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Amphibians and reptiles from the Early Miocene of the Bardenas Reales of Navarre (Ebro Basin, Iberian Peninsula)

Amphibiens et reptiles du Miocène inférieur des Bardenas Reales de Navarre (Dépression de l'Ebre, Péninsule ibérique)

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Abstract

The Lower Miocene deposits of the Bardenas Reales of Navarre (NW Ebro Basin, northern Iberian Peninsula) have yielded a diverse vertebrate fauna, including remains of amphibians and reptiles. These remains occur in several localities in the Tudela Formation. The fossiliferous levels belong to the Biozones MN2b-3 (Biozones Z-A of the Ramblian, i.e., Late Aquitanian to Early Burdigalian in age). The amphibians and reptiles represent at least 13 out of 37 vertebrate species. Amphibians consist of a salamandrid urodele and two or three anurans. All the turtles are cryptodirans and consist of the chelydrid *Chelydropsis apellanizi*, the testudinids *Ptychogaster* (*Temnoclemmys*) *bardenensis* and *Ptychogaster ronheimensis*, and a Trionychinae indet. Squamates are represented by the anguid lizard *Ophisaurus* sp., a non-anguid lacertilian, an amphisbaenian, the erycine boid? *Eryx* sp., and indeterminate colubrids. Crocodilian remains are assigned to the basal alligatoroid *Diplocynodon* sp. The fossil associations of the Bardenas Reales of Navarre suggest that the vertebrates lived in the centre of an endoreic basin with stretches of water under intertropical to subtropical climatic conditions. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Résumé

Les sédiments du Miocène inférieur des Bardenas Reales de Navarre (NO du bassin de l'Ebre, nord de la péninsule ibérique) ont livré une faune variée de vertébrés incluant des restes d'amphibiens et de reptiles. Ces restes ont été trouvés dans plusieurs localités de la formation Tudela. Les niveaux fossilifères appartiennent aux biozones MN 2b-3 (Biozones Z-A du Ramblien, c'est à dire Aquitanien supérieur-Burdigalien inférieur). Les amphibiens et reptiles représentent au moins 13 des 37 espèces de vertébrés trouvés dans les localités. Les amphibiens comportent un urodèle salamandridé et deux ou trois anoures. Les tortues sont toutes cryptodires et comportent le chélydridé *Chelydropsis apellanizi*, les testudinidés *Ptychogaster* (*Temnoclemmys*) *bardenensis* et *Ptychogaster ronheimensis* et un Trionychiné indéterminé. Les squamates sont repésentés par le lézard anguidé *Ophisaurus* sp., un lacertilien non anguidé, un amphisbénien, le boïdé éryciné ? *Eryx* sp. et des colubridés indéterminés. Les restes crocodiliens sont attribués à l'alligatoroïde basal *Diplocynodon* sp. Les associations de fossiles des Bardenas Reales de Navarre suggèrent que les vertébrés vivaient au centre d'un bassin endoréique sillonné de cours d'eau en chenaux plus ou moins importants, sous des conditions climatiques intertropicales à subtropicales. © 2002 Éditions scientifiques et médicales Elsevier SAS. Tous droits réservés.

Keywords: Early Miocene; Iberian Peninsula; Amphibians; Reptiles; Palaeoecology

Mots clés: Miocène inférieur; Péninsule ibérique; Amphibiens; Reptiles; Paléoécologie

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1. Introduction

The first fossil reptiles recovered in Navarre were turtle plates found in Miocene deposits near Tudela. They were assigned to *Trionyx* by Ezquerra del Bayo (1850). Later, Crusafont et al. (1966) mentioned a crocodilian skull found in the locality of Tudela 2; this material has never been described. So far, amphibians were unknown from this area. Since 1995, fieldworks in the Bardenas Reales of Navarre have yielded abundant remains of reptiles and amphibians, and also of bony fish (Cypriniformes), birds (Charadriiformes) and mammals (insectivores, chiropteres, rodents, lagomorphs, artiodactyls and perissodactyls) (Astibia et al., 1995; Murelaga, 2000). The amphibians consist of anurans and urodeles; the reptiles are represented by squamates (lizards, amphisbaenians, snakes), turtles and crocodilians (Pereda Suberbiola et al., 1996; Murelaga et al., 1999). As compared to other areas of the Ebro Basin (see Cuenca et al., 1992), the Bardenas Reales of Navarre have been poorly studied from a palaeontological point of view. The purpose of this paper is to describe in detail the fauna of amphibians and reptiles.

2. Geographical and geological setting

The region of the Bardenas Reales is located in the southwestern part of Navarre (Fig. 1). It is situated in the northwestern area of the Ebro Basin which is mainly composed of alluvial, lacustrine and palustrine deposits of Middle Eocene to Late Miocene age. During the Early Miocene, the study area was situated between two high chains of mountains, the Pyrenees and the Iberian Chain. Between these two ranges, an alluvial system was developed; the fossiliferous beds of the Bardenas area correspond to the distal alluvial facies.

The deposits of Lower Miocene age (Ramblian–Aragonian, i.e., Aquitanian–Burdigalian in age) which outcrop in the Bardenas Reales belong to the Tudela Formation. They consist of clays, sandstones, marls and limestones, with some intercalations of gypsum (Fig. 2). Most of the vertebrate fossils have been found in blue to grey marls. The clays are brown, reddish to orange-coloured. The limestones show mudcracks and, in some cases, abundant bioturbation. These evidences suggest that the bulk of water was shallow and sporadic. In other words, the sedimentary environment was probably a wetland (see below).

The micromammal association found in the Bardenas Reales sites indicates that the fossiliferous levels belong to the Biozones Z-A of the Ramblian (sensu Daams and Freudenthal, 1990; see Astibia et al., 1995; Murelaga, 2000). They are approximately equivalent to the Biozones MN2b-3 of the European Neogene (Mein, 1990), i.e., to the Late Aquitanian and Early Burdigalian (Agenian–Orleanian in "Europan Land Mammal Mega-Zones"; see Steininger, 1999).

Nineteen vertebrate localities are known in the Bardenas Reales of Navarre (Fig. 1): Barranco del Congosto (BCo),

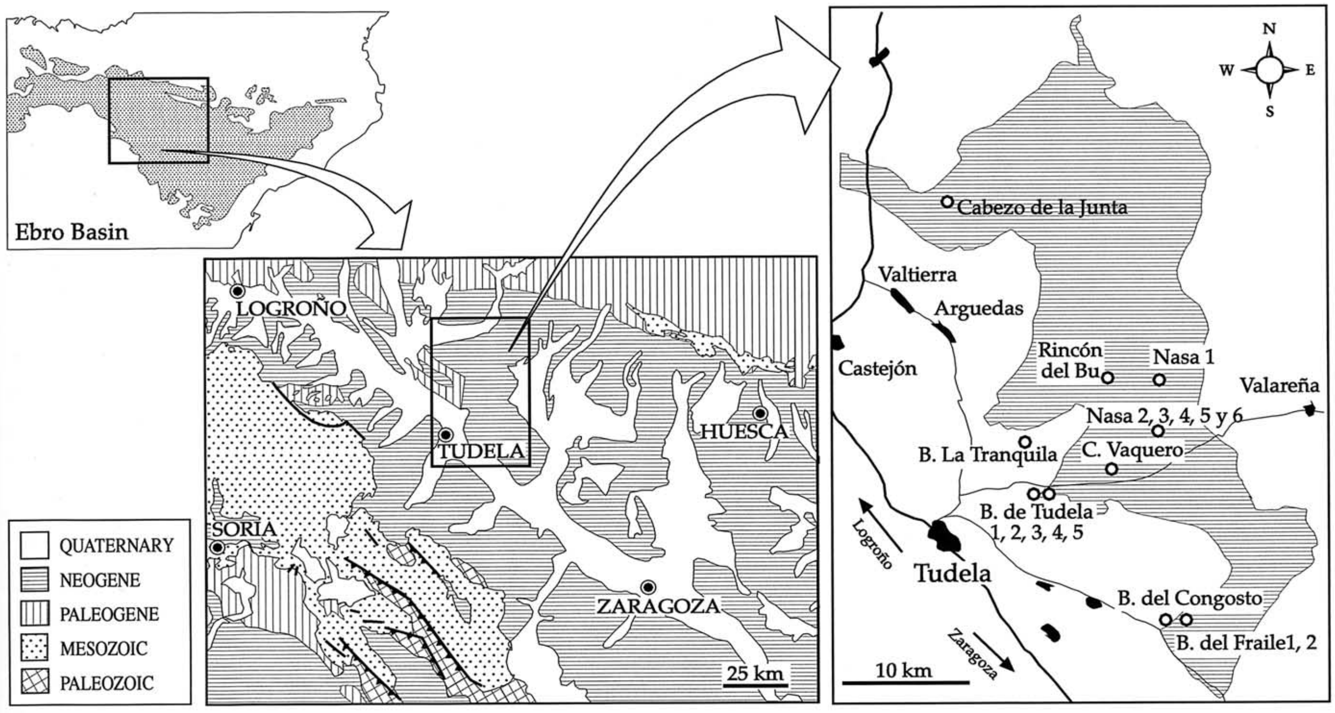

Fig. 1. Location map of the studied area: regional geologic context and geographical position of the Lower Miocene sites of the Bardenas Reales of Navarre (modified from Azanza, 1986).

Fig. 1. Carte de la région étudiée: contexte géologique régional et situation géographique des gisements du Miocène inférieur des Bardenas Reales de Navarre (d'après Azanza, 1986; modifié).

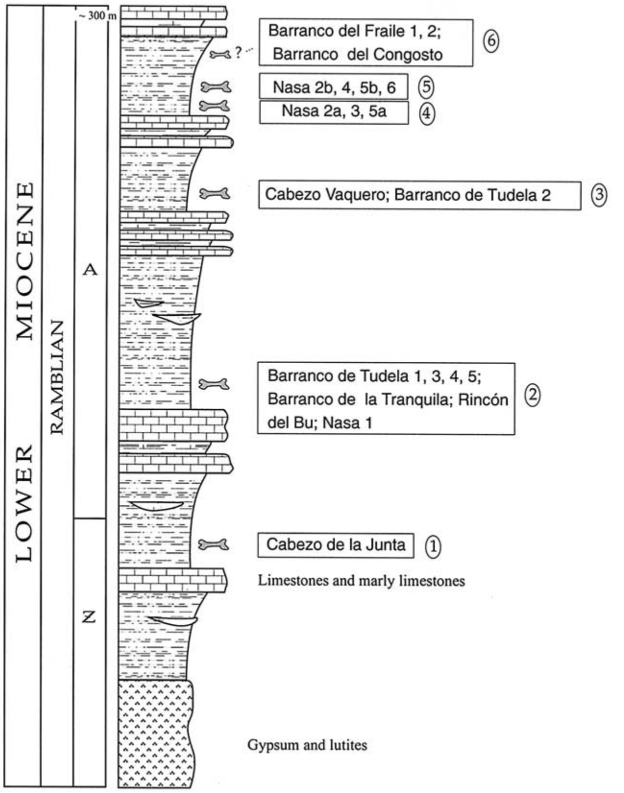
~300 m
LOWER MIOCENE
RAMBLIAN
A
Z
Barranco del Fraile 1, 2; Barranco del Congosto ⑥
?
Nasa 2b, 4, 5b, 6 ⑤
Nasa 2a, 3, 5a ④
Cabezo Vaquero; Barranco de Tudela 2 ③
Barranco de Tudela 1, 3, 4, 5; Barranco de la Tranquila; Rincón del Bu; Nasa 1 ②
Cabezo de la Junta ①
Limestones and marly limestones
Gypsum and lutites

Fig. 2. Stratigraphical column and position of the sites of the Bardenas Reales of Navarre, NW Ebro Basin. Numbers correspond to chronostratigraphic units as defined in the text.

Fig. 2. Coupe stratigraphique et position des gisements des Bardenas Reales de Navarre, nord-ouest du bassin de l'Ebre. Les numéros correspondent aux unités stratigraphiques telles qu'elles sont définies dans le texte.

