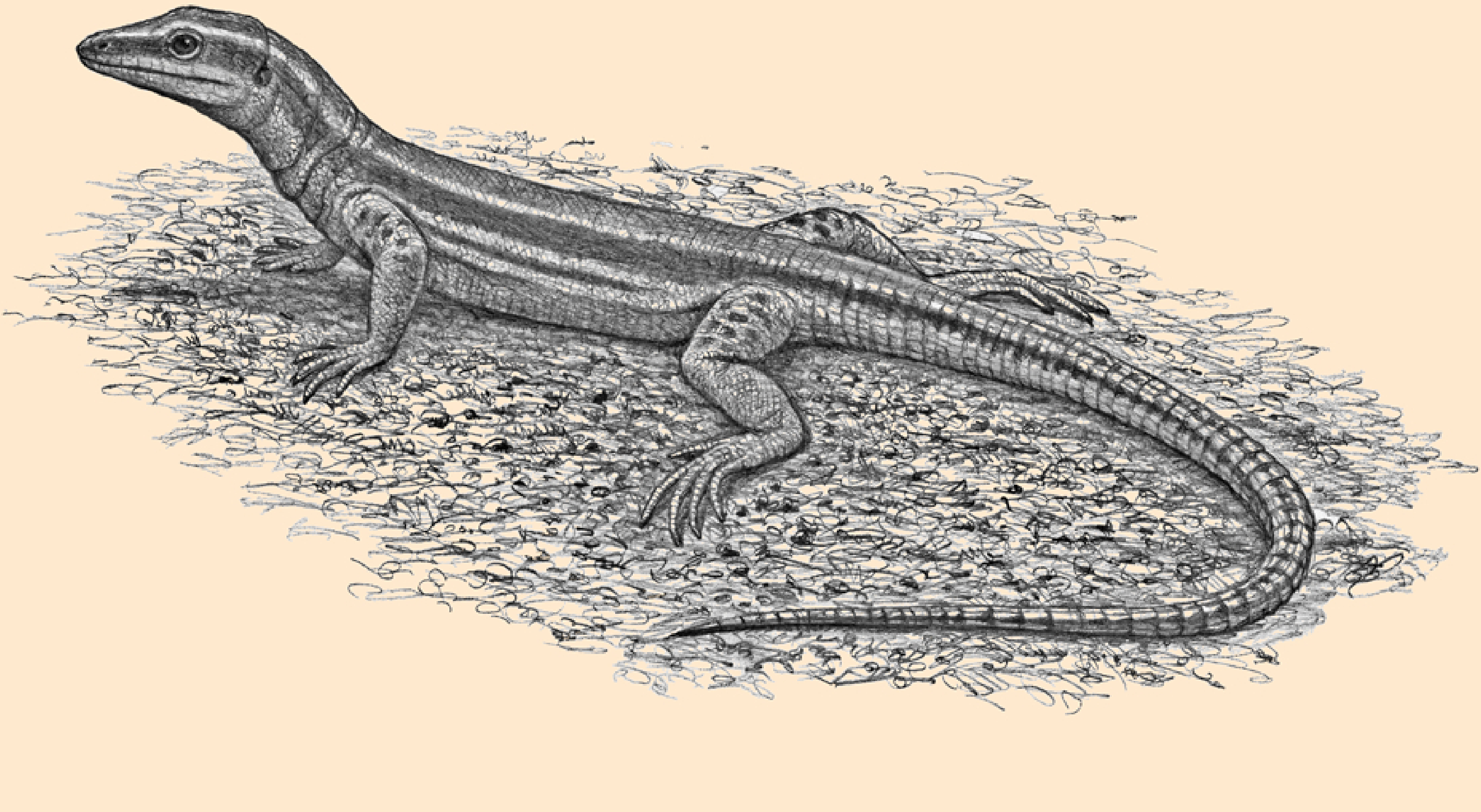
THE EVOLUTIONARY HISTORY OF LIZARDS ON THE IBERIAN PENINSULA

Arnau Bolet Mercadal

PhD Dissertation



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Front cover illustration: Reconstruction of *Pedrerasaurus* by Mauricio Antón, image courtesy of Institut Català de Paleontologia Miquel Crusafont

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Memoir presented by Arnau Bolet Mercadal in order to apply for the degree of Doctor in Geology by the Universitat Autònoma de Barcelona, Departament de Geologia, Unitat de Paleontologia, completed under the tutelage of Ricard Martínez Ribas and the supervision of:

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“Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.”

Charles Darwin, *The Origin of Species by Means of Natural Selection, or The Preservation of Favoured Races in the Struggle for Life*

A la meva família

CONTENTS

ABSTRACT/RESUM

Abstract

The remarkable squamate fossil record from the Iberian Peninsula represents an invaluable opportunity to unveil the evolutionary history of lizards and amphisbaenians during a long time span (Jurassic-Quaternary) in a key area of intermittent contact between Europe and Africa. Only Mesozoic (mainly Late Jurassic and Early Cretaceous) and Quaternary lizard assemblages had been systematically described previously.

The description of new material from the Early Cretaceous improves our knowledge of the exceptional Mesozoic assemblages through the erection of *Pedrerasaurus latifrontalis* from La Pedrera de Meià and *Jucaraseps grandipes* from Las Hoyas, as well as the description of the second known specimen of *Scandensia ciervensis*.

The diverse assemblage from Sossís (late Eocene) represents the first late Eocene lizard assemblage from Southern Europe, and includes the highly characteristic new taxon *Pyrenasaurus evansae*, as well as specimens that increase geographical and/or temporal ranges of several groups in the Iberian Peninsula, such as pleurodont iguanians, gekkotans, lacertids, scincids, cordyliformes, glytposaurines, anguines and amphisbaenians. The assemblage of Sossís provides insights from paleobiogeographical and paleoecological viewpoints, and compares well with contemporaneous French localities, supporting previous hypotheses based on mammals.

In the Miocene, the diversity of varanines is reduced to the genus *Varanus* through the synonymization of *Iberovaranus* with the former. A new species of *Blanus*, based on the first amphisbaenian skull from the European fossil record, is described. Both studies contribute to an ongoing refinement of a rather incomplete knowledge on Miocene squamate faunas resulting from a superficial treatment received by many preceding works.

Previous knowledge of fossil Iberian lizards and amphisbaenians is reviewed in the light of these new findings, and placed in a modern framework, shedding light on issues such as the composition of the assembages, paleobiogeography and paleoenvironment. The result is one of the most complete visions of their evolution most of its time of existence in a given area, in this case, the Iberian Peninsula.

Resum

L'excepcional registre fòssil d'escamosos a la Península Ibèrica representa una oportunitat inestimable per revelar la història evolutiva de llangardaixos i amfisbenes al llarg d'un llarg lapse de temps (Juràssic-Quaternari) en una zona clau de contacte intermitent entre Europa i Àfrica. Pel que fa als llangardaixos, només les associacions mesozoiques (principalment les del Juràssic Superior i Cretaci Inferior) i quaternàries s'han descrit sistemàticament amb anterioritat.

La descripció de nou material del Cretaci Inferior millora el coneixement existent quant a les notables associacions mesozoiques, permetent l'erecció de *Pedrerasaurus latifrontalis* de La Pedrera de Meià i *Jucaraseps grandipes* de Las Hoyas, així com la descripció del segon exemplar conegut de l'interessant *Scandensia ciervensis* provinent de la segona localitat.

La diversa asssociació de Sossís (Eocè superior) proporciona informació sobre els primers llangardaixos descrits d'aquesta edat al sud d'Europa, i inclou el nou tàxon *Pyrenasaurus evansae*, aixi com exemplars que amplien el rang geogràfic i/o temporal de diversos grups, com els iguànids pleurodonts, gekkos, lacèrtids, possibles scíncids, cordiliformes, glyptosaurins, anguins i amfisbenes. L'associació de Sossís proporciona noves dades des d'un punt de vista paleobiogeogràfic i paleoecològic, assemblant-se molt a les localitats contemporànies de França, recolzant hipòtesis prèvies basades en les faunes de mamífers.

