a new species of *Testudo* Linnaeus, 1758 (Testudines: Testudinidae). *Papers in Paleontology*. <https://doi.org/10.1002/spp2.1031>
- ZAHER H., GRAZZIOTIN F. G., CADLE J. E., MURPHY R. W., MOURALEITE J. C. & BONATTO S. L. 2009. — Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American Xenodontines: a revised classification and description of new taxa. *Papeis Avulsos de Zoologia* 49: 115-153. <https://doi.org/10.1590/S0031-10492009001100001>
- ZEROVA G. & ČHKHIKVADZE V. M. 1983. — [*Varanus tyrsiensis* G. Zerova et Chkhikvadze sp. nov.], in LUNGU A. N., ZEROVA G. A. & ČHKHIKVADZE V. M. (eds), [Primary evidence on the Miocene *Varanus* of the north Black Sea littoral]. *Bulletin of the Academy of Sciences of the Georgian SSR* 110: 417-420 (in Russian).
- ZEROVA G. A. & ČHKHIKVADZE V. M. 1986. — Neogene varanids of the USSR, in ROČEK Z. (ed.), *Studies in Herpetology*. Proceedings of the European Herpetological Meeting, Charles University, Prague: 689-694.

Submitted on 26 March 2019;
accepted on 20 September 2019;
published on 17 September 2020.