Barranco del Fraile 1 (BF1) and 2 (BF2), Barranco de Tudela 1 (BT1), 2 (BT2), 3 (BT3), 4 (BT4) and 5 (BT5), Barranco de la Tranquila (BTr), Cabezo de la Junta (CJ), Cabezo Vaquero (CV), La Nasa 2 (N2a, N2b), 3 (N3), 4 (N4) and 5 (N5a, N5b), Rincón del Bu (RB) and Tripazul, also called La Nasa 1 (N1). All the localities have yielded reptile remains; amphibian bones are known in three sites (see Table 1). In addition to vertebrate remains, charophytes and invertebrates (mainly gastropods) are known.

Based on stratigraphic correlations using marker-horizons such as limestone bars of great lateral continuity, we have distinguished six chronostratigraphic units (Fig. 2), i.e., from the bottom to the top (localities are in brackets): unit 1 (CJ), unit 2 (BT1, 3, 4, 5, BTr, N1, RB), unit 3 (CV, BT2), unit 4 (N2a, N3, N5a), unit 5 (N2b, N4, N5b, N6) and unit 6 (BF1, BF2, BCo). It should be noted that the sites are very close from each other and that the tectonic activity in the area was minimal, so that the levels are subhorizontal.

Cabezo de la Junta (CJ) is the most northern outcrop and corresponds to the Biozone Z (Fig. 2). The other outcrops belong to the Biozone A, as suggested by the absence of cricetid rodents ("cricetid-vacuum"; Daams and Freudenthal, 1990) (see Astibia et al., 1995; Murelaga, 2000).

The fossils belong to the palaeontological collections of the Government of Navarre; they are provisionally housed in the Laboratory of Palaeontology of the Universidad del País Vasco/EHU (Bilbao).

3. Systematics

Amphibia LINNAEUS, 1758

Remains of amphibians are rare; they were recovered from only three localities: Barranco de la Tranquila, Barranco del Fraile 1, and Rincón del Bu. Anurans are present in the three localities but salamanders are lacking at Rincón del Bu. The preservation of the specimens does not permit identification of the anurans (even at family level) although two forms may be distinguished.

Caudata Scopoli, 1777

Salamandridae Goldfuss, 1820

Indeterminate salamandrid

Material: Barranco de la Tranquila: 1 atlas (BTr-55), 1 trunk vertebra (BTr-56); Barranco del Fraile 1: 1 trunk vertebra (BF1-159) (Fig. 3(1)).

Description: only the centra of trunk vertebrae are preserved. They are elongate, approximately rectangular, and opisthocoelous. The condyle is clearly distinct from the centrum. These features are characteristic of the Salamandridae. The atlas is small and bears an interglenoid process that clearly projects anteriorly although it is incomplete (Fig. 3(1)). Apparently, because of its elongate interglenoid process, this atlas more resembles Triturinae than Salamandrinae. However, referral to Triturinae cannot be secured.

Anura Rafinesque, 1815

Indeterminate anuran A

Material: Barranco de la Tranquila: 1 humerus (BTr-57), 1 sacral vertebra (BTr-58), 3 ilia (BTr-59, 60, 61); Barranco del Fraile 1: 1 ilium (BF1-160), 1 urostyle (BF1-161) (Fig. 3(2)).

Description. The humerus is not complete. Its condylar ball is slightly shifted laterally and the cubital fossa is poorly marked, which might be reminiscent of the Discoglossidae (Hossini, 1992). The ilia are mainly characterized by the presence of a deep and broad supraacetabular fossa. The shaft bears a relatively high iliac crest. The *tuber superius* is high and anteroposteriorly long, but it does not markedly project dorsally above the iliac crest. Unfortunately, the four ilia are incomplete and it is not possible to determine whether the iliac crest was high through the whole length of the shaft. However, the ilium from Barranco del Fraile 1 (the best preserved specimen) suggests that the height of the crest decreased anteriorly (Fig. 3(2)). The observable features of the ilia do not permit assignment at family level, but they are consistent with the Discoglossidae, Ranidae, and Leptodactylidae. Unfortunately, the *pars descendens* and the posterodorsal part of the *pars ascendens* are not preserved; consequently, referral to one of these families cannot be determined. The sacral vertebra has one

Table 1
Faunal list of amphibians and reptiles from the Lower Miocene sites of the Bardenas Reales of Navarre
Liste faunique des amphibiens et reptiles des gisements du Miocène inférieur de Bardenas Reales de Navarre

TAXA	Biozones	Z	A																	
	Chronostratigraphic Units	1	2						3		4			5				6		
	SITES	CJ	N1	RB	BT1	BT3	BT5	BTr	CV	BT2	N3	N2a	N5a	N2b	N4	N5b	N6	BF1	BF2	BCo
AMPHIBIANS	Salamandridae indet.							●										●		
	anuran A							●										●		
	anuran indet.			●				●												
TURTLES	*Chelydropsis apellanizi*																	●		
	Chelydropsis cf. *apellanizi*			●	●	●	●	●	●	●	●	●	●	●		●	●		●	●
	Trionychinae indet.		●	●		●				●	●	●		●	●		●	●	●	
	Ptychogaster ronheimensis												●							
	Ptychogaster (Temnoclemmys) bardenensis		●	●	●	●				●	●	●		●				●		
	Ptychogaster sp.	●	●	●	●	●		●	●	●	●	●	●	●		●	●	●		●
SQUAMATES	lacertilian indet. (non anguid)			●		●														
	Ophisaurus sp.		●	●		●												●		
	amphisbaenian indet.		●						●											
	?*Eryx* sp.		●	●		●		●	●				●	●				●		
	?Colubridae indet.			●										●				●		
CROCODILIANS	*Diplocynodon* sp.	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●

anterior and two posterior condyles, a morphology known in the Discoglossidae and Ranidae. The anterior part of the urostyle does not bear the lateral processes that are characteristic of the Discoglossidae.

Indeterminate anurans

Material: Rincón del Bu: 1 ilium (RB1-187); Barranco de la Tranquila: 1 sacral vertebra (BTr-62), 1 humerus (BTr-63) (Fig. 3(3)).

Description: the ilium is small; it lacks an iliac crest but bears a strong *tuber superius* (Fig. 3(3)). Among recent families from Europe, this morphology is consistent only with the Bufonidae and Hylidae (Rage, 1974; Bailón, 1999). However, the high *pars ascendens* clearly differs from that of these two families. The sacral vertebra appears to be procoelous; therefore, it cannot be referred to the anuran referred to as "anuran A". It bears two posterior condyles. The humerus probably represents a juvenile individual; it cannot be identified.

The proper association of these bones cannot be determined. The humerus affords no information. The ilium and the sacral vertebra may belong either to the same taxon or to two distinct taxa.

Conclusions on amphibians: this small fauna of amphibians includes one salamander (indeterminate Salamandridae) and two or three anurans that cannot be identified at family level. These amphibians only indicate that the environment was not dry.

Chelonii Brongniart (Latreille) 1800
Cryptodira Cope, 1868
Chelydridae Gray, 1831
Chelydropsis Peters, 1868
Chelydropsis apellanizi Murelaga et al., 1999

Material: Barranco del Fraile 1: 21 specimens (BF1). Specimens figured in Murelaga et al. 1999: holotype, BF-58, left hyoplastron; paratypes: BF-131, left epiplastron, posterior part; BF-64, right hypoplastron; BF-113, right xiphiplastron; BF-20, right peripheral 9; BF-19, left peripheral 10; BF-21, pygal; BF-23, neural 1, BF-74, odd neural. Other localities with *Chelydropsis* presence (51 specimens): Bco; BF2; BT1, BT2, BT3, BT5; BTr; CV; N1; N2a, N2b, N3, N5a, N5b, N6; RB. The material does not indicate the presence of several species of the family; therefore, all the specifically undefined material is attributed to *Chelydropsis* cf. *apellanizi* (Figs. 4 and 5).

Description: the carapace is reconstructed from isolated elements. *C. apellanizi* has a typical chelydrid flattened carapace with a cruciform flat plastron, a ligamentous carapace–plastron link and a decoration of short vascular sulci frequently dichotomic or anastomosed and delimitating small polygons. It is rounded, ca 28 cm long and 25 cm wide. There is a weak medial keel. The vertebral 1 covers all the nuchal laterally and a part of the pleurals 1 up to the posteromedial border of the peripheral 1. The nuchal processes reach the peripherals 2 or 3, depending on specimens. The costomarginal sulcus is at mid-length between the external border of the peripherals 1–4 and the pleuro-peripheral suture and, posteriorly, the costomarginal sulcus is closer to the pleuro-peripheral suture. The border of the peripherals is curved upwards between the first, second or third peripherals and the seventh; posteriorly, it is flattened.

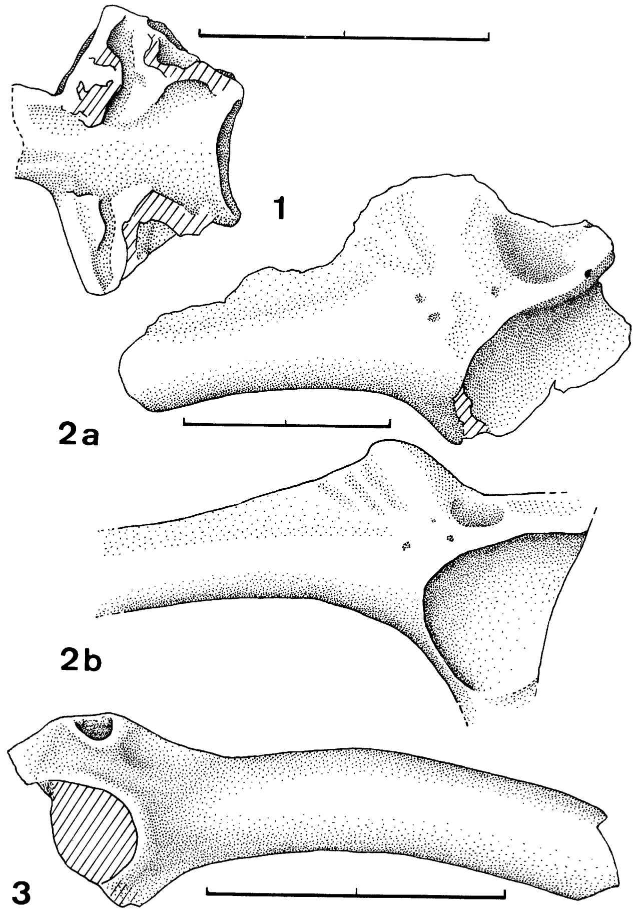

Fig. 3. Amphibians, Early Miocene, Bardenas Reales of Navarre; 1, Salamandridae indeterminate, fragmentary atlas (BTr-55), dorsal view; 2, Anura indeterminate A, left ilium (BF1-160) (2a, lateral view; 2b, tentative reconstruction in lateral view); 3, Anura indeterminate, right ilium, lateral view (RB1-187). Scale bars represent 2 mm.

Fig. 3. Amphibiens, Miocène inférieur, Bardenas Reales de Navarre; 1, Salamandridae indéterminé, atlas incomplet (BTr-55), vue dorsale; 2, Anoure indéterminé A, ilion gauche (BF1-160) (2a, vue latérale; 2b, reconstitution hypothétique en vue latérale); 3, Anoure indéterminé, ilion droit, vue latérale (RB1-187). Echelles = 2 mm.

The peripherals 10 and 11 are dentated as the pygal. The vertebral 5 does not reach the pygal. The pygal notch is narrow (its width is ca 1/3 the pygal width). The cruciform plastron has no medial fontanelles and the bridge is relatively long. The digitations of the processes of the plastron enter into the pits of the peripheral ventral border. The lateral borders of the epiplastra are rounded, converging anteriorly indicating that the gular border (not preserved) was not anteriorly widened; the anterior lobe is wider than the posterior one. The humeropectoral sulcus touches the posterior extremity of the rhomboid, relatively wide entoplastron. The pectoroabdominal sulcus is one and a half times longer than the femoroabdominal sulcus. The angle between the two sulci is ca 85–90. The anal covers the lateral extremity of the hypoplastron.