Quant al Miocè, la diversitat de varanins queda reduïda al gènere *Varanus* mitjançant la sinonimització d'*Iberovaranus* amb el primer. Es descriu també una nova espècie del blànid *Blanus* basada en el primer crani fòssil d'amfisbena recuperat a Europa. Ambdós estudis contribueixen a un refinament del coneixement més aviat parcial que es té dels llangardaixos i amfisbenes miocens, resultat d'un tractament superficial d'aquest tipus de faunes en treballs anteriors.

El coneixement previ sobre llangardaixos i amfisbenes fòssils de la Península Ibèrica és revisat a la llum d'aquestes noves troballes i sota un enfocament modern, incrementant el coneixement existent sobre la composició de les associacions i proporcionant informació paleobiogeogràfica i paleoecològica, esdevenint una de les visions més completes disponible de la evolució del grup al llarg de la major part de la seva existència en una zona determinada, en aquest cas, la Península Ibèrica.

INTRODUCTION

1

1. Introduction

Squamates are an extremely diverse and widely distributed group that includes more than 9000 extant (Sites et al., 2011) and about 1000 fossil species (Caldwell, 2005). They are present in the fossil record since at least the Early or Middle Jurassic (e.g. Evans, 2003; Hutchinson et al., 2012), and they have been found in all continents, including Antarctica. The earliest rhynchocephalian, the sister group of squamates, is Middle Triassic in age, and latest calibrations reported that crown-group Squamata originated around 193 Mya (Jones et al., 2013). The earliest representatives of the group are expected to provide information on key evolutionary features that are not observable in more derived forms. It seems, however, that the earliest known fossils occur relatively late in the fossil record and that there is a gap for the time that should contain the earliest representatives of squamate evolution, at least from the Middle Triassic to the earliest part of the Early Jurassic. This lack of early forms clearly hampers discussion, but efforts in this direction, mainly focused on available slightly younger forms (i.e. Late Jurassic and Early Cretaceous) are necessary in order to assess the complicated phylogenetic relationships of Mesozoic squamates and the timing of evolutionary changes that lead to the modern clades.

The Iberian record is interesting in presenting an uneven but rather good fossil record of squamates starting in the Late Jurassic, thus allowing the study of the evolution of lizard assemblages through a span of time of more than 150 Myrs. This introduction is intended to present the framework that served as a start point for the elaboration of publications included in this dissertation, approaching important issues such as the phylogenetic context, the adopted terminology and the state of the art on global and Iberian fossil record of lizards and amphisbaenians.

1.1 Morphological vs. molecular data in lizard phylogeny

The term Lacertilia, as defined by Günther (1867), was intended to group lizards in contraposition to Ophidia (snakes), and this view was followed in many subsequent publications (e.g. Romer, 1956; Underwood, 1971; Sukhanov, 1962, 1976; Rieppel, 1978; Rage, 1982). However, in modern phylogenetic analyses based on morphology (e.g. Estes et al., 1988; Conrad, 2008; Gauthier et al., 2012), molecular data (e.g.

Townsend et al., 2004; Vidal and Hedges, 2005; Wiens et al., 2012, Pyron et al., 2013), and combined datasets (e.g. Lee, 2009; Wiens et al., 2010; Conrad et al., 2011; Hutchinson et al., 2012), 'Lacertilia' is not monophyletic to the exclusion of snakes. The term 'lizard' used informally, however, is acceptable to mean a squamate that is neither an amphisbaenian nor a snake. In Spanish, an additional problem arises from the use of the term 'lagarto' applied only to large lacertids (e.g. *Lacerta*, *Timon*), the term 'lagartija' for small lacertids (e.g. *Podarcis*, *Psammodromus*), and a collection of names for other groups (such as 'salamanquesa' for gekkotans). The term 'lagarto', as a translation of lizard, should refer to each and all lizards, including all those for which the term is never used in Spain, such as gekkotans, anguines and scincids.

The systematic scheme proposed by Camp (1923) established the foundations for the study of squamate phylogeny. Camp illustrated (see Fig. 1) iguanians (iguanids, agamids and chamaelontids) branching off from the rest of squamates in what would later be named as Scleroglossa (Estes et al., 1988, see tree in Fig. 1). The next dichotomy was between Gekkota and Autarchoglossa, the latter containing Scincomorpha and Anguimorpha. Scincomorpha was composed of xantusiioids, lacertoids (Teiidae, Lacertidae and Gerrhosauridae) and scincoids (Scincidae, Dibamidae, Feyliniidae, and Anelytropsidae). Anguimorpha was, in its turn, composed of Platynota (Varanidae, mosasaurs and relatives) and Diploglossa (Zonuroidea and Anguioidea, the latter including glyptosaurs, helodermatids, xenosaurids, anguids and anniellids). Amphisbaenians were tentatively included in Scincomorpha, and snakes and pygopods in Anguimorpha, inside Diploglossa and Platynota respectively (Camp, 1923). The situation and composition of most of these groups remained stable until the use of molecular data in squamate phylogeny in the last decade, with a few notable exceptions (see below).

The extensive cladistic analysis of Estes et al. (1988) supported most of the groups proposed by Camp (with minor adjustments on the composition of some of them) and proposed the name Scleroglossa for the sister group of Iguania (representing, in fact, all non-iguanian squamates). Iguania was composed of the metataxon Iguanidae and Acrodonta, formed at its time by Chamaeleontidae and the metataxon Agamidae. Gekkota was again regarded as the sister-taxon to Autarchoglossa. Scincomorpha encompassed Lacertoidea and Scincoidea, the former including Teiidae, Gymnophthalmidae (their Teiioidea), Lacertidae and Xantusiidae, and the latter including Scincidae and Cordylidae. Anguimorpha was composed of Xenosauridae, Anguidae, Helodermatidae and Varanidae. The analysis recovered an amphisbaenian-dibamid-snake clade as sister group to Scleroglossa, however, the preferred conservative hypothesis, as illustrated by Estes et al. (see Fig. 1), highlighted that the authors were not confident with this result. Camp's Zonuridae, under the name Cordylidae, was considered as part of the Scincoidea, and Pygopodidae was considered to belong to the Gekkota (e.g. Estes et al., 1988, see tree in Fig. 1). Other minor changes of position included the recognition of Gerrhosauridae as part of Cordylidae, rather than Lacertoidea. Many subsequent studies used the matrix of Estes et al. (1988), most of them including new taxa and/or new characters, and also reported differences regarding the possible non-monophyly of Scincomorpha, the position of snakes and the position of fossorial groups such as amphisbaenians and dibamids (e.g. Wu et al., 1996; Evans and Barbadillo, 1997, 1998a, 1999; Caldwell, 1999; Evans et al., 2005; Evans and Wang, 2005; Lee, 1998, 2000; Lee and Caldwell, 2000; Townsend et al., 2004; Vidal and Hedges, 2005).

The phylogenetic analysis of Conrad (2008) was based on a large new matrix, but again the basic structure recovered (Fig. 1) was similar to that of the tree reported by Estes et al. (1988). However, Conrad's analysis resolved the position of amphisbaenians, dibamids and snakes. Scincomorpha was found to be monophyletic (contra some previous works on morphology, see above) and included Dibamidae, Amphisbaenia and Serpentes. His position for snakes was against the proposed placement with mosasaurs recovered by some previous studies (Lee, 1997, 1998, 2000; Caldwell, 1999; Lee and Caldwell, 2000; Lee and Scanlon, 2001; Scanlon and Lee, 2002; Caldwell and Dal Sasso, 2004). The term Scincogekkonomorpha was used for scleroglossans (as defined by Estes et al., 1988) plus their extinct sister-taxa. Similarly, he coined the term Evansauria for autarchoglossans plus related fossil taxa such as bainguids. Moreover, Conrad remained open to the possibility of convergence being involved in the recovery of his Scincophidia, a group formed by limbless or limb-reduced forms including feyliniids, acontids, dibamids, amphisbaenians and snakes.

The morphological analysis by Gauthier et al. (2012) is the most extensive to date and was based on a collection of CT-scans that allowed the codification of a new set of previously unavailable characters. The same basic scheme of Estes et al. (1988) tree was recovered, and no support for the molecular results (gaining acceptance at that time, see below) was found. Minor changes were the inclusion of xantusiids inside Scincoidea rather than Lacertoidea, variation of the interrelationships of some anguimorphs, and the recovery of a fossorial group including dibamids, amphisbaenians and snakes (although the authors regarded the latter as a result of convergence).

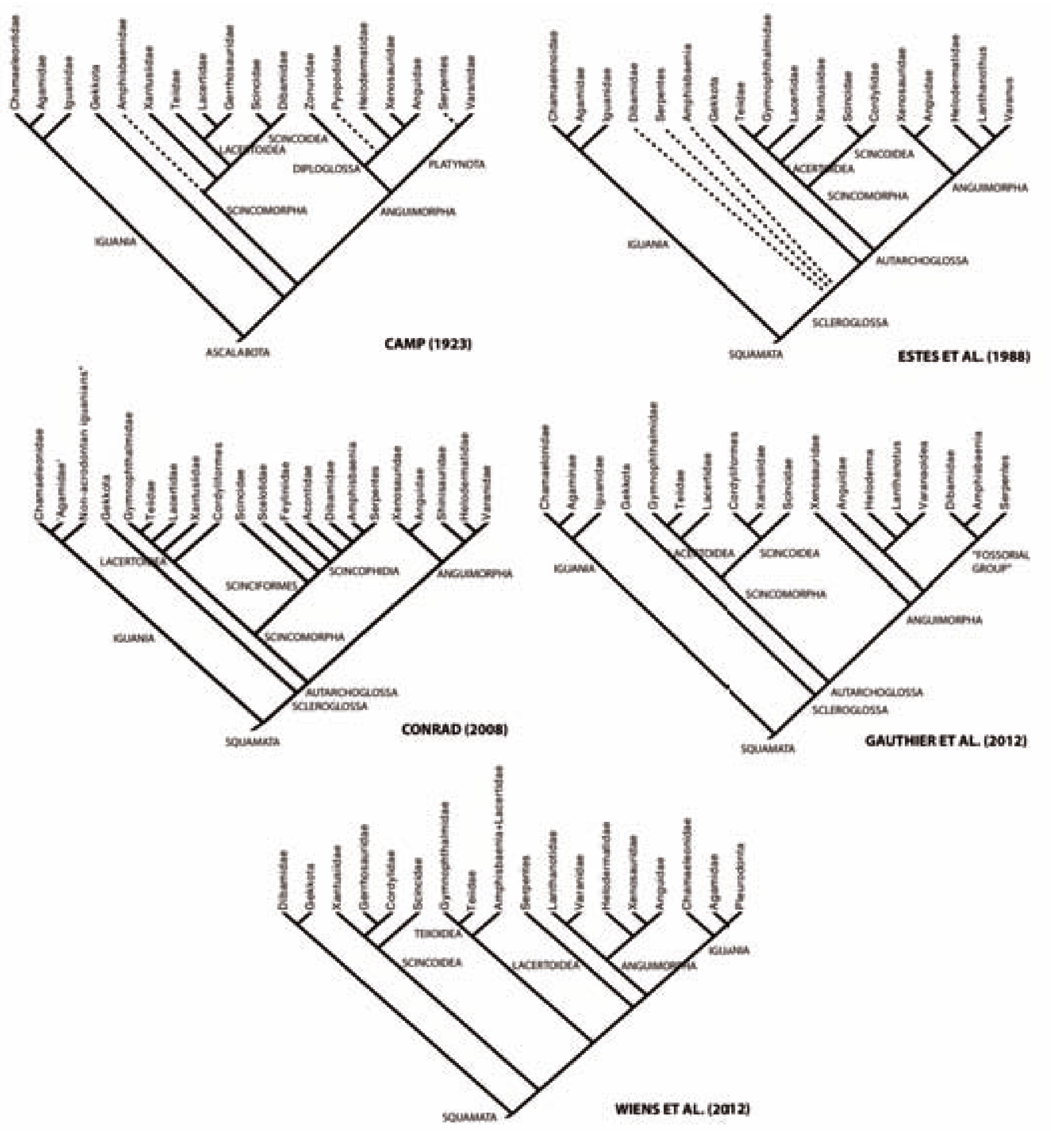

Figure 1. Proposed phylogenies from selected studies based on morphology (Camp, 1923; Estes et al., 1988; Conrad, 2008; Gauthier et al., 2012) and molecular data (Wiens et al., 2012). Trees represented are in simplifications of the original, but names for clades have been retained.

Molecular analyses (e.g. Vidal and Hedges, 2004, 2005, 2009; Townsend et al. 2004; Wiens et al., 2010, 2012) have recently presented a novel scheme with important modifications over the classical squamate phylogenetic tree. The greatest difference obtained by such molecular analyses is the movement of the position of iguanians to become closely related to anguimorphs (see Wiens et al., 2012 tree in Fig. 1). As explained below, this and other novel results of molecular analyses highlight the potential conflict in the application of widely used terms such as Scleroglossa, Autarchoglossa and Scincomorpha. The results of recent molecular studies have changed a scheme that had been stable for almost a century, since Camp's work (1923) (Fig. 1). The novel scheme, with iguanians nested inside Autarchoglossa as the sister taxon of Anguimorpha (e.g. Vidal and Hedges, 2004, 2005, 2009; Townsend et al. 2004; Fry et al., 2006; Wiens et al., 2010, 2012; Pyron et al., 2013; Jones et al., 2013), is in contrast with the basal split between Iguania and Scleroglossa presented by most morphological studies (e.g. Camp, 1923; Estes et al., 1988; Conrad, 2008; Gauthier, 2012). Molecular analyses agree in that Scincomorpha as traditionally defined (to include scincoids and lacertoids) is a paraphyletic assemblage, because scincoids appear as the sister taxon of Anguimorpha + Lacertiformes (e.g. Vidal and Hedges, 2005, 2009, Wiens et al., 2012), instead of Lacertiformes alone.

The major points of disagreement between the different molecular studies are: (1) whether the sister group to all other squamates is Dibamidae (Vidal and Hedges, 2005; Wiens et al., 2006; Mulcahy et al., 2012), Gekkota (Hugall et al., 2007), or Dibamidae + Gekkota (Wiens et al., 2010, 2012); and (2) whether the sister group to snakes is Anguimorpha (Hugall et al., 2007; Lee, 2009) or Anguimorpha + Iguania (Townsend et al., 2004; Vidal and Hedges, 2005; Wiens et al., 2006, 2010, 2012; Mulcahy et al., 2012).

If the results of molecular analyses are correct, widely used names such as 'Scleroglossa' and 'Autarchoglossa', among others, should also be avoided because these are not monophyletic groups to the exclusion of Iguania. The possibility of redefining 'Autarchoglossa' to include Iguania was rejected by Vidal and Hedges (2005) because a conflict with the meaning of the name ('free-tongued') would have lead to confusion over the content. The term 'Scleroglossa' was considered obsolete in terms of its meaning and content in the same work (if Iguania is moved inside 'Scleroglossa', the latter becomes a synonym of Squamata). New terms were defined to accommodate the newly recovered taxa (e.g. Unidentata, Episquamata), but these have not been followed by authors working on fossils or morphology alone, pending the resolution of the conflict between morphological and molecular studies. Moreover, parts of the taxonomy proposed by Vidal and Hedges (2005) are considered problematic in several aspects (see Conrad, 2008). Nonetheless, no subsequent molecular phylogeny has recovered a monophyletic 'Scleroglossa' that excludes Iguania. This creates a difficulty when discussing the results of morphology-based analyses that yield the more traditional tree. In the sections that follow, I have avoided the use of such problematic terms where possible. Where it cannot be avoided, for example in reporting the results of morphology only analyses, I use 'Scleroglossan', 'Autarchoglossa', 'Scincomorpha', 'Scincogekkonomorpha' and 'Evansauria'. These terms are used in quotes to indicate its possible non-monophyly within the Introduction, Discussion and Conclusions, but some chapters (mainly Chapters 5, 6 and 7) contain the same terms unquoted because at the time they were written the molecular results were not yet so widely accepted.