Comparison: the carapace of *C. apellanizi* has four preserved characters of the five essential apomorphic che-

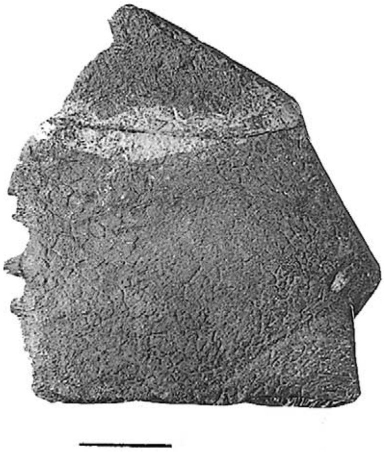

Fig. 4. *Chelydropsis apellanizi* Murelaga et al., 1999, Early Miocene, Bardenas Reales of Navarre; holotype, BF-58, left hyoplastron, ventral view. Scale bar represents 1 cm.

Fig. 4. *Chelydropsis apellanizi* Murelaga et al., 1999, Miocène inférieur, Bardenas Reales de Navarre; holotype, BF-58, hyoplastron gauche, vue ventrale. Echelle = 1 cm.

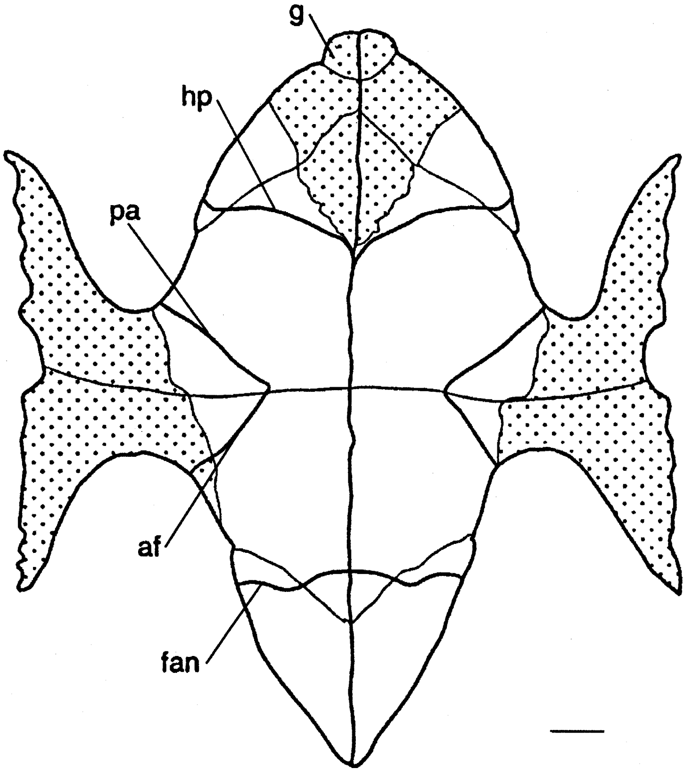

Fig. 5. *Chelydropsis apellanizi* Murelaga et al., 1999, Early Miocene, Bardenas Reales of Navarre; reconstructed plastron, ventral view, after: BF-131, left epiplastron; BF-58, holotype, left hyoplastron; BF-64, right hypoplastron; BF-113, right xiphiplastron. af, abdomino femoral sulcus; fan, femoro anal sulcus; g, gular; hp, humero pectoral sulcus; pa, pectoro-abdominal sulcus. Scale bar represents 1 cm.

Fig. 5. *Chelydropsis apellanizi* Murelaga et al., 1999, Miocène inférieur, Bardenas Reales de Navarre; reconstitution du plastron, vue ventrale, d'après: BF-131, épiplastron gauche; BF-58, holotype, hyoplastron gauche; BF-64, hypoplastron droit; BF-113 xiphiplastron droit. af, sillon abdomino-fémoral; fan, sillon fémoro-anal; g, gulaire; hp, sillon huméro-pectoral; pa, sillon pectoro-abdominal. Echelle = 1 cm.

lydrid characters (Lapparent de Broin, 2000): the posterior reduction in width of the posterior lobe with pointed xiphiplastra and widened inguinal notches; the medial union of the pectorals and femorals; the very long nuchal processes. As the anterior part of the epiplastra is missing, the last character, elongation of the epiplastral symphysis anterior to the gularo-humeral sulcus, is not verified. But the preserved parts show that the form was very close to *C. sanctihenrici* of the "*decheni-sanctihenrici*" group of *Chelydropsis* (see Broin, 1977; Murelaga et al., 1999). The form belongs to the latter group and differs from the "*murchisoni*" group by the narrow pygal notch, vertebral 5 not contacting the pygal, narrow anterior epiplastra, greater width of the entoplastron and hyoplastra, longer bridge, and peripherals not narrowed by presence of fontanelles. It differs from *C. decheni* in the narrower pygal notch which is approximately three times smaller than the total pygal width (29% of the pygal width; 28.6% in *C. sanctihenrici*, 45.8% in *C. decheni* and 62% in *C. sansaniensis* of the *murchisoni* group), margins of horned scutes of the pleural disk not accompanied by growth annuli (double or numerous costovertebral sulci in Broin, 1977) and the heavier construction of the plastron (central plastral body wider, more rounded lobes, posterior part of epiplastral branches shorter). It differs from *C. sanctihenrici* in having a pectoroabdominal sulcus only one and a half times longer than the femoroabdominal sulcus and the relative thickness of the plates: for epiplastra 4.4 cm medially long, the depth is 0.53 cm in *C. apellanizi* and 0.7–0.8 cm in *C. sanctihenrici*; while for a 9 cm medially long epiplastron, it is 0.5 cm in *C. sansaniensis*. Its age is consistent with that of the group (which ranges from the Bartonian to the Early Miocene), while the "*murchisoni*" group is Middle Miocene–Pliocene (Broin, 1977; Chkhikvadze, 1989; Mlynarski, 1980; Gaffney and Schleich, 1994; Lapparent de Broin, 2000) . The ratio of the humeropectoral and femoroabdominal sulcus is intermediate (1.5) between that of *C. sansaniensis* (1.2–1.3) of the *murchisoni* group and that of *C. sanctihenrici* (2.3). The angle between the two sulci is 85–90 in *C. apellanizi*, similar to that of *C. sanctihenrici* (85) and different from that of *C. sansaniensis* (100). A fossil intermediate between *C. apellanizi* and *C. sansaniensis* is the unnamed form from Artenay, France, end of the Lower Miocene, MN 4 (Broin, 1977), with an angle of 98–100 and a ratio of 1.1. This form is probably close to the type species *C. carinata* PETERS, 1868 (and see Peters, 1869), from the Middle Miocene of Eibiswald, Austria, basal MN5, as shown by the long peripherals, their massiveness and the absence of fontanelles.

C. cf. *apellanizi* is also reported from Miranda de Arga, a locality close to the Bardenas Reales of Navarre, same biozone Z of Ramblian as Cabezo de la Junta. *Chelydropsis* is a genus from Europe; *C. apellanizi* is the first find in Spain and the most occidental representative of the genus.

Discussion on the genus Chelydropsis: Chkhikvadze (1999) erected the genus *Chelydrasia*, type species *Chelydropsis minax* Chkhikvadze, 1971, from the Lower Oligocene of Zajsan basin, East Kazakhstan, in which he included *C. sanctihenrici*. He also suggested that all the species of the *decheni-sanctihenrici* group and the undefined Artenay form (MN4) must be assigned to this genus. Therefore, *C. apellanizi* should be also included in this genus. Chkhikvadze (1999) opposes the genus *Chelydrasia* to an unprecise "*Chelydropsis*", the type species of which is not mentioned. It seems that in his mind it represents the *murchisoni* group. Unfortunately, the type species of *Chelydropsis* is not *C. murchisoni* but *C. carinata*, from Eibiswald, the plastron of which is unknown; this species might be close to the species from Artenay, which has narrow gulars. Five differential characters of *Chelydrasia* occur on the plastron and are, therefore, not available for the definition of the genus *Chelydropsis* on the type specimen. The others are relevant to the size (smaller than in *C. murchisoni* but identical to that of *C. carinata* and to that given for *Chelydrasia*), the absence of lateral carenae (in fact, they are represented by simple elevations or are lacking in slender forms, and they are more marked only in the figured holotype of *C. sanctihenrici* in Europe and the character "absence" does not justify the attribution to a new genus). As already noted (Lapparent de Broin, 2000), if a new genus has to be erected in Europe, it should be erected for the reception of the *C. murchisoni* group, Upper Miocene–Pliocene, based on some characters such as the paedomorphic fontanelles remaining late in the adult, and, therefore, shorter and less massive peripheral plates, longer vertebral 5 and the much wider anterior border of the epiplastron (possibly also the less globular and slender skull). Other characters such as the elevation of the posterior part of the lower jaw, the widening of the pygal notch, the shortening of the bridge and plastral processes apparently derived progressively from the Oligocene *C. sanctihenrici* to Upper Miocene forms of *Chelydropsis*. In any case, since the plastron and lower jaw of *C. carinata* are unknown from Eibiswald, a generic difference is difficult to establish between this possible new genus and the *C. sanctihenrici* group including the Artenay undefined form. It is however possible that the genus *Chelydrasia* could be retained only for the species from Kazakhstan, *C. minax* (Oligocene) and *C. poena* Chkhikvadze, 1971 (Upper Miocene) and *C. kusnetzovi* Gajduchenko and Chkhikvadze, 1985 (Pliocene), that are distinguished from European chelydrids by the longer gular part of the epiplastral symphysis. As North American forms, these Asiatic species evolved by the lengthening of the gular part but they have wider gulars than in the North American forms. While the symphysis is always shorter (gular included) in European chelydrids, the *C. murchisoni* group alone evolved by the widening of the anterior epiplastra, which is stronger than in the "*Chelydra sia*" lineage. Due to its similarity with *C. sanctihenrici*, *C. apellanizi* is, therefore, considered a *Chelydropsis* species.

Testudinidae BATSCH, 1788

Testudininae BATSCH, 1788

Geoemydinei THEOBALD, 1868

Ptychogaster POMEL, 1847

Material: a great amount of specimens are indeterminate, representing either adults of the small *Ptychogaster* (*Temnoclemmys*) *bardenensis* or young and adults of the *large P. ronheimensis*. They are present in the localities Bco, BF1, BT1, BT2, BT3, BTr, CJ, CV, N1, N2a, N2b, N3, N5a, N5b, N6, RB and, when the species is indeterminated, they are referred to as *Ptychogaster* sp. in the lists of taxa. As *Chelydropsis*, *Ptychogaster* sp. is also present at Miranda de Arga, Navarre (Murelaga, 2000).

Ptychogaster ronheimensis GROESSENS-VAN DYCK and SCHLEICH, 1985

Material: La Nasa 5a, N5a, N5-28, partial dorsal carapace and plastron of one individual. Numerous isolated indeterminate fragments (Fig. 6(1–5)).

Description: the dorsal carapace is oval, slender, approximately 27 cm long and 21 cm wide once reconstructed. It belonged to a male individual (posterior concavity of the plastron and rather narrow form of the plastron). The decoration is apparently smooth but clearly microreticular and microvermiculate in enlarged view (×6.3) as in all the *Ptychogaster* spp. and many other turtles. A part of the sutures is obliterate.

The carapace has a median posterior keel. The nuchal is moderately long with regard to the shell (18–19%), wider than long and not much concave ventrally. The neural (n) series is irregular: n1 quadrangular, n2 octogonal, n3–n5 hexagonal, short sides behind, n6 quadrangular, n7 and n8 hexagonal, short sides in front. As in some specimens of *P. emydoides*, the cervical is relatively large, as wide as long posteriorly, with rounded lateral borders and a small posterior notch. The ventral border of the marginals and cervical is long below the nuchal. The vertebral (V) series is narrow with regard to costals. V1 is narrowed in lyre anteriorly, not covering the posterolateral corners of the nuchal, V2, V3 and V4 become slightly wider as one proceeds posteriorly; V5 (partly preserved) covers the pygal.

The two plastral lobes are similar in width, the anterior shorter than the posterior. The anterior border is anteriorly truncated, concave. The gular lip is wide, very slightly prominent, semi-circular gulars short, just covering the anterior part of the entoplastron; the epiplastral dorsal lip is wide, 3.2 times wider than long, moderately elongated with regard to the more primitive condition (see, for example, in the various *Palaeochelys* s.l. and *Mauremys*), its posterior border rather transversal: it is thickened at the gularo-humeral sulcus and concave medially. The entoplastron is rhomboid, anterior to the axillar notches and posteriorly crossed by the humeropectoral sulcus. The anterior lobe has lateral borders rather straight but widened at the epi-hyoplastral suture and the posterior has gently rounded borders with a short (8.5 times shorter than the xiphiplastra) and relatively narrow anal notch. The dorsal covering of the lateral borders of the plastron by the scutes is wide, especially anteriorly on each lobe. The posterior half of the plastron is mobile with a hinge between hyo-hypoplastra and peripherals 6–7—hypoplastral lateral borders and a pectoroabdominal sulcus medially close to the hyo-hypoplastral suture. The axillar and inguinal processes were probably reduced but their extremity is not preserved.

Comparison: the presence of the plastral hinge, as it is constructed, is the principal apomorphic character of the genus *Ptychogaster*. This largest form of *Ptychogaster* from the Bardenas is very similar to *P. ronheimensis* Groessens-Van Dyck and Schleich, 1985, from the Early Oligocene (MP 22) of Ronheim, Germany. It shares the relatively large size (moderate among the large *Ptychogaster*, much larger than in subgenus *Temnoclemmys* but smaller than in many derived *Ptychogaster* s.s.) and the relative dimensions of the epiplastral lip. The anterior border is more concave in the form from the Bardenas Reales and tends to be transversal or medially protruding at each epiplastron in the type material of *P. ronheimensis*, which may indicate a specific difference in the same lineage. The bone slenderness, the moderate state of reduction of the processes, the incompletely rounded lobes not well filling the openings of the shell and the non-elongated nuchal are also primitive characters shared by this form and the small form *P.* (*Temnoclemmys*) *bardenensis* described below; these characters show a more derived condition in s.g. *Ptychogaster*. The attribution of the material from the Bardenas Reales to the species *P. ronheimensis* (or at least to its lineage) represents the second report of the taxon, after that from the type locality, Ronheim (Germany). It is the first one from Spain.

Ptychogaster (*Temnoclemmys*) *bardenensis* Murelaga et al., 1999

Material: Barranco de Tudela 3, BT3: the hypodigme includes seven specimens. Other specimens (27) come from BF1, BT1, BT2; N1, N2b, N2a, N3, RB. Specimens figured in Murelaga et al. (1999): holotype, BT3-21, right epiplastron; paratype, BT3-90, nuchal; other specimens: RB1-8, right xiphiplastron; RB1 20, pygal RB1-37, suprapygal with the anterior border of the pygal; N1-63, entoplastron (Figs. 6(6–7) and 7).

Description: small carapace, reconstructed from several specimens, approximately 12 cm long and 9 cm wide. Microvermiculate and microreticulate decoration (Murelaga et al., 1999, Fig. 4i). The cervical is longer than wide, but narrower than in *P. ronheimensis*, with concave lateral borders. The vertebral 5 covers the pygal. The nuchal, wider than long, is not much ventrally concave. The presence of the hinge of the posterior mid-plastron of the genus *Ptychogaster* is indicated by the denticles for a cartilaginous union of the inguinal process and the peripheral 7. The anterior lobe was anteriorly truncated, its anterior border transversal, gular lip wide and slightly prominent. The gulars are semi-circular, short, and wide, just covering or not covering the pyriform entoplastron which is posteriorly crossed by the humeropectoral sulcus. The dorsal epiplastral lip is

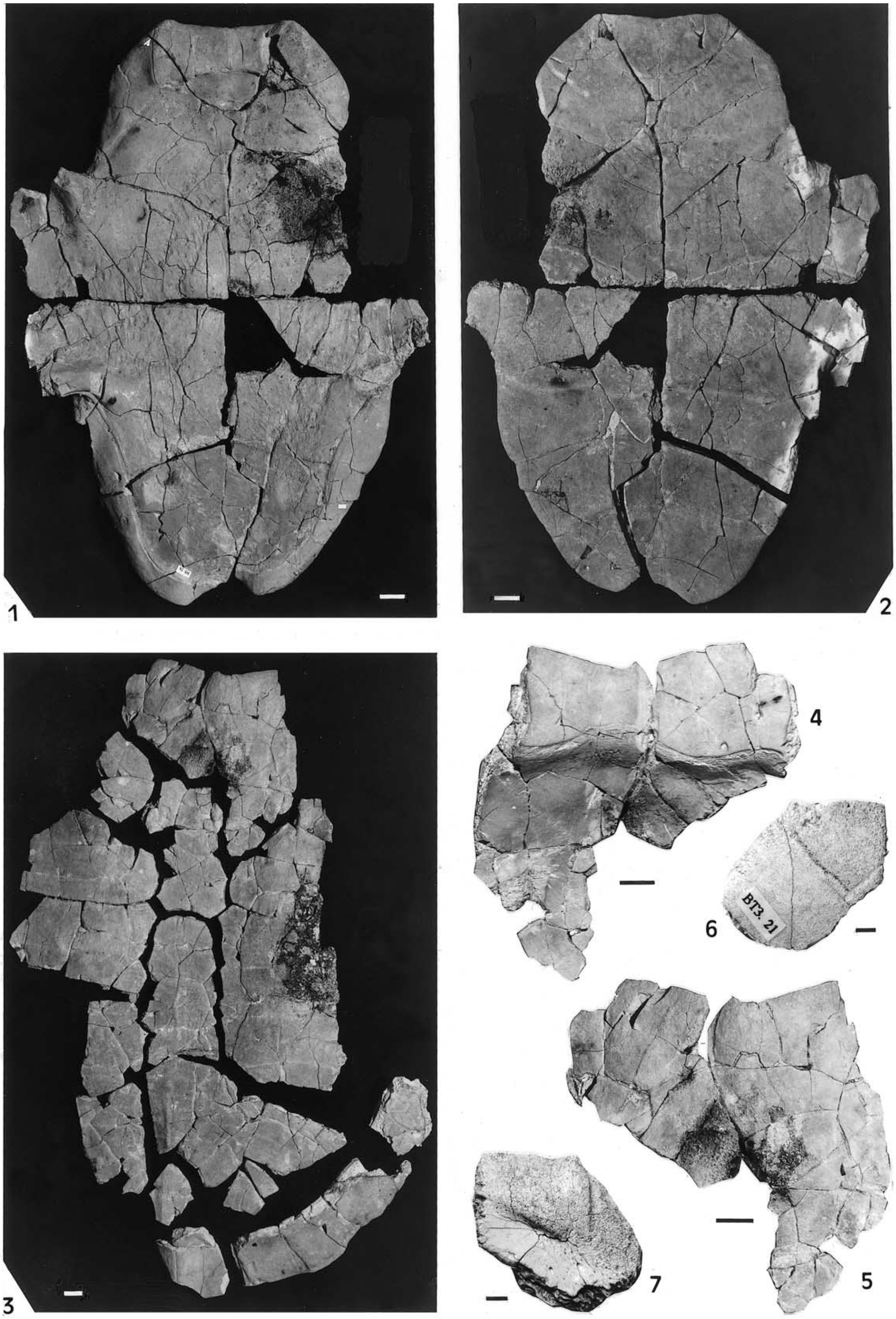

Fig. 6. *Ptychogaster ronheimensis* Groessens-Van Dyck and Schleich, 1985, Early Miocene, Bardenas Reales of Navarre; La Nasa 5a, N5-28, 1–2, plastron, dorsal and ventral views; 3, dorsal carapace, dorsal view; 4–5, nuchal, ventral and dorsal views. *Ptychogaster* (*Temnoclemmys*) *bardenensis* Murelaga et al., 1999, Early Miocene, Bardenas Reales of Navarre; 6,7, holotype, BT3-21, right epiplastron, ventral and dorsal views. Scale bars represent 1 cm.

Fig. 6. *Ptychogaster ronheimensis* Groessens-Van Dyck and Schleich, 1985, Miocène inférieur, Bardenas Reales de Navarre; La Nasa 5a, N5-28, 1–2, plastron, vues dorsale et ventrales; 3, carapace dorsale, vue dorsale; 4–5, nucale, vues ventrale et dorsale. *Ptychogaster* (*Temnoclemmys*) *bardenensis* Murelaga et al., 1999, Miocène inférieur, Bardenas Reales de Navarre, 6,7, holotype, BT3-21, épiplastron droit, vues ventrale et dorsale. Echelles = 1 cm.

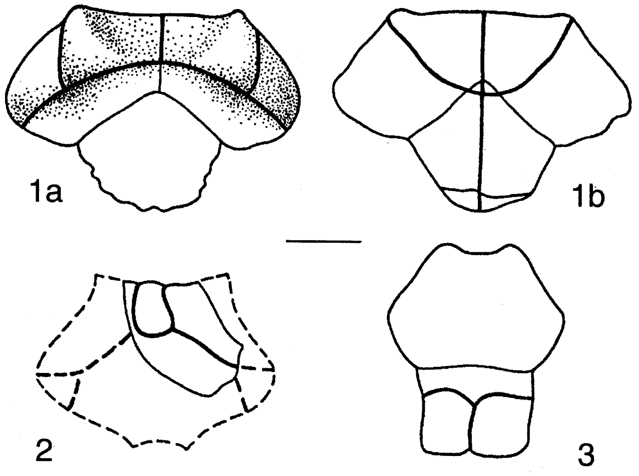

Fig. 7. *Ptychogaster* (*Temnoclemmys*) *bardenensis* Murelaga et al., 1999, Early Miocene, Bardenas Reales of Navarre; 1a,b, reconstructed anterior plastral part after the holotype, right epiplastron BT3-21, and the entoplastron NI-63, dorsal and ventral views; 2, reconstructed nuchal after the fragment BT3-90, dorsal view; 3, reconstructed pygal-suprapygal block after specimens RB1-20 and RB1-37, dorsal view. Scale bar represents 1 cm.

Fig. 7. *Ptychogaster* (*Temnoclemmys*) *bardenensis* Murelaga et al., 1999, Miocène inférieur, Bardenas Reales de Navarre; 1a,b, partie antérieure du lobe antérieur plastral reconstituée d'après l'holotype, épiplastron droit BT3-21, et l'entoplastron NI-63, vues dorsale et ventrale; 2, nucale reconstituée d'après le fragment BT3-90, vue dorsale; 3, bloc pygal-suprapygal reconstitué d'après les spécimens RB1-20 et RB1-37, vue dorsale. Échelle = 1 cm.

wider than long, medially concave, much thickened at the gularo-humeral sulcus, progressively shortening and growing thinner medially to become as shallow as the whole plate at the symphysis. The inguinal process is reduced because of the presence of the hinge, but the reduction is moderate. The precise shape of the neurals is unknown. The anal notch is wider than long, as a very obtuse U.