It seems that the way to manage these two contradictory signals (morphological and molecular) could be the use of combined morphological and molecular data. However, it is evident that the consensus reached will depend on which of the two datasets has more influence on the result, and that an intermediate solution is not necessarily the best. Wiens et al. (2010) concluded that molecular data can improve the resolution of fossil taxa in the context of a combined analysis but, and this is important, the addition of morphological data can also contribute to a better estimation of the position of living taxa. The problem of convergence in morphological phylogenetic analyses is recurrent but difficult to avoid, even when authors are aware of its influence on the results. To give an example, the recovery of a "burrowing clade" (Dibamidae, Amphisbaenia, Serpentes) has been viewed with caution since the beginning of the application of phylogenetic analyses to squamates (e.g. Estes et al., 1988), but the refinement of data and the addition of taxa and characters yielded no solution to the issue (Lee, 1998; Conrad, 2008; Gauthier, 2012). Snakes, amphisbaenians and dibamids were considered *incertae sedis* 'scleroglossans' by Estes et al. (1988) because the effect of limblessness and correlated characters on the placement of these groups was not clear. The strong signal in favour of the relationship of snakes to fossorial squamates such as amphisbaenians and dibamids recovered by Lee (1998) was artificially avoided by downweighting those characters thought to be correlated to a 'burrowing ecomorph'.

Conrad (2008) recovered snakes nested in a group of limb-reduced (some of them limbless) scincoids, including feyliniids, acontids, dibamids and amphisbaenians, but remained open to the possibility of convergence being involved. Gauthier et al. (2012) again recovered a group of ‘snake-like’ (in reference to the reduction or loss of limbs) squamates. However, when all burrowing lizards were deleted and then added individually, they failed to root at the same point on the tree, as it would be expected if the signal had been independent of characters related to fossoriality. As stated by Gauthier et al. (2012), this is probably highlighting an excessive ‘attraction’ between fossorial squamates due to convergence rather than common ancestry.

A basic problem regarding Mesozoic squamates (and, to a lesser degree, regarding early Cenozoic forms) is that, while molecular analyses have a great potential to resolve the phylogenetic relationships of crown members of squamate groups, it is possible that a large number of Mesozoic and some Cenozoic taxa formed part of the stem of such groups or of Squamata. Regarding this, it is very important that the recent taxa, the relationships of which can be established by molecular analyses, are also scored for morphological data. This is the only way to get an overlap of datasets between the ‘isolated’ fossil taxa, for which there is no possibility of obtaining molecular data, and extant taxa, for which both datasets are available. The question is, why is it so important to place early fossils in their correct phylogenetic position? First of all, many squamate groups are only known from fossils, representing a great part of the achieved diversity that cannot be evaluated by molecular-only analyses. Additionally, molecular divergence estimates rely on the existence of fossil taxa that are both well dated and accurately placed in the phylogeny. Most major crown-squamate clades are estimated to have originated in the Mesozoic, and therefore fossil squamates of this age should provide the clues needed to understand the early history of these modern groups. The subsequent appearance of less inclusive groups occurred in the Paleogene and Neogene, and thus many key fossils are also found in sediments of Cenozoic age.

1.2 Mesozoic lizard record

The earliest stages of squamate evolution during the Triassic and the earliest Jurassic are missing from the fossil record, probably because of a preservational bias resulted from the small size and fragility of their bones (Evans, 2003). A preference for habitats that provide a low potential of preservation or that represented a small fraction of the available formations from this age may also be involved. The earliest squamates have to be at least as old as the earliest representative of their sister group, Rhynchocephalia, and thus they should be as old as Middle Triassic, although the crown might have appeared later, by the Early Jurassic (Jones et al., 2013).

Rhynchocephalians may have radiated first as they were already globally widespread by the Late Triassic (Jones et al., 2009). However, the earliest recognized squamates are from the Early Jurassic (India, Evans et al., 2002) or Middle Jurassic (UK, Evans, 1994, 1998; Central Asia, Nessov, 1988; Fedorov and Nessov, 1992; Martin et al., 2006; and China, Clark et al., 2006). Rhynchocephalians disappear first from Asia (no record after the Early Jurassic) and then from the rest of Laurasia (latest record is in the Albian, latest Early Cretaceous, Evans and Jones, 2010). They are known, however, from the Late Cretaceous of South America (e.g. Apesteguía and Jones, 2012) and from scattered records in the post-Cretaceous deposits of New Zealand (Jones et al., 2009), where they are represented today by the genus *Sphenodon* (Evans and Jones, 2010).

Most taxa that have been placed as stem or basal squamates at some point occur relatively late in the fossil record, and are concentrated in the Late Jurassic (e.g. *Bavarisaurus*, *Ardeosaurus*) and Early Cretaceous (e.g. *Huehuecuetzpalli*, *Scandensia*, *Hoyalacerta*, *Eichstaettisaurus*, *Yabeinosaurus*). There is no agreement regarding their relative phylogenetic positions, and most of them have been also regarded as stem members of crown groups (e.g. Gekkota, Iguania or 'Scleroglossan'), although support for proposed relationships is usually weak. The tendency of Jurassic-Early Cretaceous lizards to fall on the stem of a crown-clade may reflect a real phylogenetic signal, but the potential effects of missing data (see Evans and Wang, 2011) cannot be discounted. *Huehuecuetzpalli* is consistently placed as the sister group of other squamates (Reynoso, 1998; Conrad, 2008; Gauthier et al., 2012), although it is the geologically youngest of those interpreted as stem-taxa. The same position was recovered by Wiens et al. (2010) in their morphology based analyses, but not in the combined analyses, where *Huehuecuetzpalli* joins iguanians to form the sister taxon to Anguimorpha (in the Bayesian analysis) or Anguimorpha + Serpentes (in the parsimony analysis). Taking into account that fossil taxa lack the molecular data that would aid their placement with respect to the crown, and are also likely to be scored for a lower percentage of morphological characters, due to incompleteness, the recovered instability is not surprising.

Tikiguania, for some time considered the earliest squamate (Datta et al., 2006), has been shown to be a Quaternary or late Tertiary agamid (Hutchinson et al., 2012) rather than a Late Triassic early acrodont iguanian. The Early Jurassic Indian *Bharatagama*, previously considered the first acrodont iguanian (Evans et al., 2002), could alternatively represent an early stem-group squamate or belong to another clade (Jones et al., 2013; Bolet and Evans, 2014). These alternative hypotheses would fit better with molecular phylogenies, where Iguania is the sister taxon of Anguimorpha, because such early records of iguanians would indicate long ghost lineages for many other groups. Squamates were certainly present in the Middle Jurassic, but they are fragmentary and difficult to attribute. Lizards from Middle Jurassic deposits from the British Isles have been interpreted as possible 'scincomorphs' and other crown- or stem-lizards harder to allocate (Evans, 1994, 1998; Waldman and Evans, 1994), but this needs to be re-evaluated in the light of recent molecular phylogenetic work. Other less secure records of indeterminate lizards exist mainly from Laurasian localities (Nessov, 1985; Meszoely, 1987; Rauhut et al., 2001).

Late Jurassic records include the widely distributed paramacellodids (possible stem-scincoids, Evans and Chure, 1998), as well as putative first anguimorphs, and some of the taxa that have been placed as basal squamates (Evans, 2003 for a revision, and Conrad, 2008 for alternative phylogenetic positions). Paramacellodids are nowadays interpreted as stem-scincoids (Evans and Chure, 1998), but their monophyly has not yet been established (e.g. Nydam and Cifelli, 2002), and alternative positions for them have been proposed (Conrad, 2008; Conrad et al., 2011). Scincoids (if paramacellodids and/or *Saurillodon* are included) may have arisen by the Late Jurassic. The record of anguimorphs, or stem-anguimorphs, in the Jurassic relies mainly on the attribution of *Dorsetisaurus* to the group, as the position of *Parviraptor* is uncertain (Conrad, 2008) although a position of the latter as a stem-'scleroglossan' is favoured (e.g. Daza et al., 2012). Estes (1983a) stated that anguimorphan affinities for *Dorsetisaurus* remained to be proved, but the position was confirmed by later phylogenetic works (e.g. Conrad, 2008; Conrad et al., 2011). If the molecular tree is correct, then gekkotans, as the sister group of other squamates, should also have arisen by this time, although again their early fossil record is unclear (Daza et al., 2012).

Early Cretaceous deposits seem to be dominated by taxa on the stem of modern groups (e.g. Evans, 2003; Evans and Bolet, in press), but paramacellodids and anguimorphs were certainly present, and these assemblages seem to be the natural continuation of those from the Jurassic. The recently described *Purbicella* from the Late Jurassic-Early Cretaceous Purbeck Limestone Group in England may represent an early lacertoid (Evans et al., 2012). In the Early Cretaceous further candidates have been attributed to Anguimorpha, (e.g. *Dalinghosaurus*, *Chometokadmon*). The position of *Chometokadmon* (Evans et al., 2006) has not been re-evaluated because it was not included in Conrad (2008), Conrad et al. (2011) or Gauthier et al. (2012), but the position of *Dalinghosaurus* as a crown-anguimorph has been corroborated by Conrad (2008) and Conrad et al. (2011). Between the Early Cretaceous and the early Late Cretaceous representatives of other groups (e.g. iguanians, anguids, xantusioids and snakes) appeared in the fossil record, although some of them may have appeared earlier. Boreoteiioids (including polyglyphanodontids) have been interpreted as the sister taxon of teiioids during the Late Cretaceous of Laurasia (e.g. Nydam et al., 2007), but Gauthier et al. (2012) and Longrich et al. (2012) placed them as stem-‘scleroglossans’. However, their presence in Europe is limited to the East, and, because they have not been found in the Iberian Peninsula, they are not discussed further in this thesis. The diversity of platynotans, including terrestrial and marine forms, underwent its greatest expansion during the Late Cretaceous. Amphisbaenians probably had their origin in the Cretaceous, but there are no confirmed fossil remains prior to the Paleocene (Kearney, 2003).

1.3. Paleogene lizard record

The generally poor record of lizards in the Paleocene makes it difficult to evaluate the role of the K/Pg event in modelling Paleogene lizard assemblages. This is especially true for the European record, and even more so for Iberian assemblages. However, in places where the Cretaceous-Paleocene record is continuous and localities at both sides of the boundary exist (e.g. North America), it has been argued that the K/Pg event had a strong influence on squamate assemblages (e.g. Longrich et al., 2012). Rage (2013) argued that squamates were not sharply affected in Europe mainly because Late Cretaceous faunas from this area were already less rich and diverse than those from, for example, North America. In any case, the Paleocene was the time of arrival of many groups to Europe, including scincids, necrosaurs and amphisbaenians (Rage, 2013). If the reported Late Cretaceous anguids from Laño and Blasi 2 (Blain et al., 2010) are correctly classified, then the group seems to disappear at the K/Pg boundary and be missing until the early Eocene, when they returned to Europe in the form of glyptosaurines and anguines, together with pleurodont iguanians, helodermatids and agamids. However, the Paleocene record of lizards in Europe is reduced to a few isolated localities (e.g. Hainin, Cernay), and apparent gaps might be an artifact of sampling. Eocene lizard records, in contrast, are extremely abundant in North America, Europe and, to a lesser degree, Asia. African records are, however, scarce. At that time there was a great degree of interchange between northern continents because the warmer temperatures allowed ectothermic vertebrates to reach higher latitudes and cross from one continent to another (e.g. Rage, 2012). It is notable that many European Paleogene lizard taxa have strong affinities with North American forms (e.g. the agamid *Tinosaurus*, 'higher' amphisbaenians, glyptosaurs, pleurodont iguanians and helodermatids, see Augé, 2012). In the early Eocene of Europe, amphisbaenians, scincids (or scincoids) and 'necrosaurs', which appeared in the Paleocene, persisted, whereas glyptosaur anguids, iguanians, lacertids and helodermatids make their appearance. The middle Eocene record in Europe is poorly known, despite the presence of two konservat-lagerstätten, Geiseltal and Messel (Augé, 2012). One of the main problems is that articulated specimens from these localities are difficult to compare to disarticulated remains from other localities, which are, at their time, comparatively rare (Augé, 2012). The late Eocene was a time when many endemic forms with a peculiar morphology appeared. This same situation has been reported for mammals (Sigé and Hugueney, 2006). It should be noted that the high degree of endemism is probably due to the isolation of small areas, probably in the form of islands. This applies, for example, to squamates from England (Holman et al., 2006) and, at least, to mammals from the western part of the Iberian Peninsula (e.g. Badiola et al., 2009). Most European Eocene lizard taxa died out in the Grande Coupure (Augé, 2005), coinciding with the Eocene-Oligocene boundary, although some may have survived elsewhere (e.g. Africa and/or Asia) permitting subsequent repopulation of Europe (Rage, 2012) later in the Oligocene. In the relatively cooler conditions of the Oligocene, European lizard faunas mainly consisted of Laurasian or Old World taxa. However, the discovery of pleurodont iguanians in the MP28 of Pech-du-Fraysse (Augé and Pouit, 2012) supports previous suggestions that extinction was delayed for some taxa until later in the Oligocene (Rage, 2012).

1.4. Neogene and Quaternary lizard record

Squamates are abundant in Neogene and Quaternary assemblages, and many extant genera have their first representatives in localities of this age. Most extant genera are represented in the Miocene by exclusively fossil species, whereas many extant species are already present in Pliocene, Pleistocene and Holocene assemblages. The faunas of localities from which human remains have been recovered have generally received greater attention because of the efforts invested in understanding their paleoenvironment and paleobiogeography. In comparison, Miocene faunas have received less attention. The Miocene Climatic Optimum, that had started by the latest Early Miocene, allowed the incursion of several thermophilic taxa into Europe, including varanines, chameleons, scincids, agamids and possible cordylids (Böhme, 2002, 2003, 2010). Some of these groups were present in the Eocene, but became extinct either during, shortly before or shortly after the Grande Coupure, and are thus absent for the greatest part of the Oligocene (agamids might be an exception because they are found throughout the Oligocene and their presence in Europe was probably continuous). The rise in temperature allowed ectothermic herpetofauna to reach higher latitudes in Central Europe (Böhme, 2003). The Miocene paleoherpetofauna has also been used to estimate paleoprecipitation using an actualistic approach (e.g. Böhme et al., 2006).

The later drop in temperatures lead to the extinction of some clades in Europe and to the restriction of others into southern refugia (e.g. blanid amphisbaenians in the Iberian, Balkan and Italian Peninsulas, although they subsequently disappeared from the Italian Peninsula). Detailed paleoclimatic reconstructions have been achieved (e.g. Blain et al., 2008a) based on herpetofaunal Pliocene-Holocene assemblages. As a result of several extinctions in Pliocene and Pleistocene times, the European herpetofaunal assemblages, including lizards, are today impoverished (Rage, 2013) but, as stated above, the Iberian Peninsula, together with other Southern European peninsulas, acted as a refugium, and became a hot spot of diversity.