Comparison: the subgenus *Ptychogaster* (*Temnoclemmys*) (see figures in Bergounioux, 1958; Broin, 1977; Lapparent de Broin, 2001) is a paedomorphic form which is derived with respect to s.g. *Ptychogaster* (*Ptychogaster*) (see Lapparent de Broin, 2000) as shown by its reduced size in adults (specimens with well closed sutures, often obliterated), and its short anal notch with straight borders, more or less wide (compare with the immature specimen of *P. emydoides* described as *P. heteroclitus*, De Stefano, 1903). The dorsal thickening at the gularo-humeral boundary ends in a clear small point forming a sharp gular angle and produces, with the transversal epiplastral border, a clearly trapezoidal anterior lobe, although the lateral borders of the anterior lobe are rounded. The cervical is not widened. As in s.g. *Ptychogaster*, there is a tendency to the thickening of the dorsal epiplastral lip that fills the concavity. Three species are defined, among possible other ones in the subgenus. The present species *P.* (*T.*) *bardenensis* Murelaga et al., 1999, is characterized, within the subgenus, by its epiplastral dorsal lip regularly reduced in length from the gularo-humeral thickening up to the symphysis, as in primitive Geoemydinei but remaining longer than in the latter and as long as in primitive members of the *Ptychogaster* group. Its primitively laterally concave, not rounded, cervical is also peculiar but may be individually variable and/or reversed with regard to other *Ptychogaster* including *Temnoclemmys*. *P.* (*T*). *batalleri* (Bergounioux, 1931), type species of the subgenus, Upper Vallesian, MN 10, Terrassa, Spain, has an epiplastral dorsal lip less concave, thickened throughout its width (individually variable). The cervical is narrow as in *P.* (*T.*) *bardenensis*, but its borders are more rounded. *P.* (*T.*) *cayluxensis* Lydekker, 1889, Oligocene, phosphorites du Quercy, type locality unprecised close to Bach, and from Pech du Fraysse and Pech Desse (new collected material), MP 28, Lot, France, has an epiplastral dorsal lip variably thickened medially, filling the concavity but always with a thickened inversed triangle in the medial part of the anterior border (see Lydekker, 1889); the anterior lobe may be less trapezoidal due to the rounded gular angles.

Discussion on the genus Ptychogaster: *Ptychogaster* belongs to a group of primitively rather large forms (carapace length more than 25 cm) of Geoemydinei that arose during the Eocene in Europe. It is derived by a feature, the narrowing of the vertebral 1, often lyre shaped anteriorly, which does not cover the posterior corners of the nuchal. This derived character is also known in freshwater Testudinidae from the Palaeocene of China (Yeh, 1979) and in Europe from the Ypresian of France (Broin, 1977) and Lutetian of Germany (Schleich, 1994) in several forms; it might be homoplastic and shared or not shared by one of these forms and the *Ptychogaster* group. The primitive members of the *Ptychogaster* group have acquired a neural irregularity, principally with neurals short sided posteriorly, rounded borders of the plastral lobes, dorsal thickening at gular–humeral boundary of the moderately elongated epiplastral lip, and an anterior position of the humeropectoral sulcus crossing the entoplastron. Among them, *Geiselemys ptychogastroides* (Hummel, 1935) (the holotype of *Geoemyda saxonica* not included), from the Lutetian (MP 13-14) of the Geiseltal, Germany, might be considered as the sister group of *Ptychogaster*, but it is not well described and poorly figured, although some reconsiderations were made (Hummel, 1935; Khozatsky and Mlynarski, 1966; Zimmermann-Rollius, 1966). Among other characters, the anterior border of the plastron is clearly concave, medially protruding in the juvenile. *Ptychogaster* principally differs from the above-mentioned forms by the formation of a hinge at the mid-posterior plastron, between hyo- and hypoplastra and peripherals 6–7 and hypoplastra, which renders the posterior mid-plastron mobile in males as in females; the anterior border tends to be less concave and sinuous or transversal; the sutural closure appears early in adults; the lateral borders of the cervical are rounded; the vertebral 5 is always extended on the pygal.

According to a preliminary hypothesis, the basal clade in *Ptychogaster* would be *P. ronheimensis* GROESSENS–

VAN DYCK and SCHLEICH, 1985, from the Early Oligocene of Ronheim (Germany), a species to which the largest *Ptychogaster* form from the Bardenas is attributed (or at least to its lineage). As *Geiselemys ptychogastroides*, *P. ronheimensis* shares with this form the large size (carapace 27 cm long in the Bardenas form), reduced in *Temnoclemmys* (carapace approximately 12 cm long in the Bardenas form), and the wide and moderately long dorsal epiplastral lip which is narrowed and elongated in the s.g. *Ptychogaster*: *P. ronheimensis* has neither the specializations of s.g. *Temnoclemmys* nor those of s.g. *Ptychogaster*. In s.g. *Ptychogaster* as in s.g. *Temnoclemmys*, the anterior epiplastral border is always more transversal and often more protruding, as in some specimens of the type series of *P. ronheimensis*, the dorsal epiplastral lip tends to thicken (except in *P.* (*T.*) *bardenensis*, which may indicate a homoplasy between the two groups) although it remains concave, and the entoplastron becomes clearly pyriform.

On the basis of characters given above in the comparison, *Temnoclemmys* is a small derived paedomorphic form which could be the sister group of s.g. *Ptychogaster*.

In the s.g. *Ptychogaster*, the dorsal epiplastral lip becomes characteristically (apomorphy) much longer and much narrower; it has a tendency to protrude and also to thicken dorsally although it remains concave dorsally, as in *Temnoclemmys*. The bones are thicker, the size of the carapace increases. The carapace is narrower relative to the length (especially in males) and higher. The nuchal is more concave ventrally and is elongated in most forms (particularly in males). The neural series has more often quadrate and octogonal plates than hexagonal short sided behind ones, with the resulting alternate short and long medial borders of pleurals, although the formula is variable (Broin, 1977, Figs. 89–93). The anterior lobe borders are more rounded. The lobes are more extended, particularly the posterior lobe filling better the posterior cavity of the shell. The processes are more reduced, especially the inguinal accompanying the better mobility of the posterior plastron. Three groups of species are recognized among the material which has been revised up to now; however, many other species of the European *Ptychogaster* which have not been revised might reveal sound species of the subgenus, if they do not belong to *Temnoclemmys* (see Lapparent de Broin, 2000).

P. laurae (Förster and Becker, 1888), Rixheim, France (Upper Eocene, MP 19) also represented at Hoogbutsel, Belgium (Lower Oligocene, MP 21) (Broin, 1977) has a posterior lobe primitively relatively less widened and primitively much narrower at anals (material of Hoogbutsel) than in *P. emydoides*.

P. emydoides POMEL, 1847, type-species, Lower Miocene (MN2a), Saint-Gérand-le-Puy, France (see Lapparent de Broin, 2000) and *P. sansaniensis* (De Stefano, 1902), Middle Miocene (MN 6), Sansan, France, are closely related. *P. sansaniensis* (only three specimens known, unknown posterior lobe) is distinguished from *P. emydoides* by its younger geological age (less than about 5 Ma), its maximum known size inferior to the majority of that of specimens of *P. emydoides*, the V1 more anteriorly narrowed as in a specimen of *P. emydoides*, not from Saint-Gérand-le-Puy but from Gannat, Upper Oligocene, and by three characters united in only one specimen from Sansan (the single specimen known by the partial plastron) and known scattered only in three different specimens of *P. emydoides*, on 43 examined: its axillar notches less deep, the exceptionally long gulars and the entoplastron fully anterior to the axillar notches. The *P. emydoides* group includes specimens from the Switzerland Molasses (Golliez and Lugeon, 1889; Pictet and Humbert, 1856; Portis, 1882).

P. emydoides and *P. grepiacensis* have an anterior lobe clearly narrower than the posterior, which is derived, i.e., more enlarged and more rounded posteriorly than in *P. laurae*. *P. emydoides* has a moderate size (carapace 26–27 cm long), as *P. laurae*, with respect to the large *P. grepiacensis* (see Lapparent de Broin et al., 2000).

P. grepiacensis (Bergounioux, 1935), Lower Miocene, MN 2b, Ariège, France, is a group of very large forms (carapace 28–35.5 cm long), very thick, with a long anterior border of the shell and medial irregular protrusion of the gulars. According to the localities and age, the entoplatron is more posterior in the type material of *P. grepiacensis*, type locality of Ariège, with regard to specimens from Laugnac and Montgaillard, MN 2b (see Lapparent de Broin et al., 2000).

Owing to the numerous possibilities of homoplasy, only a complete cladistic study of the Geoemydinei will show which are exactly the relatives of *Ptychogaster* and at which nodes appeared the derived characters in the forms of the group. It will also allow to identify the oldest and the youngest members of the subgenera.

Ptychogaster is present at least from the Upper Eocene, MP 19 (Rixheim, Alsace, see Broin, 1977) and perhaps from the Bartonian, MP 16, of a new Paris Basin locality, Aisne (Léandrat, in preparation), up to the Middle Miocene of Sansan, MN 6, France. The oldest known defined species of *Temnoclemmys* is *T. cayluxensis* (Late Oligocene, MP 28 at least), although the subgenus is probably present in France with the small undefined form of *Ptychogaster* sp. from the Upper Eocene of Lostange (Broin, 1978), also MP 19, and also represented by small elements from French Bartonian localities, MP 16: Le Bretou, phosphorites du Quercy, (Broin in Rage, 1988), Méry-sur-Oise, Oise (Magnan, priv. coll.) and the above-mentioned new locality. The youngest recognized member of the subgenus *Temnoclemmys* is, up to now, the undefined species from Aubignas II, France, beginning of MN 12 (Azanza et al., 1993). The species *P.* (*T.*) *bardenensis* from the Bardenas is the oldest member of the s.g. *Temnoclemmys* from Spain and, with the form attributed to *P. ronheimensis*, both are the oldest known *Ptychogaster* from the Iberian Peninsula.

Trionychidae FITZINGER, 1826

Trionychinae FITZINGER, 1826

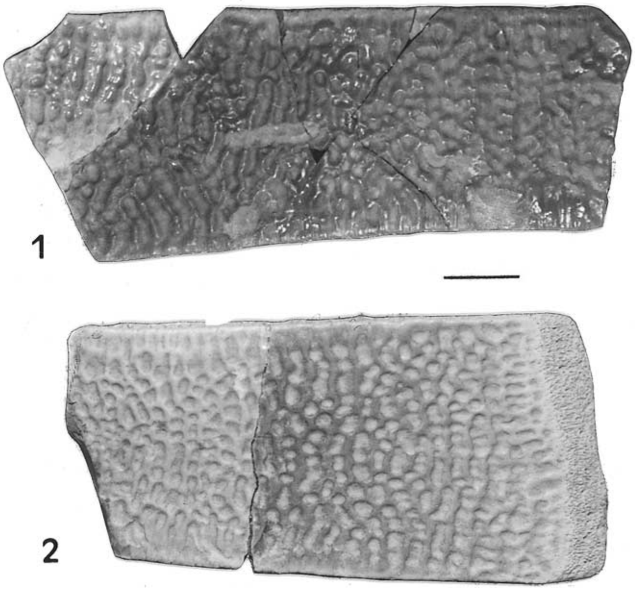

Fig. 8. Trionychinae indet., Early Miocene, Bardenas Reales of Navarre; 1, medial part of pleural; 2, distal part of pleural; dorsal views. Scale bar represents 1 cm.

Fig. 8. Trionychinae indet., Miocène inférieur, Bardenas Reales de Navarre; 1, partie médiale de pleurale; 2, partie distale de pleurale; vues dorsales. Échelle = 1 cm.

Trionychinae indet.

Material: twenty fragments of pleurals, plastron and indeterminate: BF1; BF2; BT2; BT3; N2; N2b; N3; N4; N6; RB (Fig. 8).

Description: the material indicates that the larger preserved specimens belonged to medium sized carapaces, 30 cm long and 26 cm wide. The decoration is made of rounded or elongated pits, rather large (2 × 2 or 3 mm) separated by blunt crests, narrower than the pits (ca 1 mm). The measurements of the pits and crests are only indicative and have no statistical value.