1.5. Previous work on fossil lizards from the Iberian Peninsula

1.5.1. Late Jurassic

The oldest known Iberian squamates are currently those from Guimarota (Kimmeridgian, Portugal). These are mainly represented by disarticulated but well-preserved elements that have been attributed to the putative anguimorphs *Parviraptor* (but see Conrad, 2008) and *Dorsetisaurus*, the scincoid (?scincid) *Saurillodon*, the paramacellodids *Becklesius* and *Paramacellodus*, and indeterminate forms probably more related to scincoids or lacertoids than to other lizards (Seiffert, 1973; Broschinski, 2000). Some of these taxa were also recorded by Seiffert (1973) from the Portuguese locality of Porto Dinheiro which is generally considered to be younger (Tithonian-Berriasian or Berriasian: Wilson, 1979, Mohr, 1989). Based on new material from Guimarota, Kosma (2004) erected the genus *Chalcidosaurus* and four new species of *Saurillodon*.

1.5.2. Early Cretaceous

Except for the possible Berriasian lizards from Porto Dinheiro (see above), there are no described Cretaceous lizards from Portugal. In contrast, Early Cretaceous records from Spain are numerous, and material is in some cases exceptional. In addition to the newly described *Pedrerasaurus* (Chapter 5), La Pedrera de Meià has yielded several specimens of *Meyasaurus* (Vidal, 1915; Hoffstetter, 1966; Evans and Barbadillo, 1996, 1997, 1998b) and a single specimen of *Eichstaettisaurus* (Evans et al., 2000, 2004). Upper Hauterivian-lower Barremian deposits at Galve and Las Hoyas, and upper Barremian deposits at Uña, and Buenache de la Sierra have also produced squamate remains. The specimens from Galve include records of *Meyasaurus* sp., an indeterminate 'scincomorph', and *Paramacellodus* sp. at the fossil sites of Herrero, Colladico Blanco, Cerrada Roya and Poca (Crusafont and Adrover, 1965, 1966; Kühne, 1966; Krebs, 1985; Estes and Sanchiz, 1982; Richter, 1991, 1994a, b). New material, as yet undescribed, has been recovered from screen-washing concentrates at La Cantalera and Vallipón (Ruiz-Omeñaca and Canudo, 2001), both at Galve. Las Hoyas has yielded well-preserved specimens of *M. diazromerali* (Evans and Barbadillo, 1997), *Hoyalacerta sanzi* (Evans and Barbadillo, 1999), *Scandensia ciervensis* (Evans and Barbadillo, 1998a; see also Chapter 6), and *Jucaraseps* (Chapter, 7), and fragmentary material of a paramacellodid (Evans and Bolet, in press). The material from Uña is partially or fully disarticulated, but includes *M. unaensis* (with a possible additional record at Pie Pajarón, Hahn and Hahn, 2001), the paramacellodids *Paramacellodus sinusosus* and *Becklesius cataphractus*, a putative anguimorph, *Cuencasaurus estesi* (Richter, 1991, 1994a, b), and an indeterminate lizard (Rage and Escuillié, 2003) formerly identified as a snake (Richter and Rage, 1994). Squamate eggs tentatively referred to a gekkotan have also been reported from Galve (Kohring, 1990, 1991). In addition to the above sites, Buenache de la Sierra (Cuenca) has yielded fragmentary remains of at least one indeterminate lizard (Buscalioni et al., 2008). Material recovered from the Barremian-Aptian locality of Salas de los Infantes has allowed the erection of *Arcanosaurus ibericus* (Houssaye et al., 2013a), tentatively referred to Varanoidea. If the referral is confirmed, it would represent the earliest known terrestrial varanoid (Houssaye et al., 2013a).

1.5.3. Late Cretaceous

Despite a good record of vertebrates including dinosaurs, crocodiles and turtles, microvertebrate Late Cretaceous assemblages are rare in the Iberian Peninsula. The first late Cretaceous Iberian lizard assemblage was described from Laño (upper Campanian/lower Maastrichtian, Basque country) with iguanians, 'scincomorphs', anguines and snakes (Astibia et al., 1991; Rage, 1999; Blain et al., 2010). Indeterminate squamates have also been reported from the localities Chera 0, Chera 1c (Campanian/Maastrichtian, Valencia) (Company et al., 2009a) and Fontllonga 6 (Maastrichtian, Catalonia) (Álvarez-Sierra et al., 1994). Lo Hueco (upper Campanian-lower Maastrichtian, Cuenca) (Barroso-Barcenilla et al., 2009) has yielded remains of a possible iguanian, an indeterminated 'scincomorph', and indeterminate squamate, and a pythonomorph varanoid (Narváez and Ortega, 2010; Torices et al., 2010; Houssaye et al., 2013b). The latter is interesting in that non-marine pythonomorphs are only known from the Early Cretaceous of Japan and, now, from Spain. Blasi 2 has yielded two indeterminate lizards (one iguanid or 'scleroglossan' and one possible 'scincomorph'), and the remains of an anguid and snakes (López-Martínez et al., 2001; Blain et al., 2010).

1.5.4. Paleogene

Paleogene (mainly Eocene and, to a lesser degree, Oligocene) localities from the Iberian Peninsula usually yield abundant squamate material but this has generally been overlooked. Thus the only previously described Paleogene squamate assemblage was that from the early Eocene of Silveirinha in Portugal (Rage and Augé, 2003). Reports on scattered Eocene material from Spain existed (e.g. Cuesta Ruiz-Colmenares and Jimenez-Fuentes, 1994), but the material was never described or figured. After revision of the material housed at the Institut Català de Paleontologia Miquel Crusafont (ICP), corresponding to numerous localities of early, middle and late Eocene localities from different Iberian basins, it is evident that lizards are almost invariably present in such localities, and are sometimes abundant. Preliminary results were reported in Bolet and Evans (2010a, 2012a), but studies on all localities except Sossís (see Chapter 8 and 9) are still in progress. Because many ‘exotic’ forms have appeared in Europe by the Eocene (e.g. pleurodont iguanians, agamids, helodermatids, glyptosaurs), the evaluation of Iberian faunas is interesting in that it could shed light on the origin and dispersal routes followed by these immigrants.

1.5.5. Neogene and Quaternary

A similar situation, with rich but understudied lizard asssemblages, applies to the Neogene of the Iberian Peninsula. The revision of the ICP collections, focused on but not restricted to the Vallès-Penedès Basin, highlighted that paleoherpetofaunal material is abundant. However, until now, most studies have been focused on macrovertebrates or micromammals, and lizard assemblages have not been described in detail. In contrast, the few works reporting lizard remains usually cite their presence in faunal lists without providing figures or descriptions (e.g. Crusafont and Villalta, 1952). A preliminary report on the herpetofauna from the Vallès-Penedès Basin, including squamates, is in preparation (Delfino et al., in prep.). Among the squamates previously reported from the Vallès-Penedès Basin are *Varanus*, anguines, amphisbaenians and snakes, but collections include gekkotans, lacertids and scincids and a new taxon of uncertain affinities (pers. obs., see also Chapter 10 and Annex I).

In contrast with the Neogene lizard record, that of the Quaternary has been subject of several systematic studies, usually within a broader context encompassing the paleoherpetofauna in its entirety. The first exhaustive account on these faunas (not restricted to lizards, but to small fossil herpetofauna in general, and encompassing some assemblages from southern France) was that of Bailon (1991). These studies were complemented by Barbadillo (1989), Bailon and Augé (2012), Blain (2009), Blain and Bailon (2010), Blain et al. (2007, 2008a, b, c, 2009, 2011, 2013), López-García et al. (2008a, b, 2010, 2013), and Laplana et al. (2013), among others. This recent work is usually focused on the paleoclimatic inferences that can be drawn from the analysis of the paleoherpetofauna or the microvertebrate assemblage in general.