Discussion: the decoration is typical of the subfamily but no precise identification of the genus and species can be made on the basis of such isolated elements. A similar decoration is known in adult Trionychinae from other European localities such as Saint-Gérand-le-Puy (MN 2a) and in *Trionyx stiriacus* from Artenay (MN 4) (pits: ca 2 × 3.7; 1.9 × 3.5; 2.3 × 2.3 mm; crests: ca 1–1.3 mm). It differs from that of undefined species from other localities such as La Milloque, MP 29, including narrower pits (ca 1–1.3 × 2 to 3 mm) and relatively wider crests (ca 1–1.7 mm) and Avenay, Lower Eocene MP 8-9, with similar pits (1.1 × 2.5; 3.1 × 2.5 mm) separated by wider crests (1.3–1.6 mm) and *T. michauxi* from Grauves, Lower Eocene, MP 9, with very narrow pits (1.8 mm) and much wider rounded crests (4.12 mm) (Broin 1977). Although “*Trionyx*” was already mentioned in Navarre at Tudela (see above), the present fragments are the first figured specimens of Trionychinae of the area.

Conclusions on chelonians: the fauna includes four European species (three genera). *Chelydropsis apellanizi* is the first find of the genus in the Iberian Peninsula and the most occidental representative of the genus. *Ptychogaster* is represented by two subgenera: *P. ronheimensis*, a basal member of the group, first representative of this lineage out of the type locality in Germany, and *P.* (*Temnoclemmys*) *bardenensis*, a recently recognized lineage. The latter is the oldest member of the subgenus from Spain. Both *Ptychogaster* species are the oldest known ones of the genus from the Iberian Peninsula. The Trionychinae are known in Spain from the Early Oligocene (Bergounioux, 1958) and they were already mentioned in the Bardenas area. The European Trionychinae invaded Africa, where they are still present, by the Late Miocene–Early Pliocene. All chelonian taxa discussed here disappeared from Europe during the Pliocene.

Squamata OPPEL, 1811
Lacertilia OWEN, 1842
Anguidae GRAY, 1825
Anguinae GRAY, 1825
Ophisaurus DAUDIN, 1803 s.l.
Ophisaurus sp.

Material: Barranco del Fraile 1: 1 trunk vertebra (BF1-132), 3 caudal vertebrae (BF-133 to 135), 1 osteoscute (BF1-136); Barranco de Tudela 3: 1 caudal vertebra (BT3-187), 1 osteoscute (BT3-188); La Nasa 1: 5 trunk vertebrae (N1-273 to 277), 3 caudal vertebrae (N1-278 to 280); Rincón del Bu 1: 3 trunk vertebrae (RB1-82 to 84), 2 caudal vertebrae (RB1-85, 86) (Fig. 9(1)).

Three distinct lineages of limbless anguine lizards have long been lumped together as *Ophisaurus*. The latter genus is currently regarded as a paraphyletic assemblage; here this assemblage is referred to as *Ophisaurus* s.l. It probably represents the stem group of *Anguis*. At present, the three lineages are generally regarded as three distinct genera: *Ophisaurus* s.s. (the American species), *Dopasia* (European and Asian species) and *Pseudopus* (primarily European) (Augé, 1992; Gauthier, 1982; Klembara, 1981; Rocek, 1984; Sullivan, 1987; Sullivan and Holman, 1996). Unfortunately, these genera are distinguished on the basis of cranial bones, whereas only vertebrae and osteoscutes were recovered from the localities from the Spanish Miocene. These skeletal elements do not permit identification within *Ophisaurus* s.l.

Description: the trunk vertebrae are very characteristic of *Ophisaurus* s.l. They are markedly depressed, comparatively elongate, and the cotyle and condyle are flattened dorsoventrally. In ventral view, the centrum is triangular and narrow; its ventral face is weakly convex ventrally. On the posteriormost available vertebra, the ventral face appears to be nearly flat and even slightly depressed.

The caudal vertebrae are narrower, more elongate and less depressed than those from the trunk region (Fig. 9(1)). The subcentral ridges are almost parallel. The haemapophyses, that are fused to the centrum, occupy approximately the posterior part of the centrum. Between the prezygapophyses, the anterior part of the neural arch forms two concave surfaces that are posterioly limited by a crest.

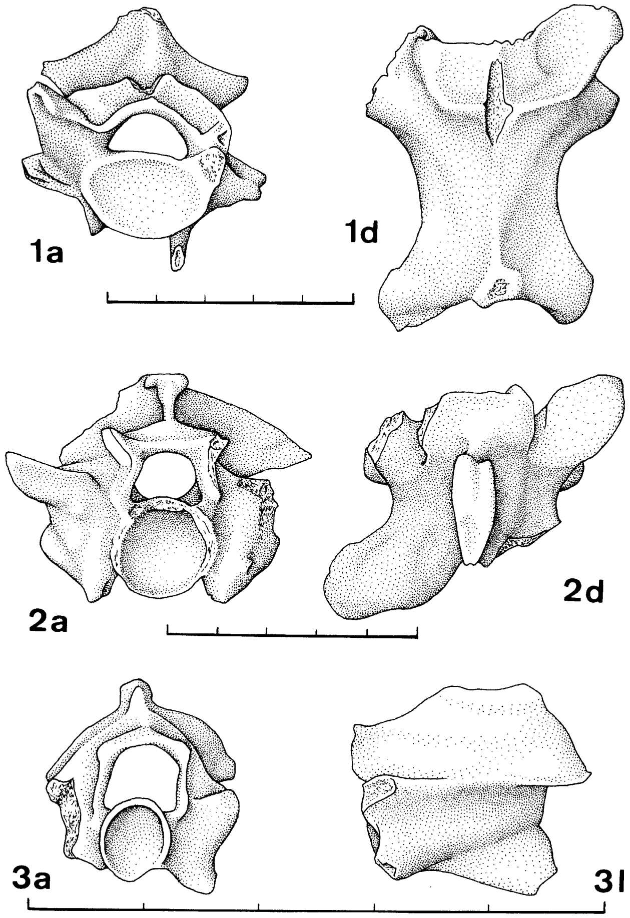

Fig. 9. Squamates, Early Miocene, Bardenas Reales of Navarre. 1, Anguidae, *Ophisaurus* sp., caudal vertebra (RB1-85); 2, ? *Eryx*, trunk vertebra (BF1-137); 3, Colubridae indeterminate, caudal vertebra (N2-122); **a**, anterior view; **d**, dorsal view; **l**, lateral view. Scale bars represent 5 mm.
Fig. 9. Squamates, Miocène inférieur, Bardenas Reales de Navarre. 1, Anguidae, *Ophisaurus* sp., vertèbre caudale (RB1-85); 2, ? *Eryx*, vertèbre dorsale (BF1-137); 3, Colubridae indéterminés, vertèbre caudale (N2-122); **a**: vue antérieure, **d**: vue dorsale, **l**: vue latérale. Echelles = 5 mm.

Two fragmentary osteoscutes show the morphology that is characteristic of the Anguinae: the external surface bears irregular shallow grooves and small tubercles on its posterior part, whereas its anterior part is not ornamented; the inner face is entirely smooth.

Discussion: no difference has been noticed between fossils from distinct localities of the Bardenas. This lizard is the largest one from these Miocene localities. Based on the size of most vertebrae, a length estimate of 40–50 cm may be inferred. However, a fragment of vertebra (neural arch) is large; the length of the individual from which this vertebra came was about 70–80 cm long. In Europe, *Ophisaurus* s.l. is frequent in localities from the whole Tertiary. Apparently, these lizards were ecologically tolerant. Today, only one species (*Pseudopus apodus*) survives in Europe, from the Balkan Peninsula to the Caspian Sea (Obst, 1997).

Indeterminate lacertilians

Small fragments of dentaries belong to undeterminable lizards. Only two of them, from Barranco de Tudela 3 and Rincón del Bu, provide information. They do not pertain to anguids and they perhaps represent two distinct taxa.

Amphisbaenia GRAY, 1844

Indeterminate amphisbaenians

Material: La Nasa 1: 1 trunk vertebra (N1-270), 2 fragments of vertebrae (N1-271, 272); Cabezo Vaquero: 3 trunk vertebrae (CV-87 to 89).

Description and discussion: the vertebral morphology of amphisbaenians is very characteristic, which permits unquestionable allocation to that group, even on the basis of fragmentary specimens. The centrum has a flattened ventral face, its lateral limits are parallel and often slightly concave, the neural spine is strongly reduced, and vertebrae lack a zygosphene–zygantrum system. However, identification within amphisbaenians is not possible on the basis of the available specimens. In Europe, amphisbaenians have a substantial Cenozoic record. These squamates are fossorial; today, only one species remains in Europe (*Blanus cinereus*, in the Iberian Peninsula).

Serpentes LINNAEUS, 1758

Boidae GRAY, 1825

? Erycinae BONAPARTE, 1831

? *Eryx* DAUDIN, 1803

Material: Barranco del Fraile 1: 19 trunk vertebrae (BF1-137 to 155); Barranco de Tudela 3: 3 trunk vertebrae (BT3-184 to 186); Cabezo Vaquero: 2 trunk vertebrae (CV-85, 86); La Nasa 1: 2 trunk vertebrae (N1-268, 269); La Nasa 2b: 1 trunk vertebra (N2-123); La Nasa 5a: 5 trunk vertebrae (N5-55 to 59); Rincón del Bu: 17 trunk vertebrae (RB1-165 to 181); Barranco de la Tranquila: ? two trunk vertebrae (BTr-53, 54) (Fig. 9(2)).

Description: several small trunk vertebrae display the typical morphology of Boidae: vertebrae short and wide, massively built, section of the neural canal small, prezygapophyseal processes reduced (Fig. 9(2)). Moreover, their neural arch is depressed, the neural spine is low, and the haemal keel is shallow. The latter three characters are consistent with the Erycinae.

Discussion: it is not possible to confidently refer a snake to the Erycinae on the basis of trunk vertebrae only. Only caudal vertebrae secure assignment to this subfamily (Szyndlar and Böhme, 1996). However, the morphology of the trunk vertebrae from the Miocene of Spain closely resembles that of the erycine boids *Eryx* and *Bransateryx*. *Eryx* is a living genus of the Old World (including southeastern Europe). The extinct European genus *Bransateryx* ranges from the Early (MP 22) to the Latest (MP 30) Oligocene, and perhaps the Early Miocene (Rage and Augé, 1993; Szyndlar, 1994; Müller, 1998). The antero-posterior length of the neural spine suggests that these fossils represent *Eryx* (it is shorter in *Bransateryx*), but this cannot be ascertained. Szyndlar and Schleich (1994) reported two species of *Eryx* from the Neogene of Spain: *E.* cf. *jaculus* from the Late Miocene (*E. jaculus* is one of the two living European species) and the extinct *E. primitivus* from the Pliocene. The vertebrae studied in the present paper differ from those of *E. jaculus* in being stockier and in having thicker neural spines. On the other hand, trunk vertebrae of *E. primitivus* are unknown; therefore, comparisons cannot be made at specific level.

Erycinae are small, fossorial to secretive, snakes living in loose, often sandy grounds. They are very frequent in European Cenozoic localities (Hoffstetter and Rage, 1972; Szyndlar, 1991). Today, only two species (*E. jaculus* and *E. miliaris*) remain in Europe, they occupy southeastern refuge areas from the Balkan Peninsula to the Caspian Sea.

Colubridae OPPEL, 1811

Material: Barranco del Fraile 1: ? 1 caudal vertebra (BF1-156); La Nasa 2b: 1 caudal vertebra (N2-122); Rincón del Bu 1: ? 1 caudal vertebra (RB1-164) (Fig. 9(3)).

Description and discussion: three vertebrae are markedly elongate and lightly built, which points to the Colubridae. But, surprisingly, whereas the Boidae from the localities are represented only by trunk vertebrae, only caudal vertebrae are referable to the Colubridae (Fig. 9(3)). Such vertebrae do not permit unquestionable referral within colubroids, even at family level. However, at least one of them (from Nasa 2) may be assigned to the Colubridae.

In Europe, the Colubridae first appear in the Early Oligocene (MP 22) and they have been the dominant constituents of snake faunas since the Miocene (Rage, 1987).

Conclusions on Squamates: the fauna includes one anguid lizard (*Ophisaurus* s.l. indeterminate), one, or perhaps two, indeterminate non-anguid lizards, an indeterminate amphisbaenian, one boid snake (? *Eryx*, Erycinae), and at least one indeterminate colubrid snake. This small fauna cannot provide stratigraphic and palaeoenvironmental information. However, it should be noticed that erycine snakes are fossorial, generally in sandy grounds. Today, in Europe, three of these taxa inhabit refuge areas in southernmost parts of the continent: *Ophisaurus* s.l. (i.e., *Pseudopus*) and erycine snakes are restricted to southeastern Europe (from the Balkan Peninsula to the Caspian Sea) whereas amphisbaenians live in the Iberian Peninsula.

Crocodylia GMELIN, 1788

Eusuchia HUXLEY, 1875

Alligatoroidea GRAY, 1844 (sensu Norell et al., 1994)

Incertae familiae

At the family level, *Diplocynodon* was placed either (Berg, 1966) in the Crocodylidae Alligatorinae, or (Rauhe and Rossman, 1995 in the Leidyosuchidae Rauhe and Rossman, 1995), or (Ginsburg and Bulot, 1997) in the Crocodylidae Crocodylinae. It is incertae familiae (de facto) in Buscalioni et al. (1992). Brochu (1999) established the paraphyly of the Leidyosuchidae and placed his new clade Diplocynodontinae BROCHU, 1999, within the Alligatoroidea GRAY, 1844, as a stem-based group basal to some fossil genera and to Alligatoridae. Being established at a subfamilial level, out of the rules of the ICZN (International Code of Zoological Nomenclature) and partly following De Queiroz and Gauthier (1994), the family level is not given. To agree with the ICZN, the nomenclatural rank of each of the involved taxa should be discussed. Anyway, further study is necessary to define the family that includes *Diplocynodon*; such a work should include all European fossils.

Diplocynodon Pomel, 1847

Diplocynodon sp.

Material: about 200 specimens coming from all localities of the Bardenas (see Table 1), including skull and lower jaw remains, isolated teeth, and postcranial bones (cervical, dorsal and caudal vertebrae, hindlimb bones, and osteoscutes) (Fig. 10).

Description: most of the remains are disarticulated and have been collected as isolated bones and teeth. A number of individuals, including immature and adult specimens, are known. A large surangular (Fig. 10(5)) corresponds to an individual with a lower jaw, the estimated length of which is over 40 cm and the total length of the animal was approximately 3 m. Small dentaries and teeth probably come from immature individuals less than 1 m long. The low amount of variation observed in the assemblage suggests that all the remains belong to a single species (Pereda Suberbiola et al., 2001).

The specimen BF2-2 consists of skull and lower jaw remains, teeth, the axial odontoid process, and osteoscutes from a single adult individual. This material was recovered on the surface, so that the bones are damaged by weathering. Among the skull remains, the frontal, quadrate, quadratojugal, pterygoid and maxilla remains have been recognized. Additional fragments from the orbital and postorbital regions could be also represented. The frontal participates posterolaterally to the border of the supratemporal fossa and it prevents broad contact between the postorbital and parietal (Fig. 10(1)). The frontoparietal suture is almost linear. The *foramen aerum* is located on the dorsal surface of the posterior ramus of the quadrate (Fig. 10(2)). The lateral hemicondyle of the quadrate is larger than the medial one. Posteriorly, the suture between the quadrate and quadratojugal is straight. The quadratojugal does not participate to the mandibular joint. The lower jaw is represented by angular, articular and, probably, dentary fragments. The surface of the retroarticular process is smooth. The only known vertebral element is a free odontoid process. The dermal osteoscutes are very fragmentary.

Apart from the above-described elements, the Bardenas has yielded additional isolated skull and mandibular remains. Skull bones include fragments of maxilla, frontal, postorbital, squamosal, jugal and exoccipital. The lower jaw has been partially reconstructed from dentary, angular, surangular and articular remains. The alveoli for dentary teeth 3 and 4 are nearly of same size and confluent (Fig. 10(3)). The mandibular symphysis is very short and does not extend beyond the third alveolus. The splenial is excluded from the symphysis. The imprint of the splenial on each side of the Meckelian groove indicates that the ventral tip of the splenial projected more anteriorly, near the

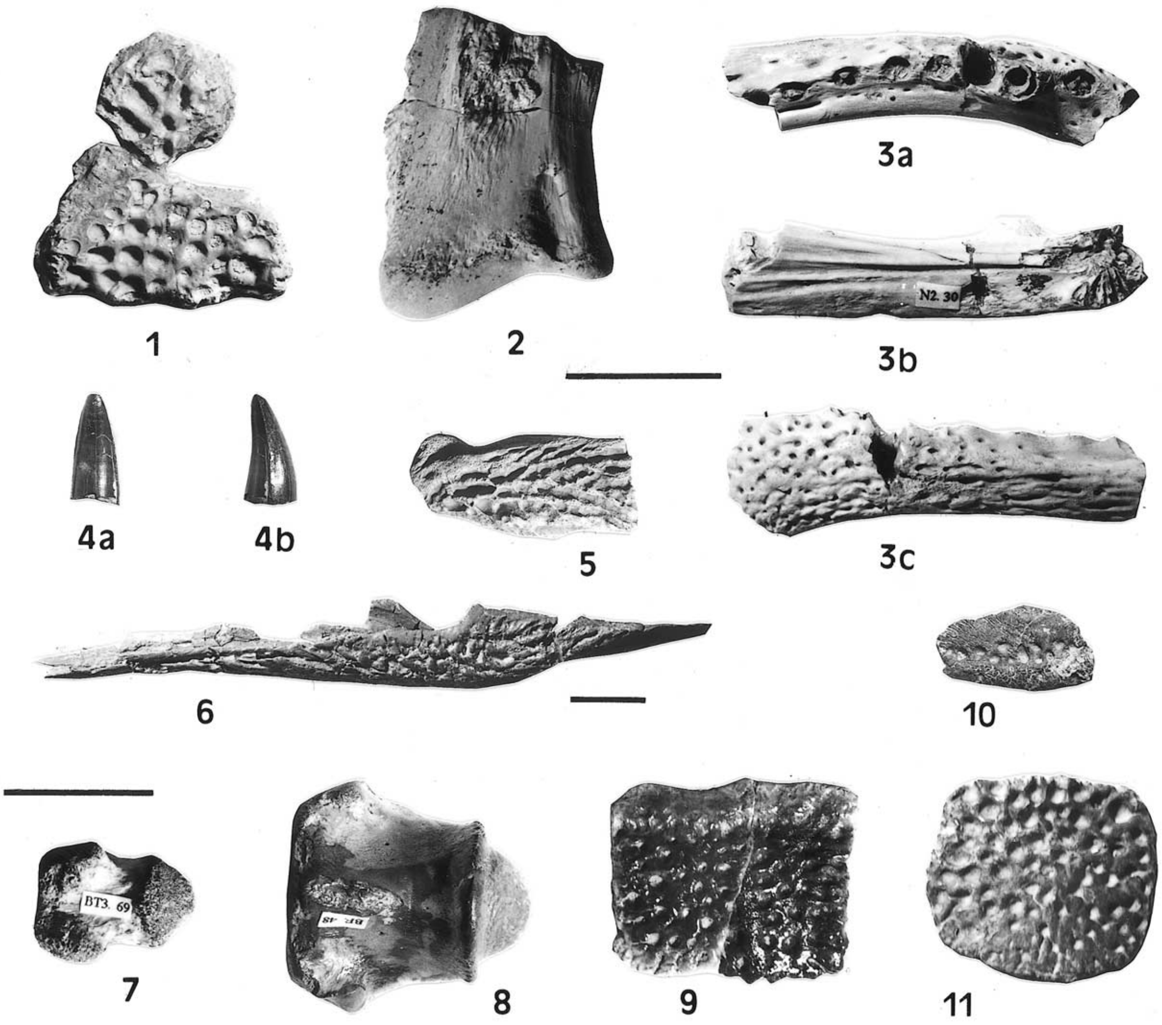

Fig. 10. *Diplocynodon* sp., Early Miocene, Bardenas Reales of Navarre. Skull, lower jaw and postcranial remains. 1, BF2-2, frontal, dorsal view; 2, BF2-2, left quadrate, dorsal view; 3, N2-30, left dentary, **a**, dorsal view, **b**, medial view and **c**, lateral view; 4, BF-47, tooth, **a**, lingual view, **b**, anterior or posterior view; 5, BT-183, right surangular, lateral view; 6, N5-26, left angular, lateral view; 7, BT3-69, first postaxial vertebra, ventral view; 8, BF-48, centrum from the cervical-dorsal transition, ventral view; 9, dorsal osteoscute; 10, CV-21, ventral osteoscute (anterior part of the paired ossification); 11, BF-45, ventral osteoscute (posterior ossification). Scales: 2 cm. All photographs at natural size except 5–6 (half size).

Fig. 10. *Diplocynodon* sp., Miocène inférieur, Bardenas Reales de Navarre. Restes du crâne, de la mandibule et du squelette post-crânien. 1, BF2-2, frontal, vue dorsale; 2, BF2-2, carré gauche, vue dorsale; 3, N2-30, dentaire gauche, **a**, vue dorsale, **b,** vue médiale, **c**, vue latérale; 4, BF-47, dent, **a**, vue linguale, **b**, vue antérieure ou postérieure; 5, BT-183, surangulaire droit, vue latérale; 6, N5-26, angulaire gauche, vue latérale; 7, BT3-69, première vertèbre post-axiale, vue ventrale; 8, BF-48, centrum de vertèbre de la transition cervicales-dorsales, vue ventrale; 9, ostéoderme dorsal, vue dorsale; 10, CV-21, ostéoderme ventral (partie antérieure de la double ossification), vue dorsale; 11, BF-45, ostéoderme ventral (ossification postérieure), vue dorsale. Echelles = 2 cm: toutes les vues grandeur nature sauf 5 et 6, ×(1/2).

symphysis, than the dorsal tip. In lateral view, the dentary is gently concave between alveoli 4 and 10. The angular–surangular suture contacts the external mandibular fenestra at posterior angle. The ascending process of the angular does not exceed in height the external mandibular fenestra (Fig. 10(6)). The latter looks relatively small, with a high lower border. The lateral surface of the angular and surangular is highly ornamented. The foramen intermandibularis is small. The teeth are conical, oval to subcircular in cross section. The crowns are ornamented with thin longitudinal ridges, which become slightly anastomosed toward the apical region. The medial and distal carinae are smooth (Fig.10(4)).

The vertebral column is represented by cervical, dorsal and caudal vertebrae from several individuals. All the centra are procoelous. With the exception of an anterior centrum, regarded here as the first postaxial (Fig. 10(7)), the cervical vertebrae bear prominent hypapophyses (Fig. 10(8)). Hypapophyses are also present on the ventral surface of the anterior dorsals. Small dorsal vertebrae show a neurocentral suture. The caudal vertebrae have relatively long centra and bear transverse processes.

The limb bones consist of femora and tibiae. They are similar in form and robustness to those of typical eusuchians. The femoral shaft has a moderately prominent fourth trochanter. The tibia is slightly curved.

Many osteoscutes are known but most of them are fragmentary. The dorsal osteoscutes are rectangular and bear a longitudinal keel (Fig. 10(9)). The anterior margin of dorsal osteoscutes is smooth. The ventral armour consists of paired ossifications that suture together. The anterior ossification is narrow and has a smooth area (Fig. 10(10)), while the posterior ossification is fully ornamented (Fig. 10(11)).