1.6. Importance of Iberian herpetofaunas

Squamates (lizards, amphisbaenians and snakes) constitute a great part of the present tetrapod diversity in worldwide continental environments. The number of extant species is roughly equivalent to the number of known extant mammals, although there are likely more species of lizards still to be discovered than of mammals. In the Iberian Peninsula, the high diversity of extant squamate assemblages is linked to the role of the area as a refugium during the last glaciations. This makes the Iberian Peninsula a valuable place to study living squamates, but also to investigate the evolutionary history of the assemblages leading to the present day. However, despite the good fossil record, squamates (mainly lizards and amphisbaenians) remain understudied at many time periods (e.g. Late Cretaceous, Paleocene, Eocene, Oligocene and, to a lesser degree, Miocene). There are two different reasons for this lack of knowledge. In some cases the fossil record is poor (e.g. Paleocene), and searching for new localities or increasing efforts to obtain squamates from previously known localities are the only ways to improve it. In other cases (e.g. Eocene, Miocene), however, the lack of knowledge is linked to the limited attention received by a rather rich herpetofauna in contrast to mammals. As already applied to post-Miocene assemblages, the amount of information that can be obtained from this herpetofauna is potentially huge. The study of lizards and amphisbaenians yields important information regarding the paleoecology, paleobiogeography and divergence times of included clades. Moreover, the position of the Iberian Peninsula in Southern Europe, and the fact that it was connected to both North America (Jurassic and Eocene) and Africa (?Eocene, Miocene) makes it an excellent place to track dispersion routes between these continents and Europe. The objectives of the present work were not only to describe new material in order to increase the known diversity of lizard and amphisbaenian assemblages, but also to explore the implications of their composition, mainly for those poorly known pre-Pliocene assemblages.

STRUCTURE OF THE DISSERTATION AND GOALS

2

2. Structure of the dissertation and goals

2.1. Structure of the dissertation

New material of lizards and amphisbaenians from different regions of the Iberian Peninsula was studied for this work. Fossil-bearing localities represented include La Pedrera de Meià (Early Cretaceous, Catalonia), Las Hoyas (Early Cretaceous, Cuenca), Sossís (late Eocene, Catalonia) and Can Mata and Can Mas (middle-late Miocene, Catalonia). One new specimen from Escamps (late Eocene, France) was included because the taxon also occurs at the roughly contemporaneous locality of Sossís.

This thesis is structured as a compendium of publications. The first Chapters (1-4) serve as an introduction, whereas Chapter 11 presents general results and discussion and Chapter 12 contains general conclusions. The remaining chapters correspond to published (Chapters 5-8), accepted (9 and 10) or submitted (Annex I) research articles in journals included in the Science Citation Index. Three new genera and three new species of lizards have been erected, and one genus has been synonymized. A new species of blanid amphisbaenian is described in Annex I, but it is still in process of review.

Included papers are:

- Bolet, A., Evans, S.E., 2010b. A new lizard from the Early Cretaceous of Catalonia (Spain) and the Mesozoic lizards from the Iberian Peninsula. *Cretaceous Research* 31, 447-457 (Chapter 5).

- Bolet, A., Evans, S.E., 2011. New material of the enigmatic *Scandensia*, an Early Cretaceous lizard from the Iberian Peninsula. *Special Papers in Palaeontology* 86, 99-108 (Chapter 6).

- Bolet, A., Evans, S.E., 2012b. A tiny lizard (Lepidosauria, Squamata) from the Lower Cretaceous of Spain. *Palaeontology* 55(3), 491-500 (Chapter 7).

- Bolet, A., Evans, S.E. 2013. Lizards and amphisbaenians (Reptilia, Squamata) from the late Eocene of Sossís (Catalonia, Spain). *Palaeontologia Electronica* 16.1.8A, 1-23 (Chapter 8).

- Bolet, A., Augé, M., in press. A new minute fossorial lizard from the late Eocene of France and Spain. *Anatomical Record* (Chapter 9).

- Delfino, M., Rage, J.C., Bolet, A., Alba, D.M., published online 2012. Synonymization of the Miocene varanid lizard *Iberovaranus* Hoffstetter, 1969 with *Varanus* Merrem, 1820. *Acta Palaeontologica Polonica* (Chapter 10).

- Bolet, A., Delfino, M., Fortuny, J., Almécija, S., Robles, J.M. Alba, D.M., in review. An amphisbaenian skull from the European Miocene and the evolution of Mediterranean worm lizards (Annex I).

2.2. Goals

The fossil record of lizards and amphisbaenians from the Iberian Peninsula has received irregular attention depending on the fossil-bearing locality in question. The main goal of this thesis was to achieve a fuller knowledge of the well-studied assemblages (e.g. Early Cretaceous) and, at the same time, to fill gaps for previously understudied periods (e.g. Eocene, Miocene). The long span of time studied, from the Late Jurassic to the Miocene, with Quaternary assemblages also taken into account, provides a comprehensive view of the evolutionary history of the group in an area with a privileged fossil record. These novel observations provide a basis from which to intepret the present composition of the diverse Iberian extant lizard faunas.

The main goal described above was addressed through the identification, description and comparison of lizard and amphisbaenian fossil material and, when appropriate, the erection of new taxa. Paleoenvironmental and palebiogeographical inferences based on this new information were provided when possible, and a global view of the evolutionary paths followed by lizard assemblages is addressed.

CONTEXT OF THE STUDIED LOCALITIES

3

3. Context of the studied localities

Material described in this PhD dissertation comes from classical localities (e.g. La Pedrera de Meià or Sossís), or from localities that have undergone exhaustive fieldwork during recent years (e.g. Las Hoyas or Abocador de Can Mata). Only a short explanation of the geographic and geologic context of each locality (Fig. 2) is provided, because the literature on each is already extensive.

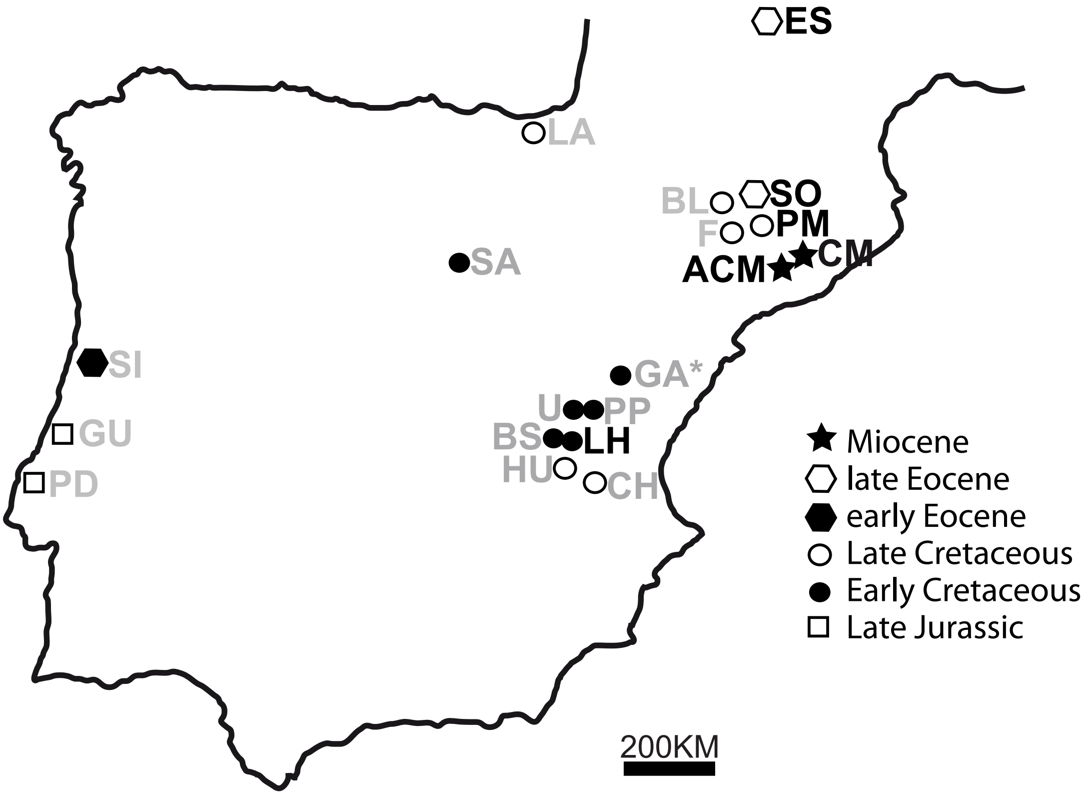

Figure 2. Map of main Iberian localities providing fossil lizards and amphisbaenians discussed in the text. The French locality of Escamps is included because material from this locality is discussed in Chapter 8. Acronyms: ACM, Abocador de Can Mata; BL, Blasi 2; CH, Chera; BS, Buenache de la Sierra; CM, Can Mas; ES, Escamps (France); F, Fontllonga; GA*, Galve (several localities, including Herrero, Colladico Blanco [=Pellejón 2], Cerrada Roya, Poca, Vallipón and La Cantalera); GU, Guimarota; HU, Lo Hueco; LA, Laño; LH, Las Hoyas; PD, Porto Dinheiro; PM, La Pedrera de Meià; PP, Pie Pajarón; SA, Salas de los Infantes; SI, Silveirinha; SO, Sossís; U, Uña. Those localities with the acronym in black have yielded material described for the first time in this dissertation, those with the acronym in grey contain material used for comparison and discussed in the text.