Discussion: the presence of procoelous vertebrae is a synapomorphy of the Eusuchia, although it is paralleled in other crocodilians (Benton and Clark, 1988; Michard et al., 1990; Clark, 1994). Prominent hypapophyses on cervical centra occur in eusuchians (poorly developed in *Gavialis*), *Bernissartia* (poorly developed) and dyrosaurids (Norell and Clark, 1990). The *foramen aerum* on the dorsal surface of the quadrate is a derived character of the Alligatoroidea (Brochu, 1999). The Bardenas crocodilian shares with the Diplocynodontinae BROCHU, 1999, a clade composed of *Diplocynodon* and *Baryphracta* Frey et al., 1987, the occurrence of paired ossifications on the ventral armour. Moreover, it shares with the known species of *Diplocynodon* from the Cenozoic of Europe the occurrence of confluent third and fourth dentary alveoli and the absence of the splenial from the symphysis (Buscalioni et al. 1992). The Bardenas dentaries differ from those of species of *Diplocynodon* in having a shorter mandibular symphysis, which does not extend beyond the third alveolus. In *Diplocynodon*, the symphysis length is variable according to the species and extends from the third to fifth alveoli. The symphysis length seems to be related to size in *Alligator mississipiensis* (see Brochu, 2000), but this is not the rule in *Diplocynodon* and closely allied forms as well as in examined Crocodylidae. Pending a full revision of the European material, the Bardenas crocodilian is referred to as *Diplocynodon* sp. (Pereda Suberbiola et al., 2001).

Conclusion on the crocodilian: the European *Diplocynodon* group is known from the Palaeocene to the Late Miocene. It was already known from the Eocene of the Iberian Peninsula. Its presence at the Bardenas adds a new element for Miocene times.

4. Conclusion—Palaeoecological implications

The lithological features and sedimentary structures observed in the Bardenas sites suggest that the vertebrate remains were deposited in the distal areas of an alluvial system. The presence of mudcracks and bioturbation traces in limestones suggests a shallow, not permanent water environment. This is indicative of a wetland. Wetlands may contain enough water during an interval of time to develop abundant biological activity (Hernández, 2000). This environment was the result of water drift from the adjacent mountains, which was conveyed by small streams up to the central plains of the basin. However, in all the Bardenas sites but Cabezo de la Junta, the small-grained deposits such as marls and clays are dominant, which indicates a rather low energy level. But the abundance of charophyte fructifications and the absence of stems suggest that the streams reached the centre of the basin. In contrast, the microconglomeratic deposits of Cabezo de la Junta indicate a higher energy environment.

The Bardenas faunistic association consists of both ademic (terrestrial) and demic (aquatic to semi-aquatic) taxa (see Fernández López, 1990, 1991). The rarity of articulated bones and the mixture of elements from different habitats are indicative of transport. The taxonomical diversity is high: 37 different species are recorded, among which at least 3 are amphibians and at least 10 are reptiles (see Table 1). There are no selective accumulations of fossils belonging to a single taxon. All these data support an accumulation of the vertebrate remains in water.

Autoecology: amphibians from the localities do not provide precise information. They only indicate that the environment was not dry. The turtle assemblage consists of two aquatic forms, i.e., *Chelydropsis apellanizi* and an indeterminated Trionychinae, and two semi-aquatic ones, *Ptychogaster ronheimensis* and *Ptychogaster* (*Temnoclemmys*) *bardenensis*. The Trionychidae live in lakes and rivers with water circulation (Broin, 1977). The Chelydridae are more common in slow waters, more or less muddy and more or less shallow (Pritchard, 1979; Lapparent de Broin, 2000). The box-turtles *Ptychogaster* and *Temnoclemmys* are found in rivers, lakes and ponds and are supposed to move on firm land to a distance from the water, as extant *Terrapene* spp. In the study area, *Chelydropsis* is the more frequent turtle and is present in all sites but one. *Ptychogaster* is also well represented and more common than trionychines. Crocodilian are represented by a single species of the basal alligatoroid *Diplocynodon*. It is a small to medium-sized (up to 3 m long) generalist crocodilian, which lived in fluviatile, lacustrine or palustrine environments. Squamates are clearly terrestrial. Two of them (the amphisbaenian and erycine boid) were even fossorial animals.

This supports the sedimentological interpretation of a wetland for the Bardenas sites, but not a completely palustral area; more or less important stretches of water and firm land parts were present. Indeed, trionychines espe cially, and more frequently also crocodiles, require rather important water bodies of running waters. A part of the Bardenas macro- and micromammals (all taxa but anthracoterids and beavers), squamates and the turtle *Ptychogaster* require dry grounds. The sites represent an accumulation of allochthonous remains, coming from firm land parts or from streams ending in the fossilization sites, and autochthonous bones, fossilized in situ.

Palaeoenvironmental evolution: the available data suggest that the fossil vertebrate assemblages of the Bardenas were accumulated in the centre of an endoreic basin, with development of more or less shallow water and palustral parts and firm land. According to the sedimentological evidences, the fossiliferous deposits accumulated in a palustrine environment; the water bulk did have minor changes during the geological time considered in this study. With regard to the climatic conditions, four phases (F1–F4) could be differentiated on the basis of the study of diversity diagrams, abundance ranks and mammal cenograms (Murelaga, 2000). The locality of Cabezo de la Junta (Biozone Z) corresponds to the phase F1, characterized by a dry climate and an open country environment. During the phase F2, represented by the Nasa 1 and Rincón del Bu sites (at the beginning of the Biozone A), the climate was warmer and the humidity was higher; these conditions were favourable to the development of the wooded environments and to an increase of the diversity. At the end of the Biozone A, the phase F3 (sites: Barranco de Tudela 3 and 5, Cabezo Vaquero, La Nasa 3 and 5a) shows a temperature fall and dryness. The sites La Nasa 2b, 5b and 6, Barranco del Fraile 1 and 2 could represent a fourth phase (F4) marked by a turnover to warmer and wetter conditions (Murelaga, 2000). The climatic inferences for the phases F1 and F2 are coherent with those obtained from the study of the ostracod associations found in the Bardenas, which reflects a transition from a fresh water and warm climate (Biozone Z) to alkaline waters in a climate context where seasonality was more marked (Biozone A) (see Murelaga et al. 1997). Moreover, these climatic changes are not restricted to the studied area because they have been attested in other continental basins of the Iberian Peninsula (Van der Meulen and Daams, 1992; Daams et al., 1997), as well as in marine basins (Muller, 1984).

Anyway, there are no significant changes in the composition of the reptilian faunas, as shown by the remains found in different levels of the Bardenas (Murelaga, 2000; see Table 1). This suggests that the climatic changes between the biozones Z and A of the Ramblian, as supported by the study of mammals and ostracods, were not significant enough (i.e., temperature fall, changes in dryness) to have an ecological effect on reptiles such as turtles, squamates, and crocodilians. On the basis of an analysis of modern crocodilians, Markwick (1998) considered that temperature is the principal climatic factor responsible for limiting the global distribution of fossil crocodilians. In fact, crocodilians are good indicators of past climates and could be used for reconstructing palaeoclimates. Turtles are also often good climatic indicators, but, among them, cryptodires, such as the families present at the Bardenas, have a greater latitudinal range than crocodilians; as a group, they occupy regions that are climatically (especially thermically) too extreme for crocodilians. Markwick (1998, 240) used turtles as the taphonomic control group for crocodilians ("this concept is based on the postulate that a significant absence in a fossil group, due to environmental or climatic factors, can be constrained by the presence of another fossil group that has a similar taphonomic behaviour and only differs from the study group in the factor being investigated").

The occurrence of turtles, amphisbaenians, erycine snakes, and crocodilians in the Lower Miocene sites of the Bardenas suggests a warm, subtropical climate (Murelaga et al., 1999). The environmental or climatic changes inferred from abundance ranks and mammal cenograms, even if they have been attested at a regional scale, were probably small and not significant (i.e., minimal temperature changes, variations in wetness). Another possibility of worthy consideration is that such changes only reflect ecological differences in areas relatively distant from the centre of the basin and corresponding to most habitats of the Bardenas mammals (ademic organisms sensu Fernández López, 1990, 1991), reptiles excluded.

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Appendix

Distribution of the amphibians, turtles, squamates and crocodilians in the localities of the Bardenas Reales of Navarre, in stratigraphical order (from more recent to older), Early Miocene, Biozones M2b-3 (Table 1).

- Barranco del Congosto (BCo): *Chelydropsis* cf. *apellanizi*, *Ptychogaster* sp., *Diplocynodon* sp.
- Barranco del Fraile 2 (BF2): *Chelydropsis* cf. *apellanizi*, Trionychinae indet., *Diplocynodon* sp.
- Barranco del Fraile 1 (BF1): Salamandridae indet., anuran A, *Chelydropsis apellanizi*, Trionychinae indet., *Ptychogaster* (*Temnoclemmys*) *bardenensis*, *Ptychogaster* sp., *Ophisaurus* sp., ?*Eryx* sp., ?Colubridae indet., *Diplocynodon* sp.
- La Nasa 6 (N6): *Chelydropsis* cf. *apellanizi*, Trionychinae indet., *Ptychogaster* sp., *Diplocynodon* sp.

- La Nasa 5b (N5b): *Chelydropsis* cf. *apellanizi, Ptychogaster* sp., *Diplocynodon* sp.
- La Nasa 4 (N4): Trionychinae indet., *Diplocynodon* sp.
- La Nasa 2b (N2b): *Chelydropsis* cf. *apellanizi*, Trionychinae indet., *Ptychogaster* (*Temnoclemmys*) *bardenensis, Ptychogaster* sp., ?*Eryx* sp., ?Colubridae indet., *Diplocynodon* sp.
- La Nasa 5a (N5a): *Chelydropsis* cf. *apellanizi, Ptychogaster ronheimensis, Ptychogaster* sp., ?*Eryx* sp., *Diplocynodon* sp.
- La Nasa 2a (N2a): *Chelydropsis* cf. *apellanizi*, Trionychinae indet., *Ptychogaster* (*Temnoclemmys*) *bardenensis, Ptychogaster* sp., *Diplocynodon* sp.
- La Nasa 3 (N3): *Chelydropsis* cf. *apellanizi*, Trionychinae indet., *Ptychogaster* (*Temnoclemmys*) *bardenensis, Ptychogaster* sp., *Diplocynodon* sp.
- Barranco de Tudela 2 (BT2): *Chelydropsis* cf. *apellanizi*, Trionychinae indet., *Ptychogaster* (*Temnoclemys*) *bardenensis, Ptychogaster* sp., *Diplocynodon* sp.
- Cabezo Vaquero (CV): *Chelydropsis* cf. *apellanizi, Ptychogaster* sp., amphisbaenian indet., ?*Eryx* sp., *Diplocynodo*n sp.
- Barranco de la Tranquila (BTr): Salamandridae indet., anuran A, anuran indet., *Chelydropsis* cf. *apellanizi, Ptychogaster* sp., ?*Eryx* sp., *Diplocynodon* sp.
- Barranco de Tudela 5 (BT5): *Chelydropsis* cf. *apellanizi, Diplocynodon* sp.
- Barranco de Tudela 3 (BT3): *Chelydropsis apellanizi*, Trionychinae indet., *Ptychogaster* (*Temnoclemmys*) *bardenensis, Ptychogaster* sp., lacertilian indet. (non-anguid), *Ophisaurus* sp., ?*Eryx* sp., *Diplocynodon* sp.
- Barranco de Tudela 1 (BT1): *Chelydropsis apellanizi, Ptychogaster* (*Temnoclemmys*) *bardenensis, Ptychogaster* sp., *Diplocynodon* sp.
- Rincón del Bu (RB): anuran indet., *Chelydropsis* cf. *apellanizi*, Trionychinae indet., *Ptychogaster* (*Temnoclemmys*) *bardenensis, Ptychogaster* sp., lacertilian indet. (non-anguid), *Ophisaurus* sp., ?*Eryx* sp., ?Colubridae indet., *Diplocynodon* sp.
- La Nasa 1 (Tripazul, N1): Trionychinae indet., *Ptychogaster* (*Temnoclemmys*) *bardenensis, Ptychogaster* sp., *Ophisaurus* sp., amphisbaenian indet., ?*Eryx* sp., *Diplocynodon* sp.
- Cabezo de la Junta (CJ): *Ptychogaster* sp., *Diplocynodon* sp.

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