3.1. La Pedrera de Meià

La Pedrera de Meià is a classical locality known since the late 19th century (Vidal, 1898). It has yielded rare but articulated remains of tetrapods, fishes, invertebrates and plants. The fossil site is situated in the Serra del Montsec, province of Lleida (Catalonia, Spain), and the freshwater sequence in which is located is supposed to be Late Berriasian-Early Valanginian in age based on the ostracod fauna (Peybernès and Oertly, 1972; Brenner et al., 1974; Whalley and Jarzembowsky, 1985) and pollen (Barale et al., 1984). However, alternative studies give a Barremian (Ansorge, 1993) or late Hauterivian-early Barremian (Martín-Closas and López-Morón, 1995) age based on the regional stratigraphy and the charophyte content. An unconformity at the base separates these deposits from underlying Jurassic marine carbonates and from a lower Berriasian marine unit, while an unconformity at the top separates it from overlying Barremian coastal and shallow marine limestones. The paleoenvironment of the locality has been interpreted as a shallow, near-coastal lake, the anoxic sediments of which preserved complete and articulated specimens, often presenting soft tissues. The articulated specimen described in Chapter 5 comes from this locality.

3.2. Las Hoyas

Las Hoyas is a well-known locality situated in the Serranía de Cuenca (Iberian Ranges) in east-central Spain (Fregenal Martínez and Meléndez, 2000). The continental deposits that contain the locality belong to La Huérgina Formation (Vilas et al., 1982), and are of late Barremian (Early Cretaceous) age. The lacustrine fossiliferous beds have provided numerous exceptionally well-preserved specimens (Fregenal Martínez and Meléndez, 2000) that make this locality one of the best places in the world to study a Cretaceous wetland. The high diversity of organisms recovered (among vertebrates: fishes, sharks, salamanders, frogs, lizards, turtles, crocodiles, pterosaurs and dinosaurs, see Buscalioni et al., in press) and their exceptional preservation is rivalled only by roughly contemporaneous localities from China. Two new articulated lizard specimens from Las Hoyas are described in Chapters 6 and 7.

3.3. Sossís

Sossís is a classical late Eocene locality situated in the Pobla de Segur subbasin, within the Graus-Tremp basin (one of the two Southern Pyrenean Basins; Cuesta Ruiz-Colmenares et al., 2006). It has provided not only a window to an extremely rich and diverse late Eocene continental assemblage, but it has also allowed correlations with European Eocene localities (López Martínez, 1998), placing it at the MP17a (Peláez-Campomanes, 1998). Previous research mainly targeted micro and macro mammals (e.g. Crusafont, 1965; Casanovas-Cladellas et al., 1998; Cuenca-Bescós, 1998; Cuesta Ruiz-Colmenares et al., 2006), but ongoing research is focused on primates (e.g. Marigó et al., 2011, 2013), and preliminary results on the herpetofauna include Bolet and Evans (2010a) and Bolet and Evans (2012a). Chapters 8 and 9 of this dissertation are focused on material from this locality.

3.4. Escamps

Escamps is a late Eocene locality forming part of the “Phosphorites du Quercy”, a group of more than 100 fossiliferous fissure-filling sites situated in southwestern France (Rage, 2006). The ages of the different sites range from MP8+9 (early Eocene) to MN3 (early Miocene), and represent the only place in Europe where the Grande Coupure (the event separating the Eocene and the Oligocene) can be studied in detail with respect to amphibians and squamates (Rage, 2012). Apart from mammals, the recovered fossil faunas include an unrivalled fauna of lower vertebrates, including fishes, amphibians and reptiles (chelonians, crocodiles, birds, lizards, and snakes; Rage, 2006). Localities were both excavated and screen-washed, allowing the recovery of small disarticulated but rather well-preserved specimens (Rage, 2006). The age of Escamps is MP19 (late Eocene), and its lizard fauna was studied by Augé (2005). The type specimen of the new taxon described in Chapter 9 comes from this locality.

3.5. Can Mas (El Papiol)

The Miocene continental deposits of the Vallès-Penedès Basin (a small Neogene basin situated in Catalonia, northeastern Iberian Peninsula) consist of continental successions interrupted by several marine transgressions. Continental localities are usually loosely defined areas around the place that gives its name to the locality. Accordingly, fossils from a single locality may come from different levels. The locality of Can Mas, near El Papiol (Barcelona), is situated in the early Miocene Lower

Continental Complex of the Vallès-Penedès Basin. The different outcrops that form the locality are mainly composed of reddish terrigenous deposits of varied lithology, with an MN3 or MN4 age (Agustí et al., 1985; Casanovas-Vilar, 2011a, b). Specimens from this locality are described in Chapter 10.

3.6. Abocador de Can Mata

The area of Els Hostalets de Pierola has yielded abundant fossils over many years (e.g. Bataller, 1938; Villalta and Crusafont, 1941; Crusafont 1952; Crusafont and Truyols, 1954). However, a new paleontological project at Abocador de Can Mata in 2002 triggered the recovery of fossils as well as providing a better stratigraphical context for the fossil-bearing localities (e.g. Alba et al., 2011). More than 250 localities are distributed along the studied section, with more than 60,000 fossils recovered (Alba et al., 2006a, 2011, 2012; D.M. Alba pers. comm. 2013). The stratigraphic sequence is mainly formed by red to brown mudstones, and less abundant sandstones, conglomerates and breccias. These sediments are interpreted as representing middle to mainly distal or marginal facies of alluvial fans (Alba et al., 2006a, b, 2007, 2009; Casanovas-Vilar et al., 2008; Moyà-Solà et al., 2009). The dating of the series is based on litho-, magneto- and biostratigraphy (Alba et al., 2009; Moyà-Solà et al., 2009; Casanovas-Vilar et al., 2011a), and ranges (as a joint series from Abocador de Can Mata and Riera de Claret) from 12.5 to 10.6 Ma (Casanovas-Vilar et al., 2011a). Locality ACM/C8-A4 corresponds to the MN7+8 (late Aragonian). See Annex I for the description of a blanid amphisbaenian skull from this locality.

MATERIAL AND METHODS

4

4. Material and methods

The material studied is housed at the ICP (former Institut de Paleontologia de Sabadell), Museu de Ciències Naturals de Barcelona (Museu de Geologia de Barcelona), Museo de las Ciencias de Castilla-La Mancha, and Université des Sciences et Techniques du Languedoc. For the collection numbers of the specimens and their location see the corresponding chapters. Fossil and extant lizard and amphisbaenian material for comparison was accessed at the Institut Català de Paleontologia Miquel Crusafont (Sabadell), Museum National d'Histoire Naturelle (Paris), American Museum of Natural History (New York), Museum of the Rockies (Bozeman), and University College London (London).

4.1. Methods

4.1.1. Prospecting and surface collecting

Surface collecting is generally limited to localities with a high occurrence of fossils, and, among lizards, recovered material is usually biased toward large taxa. For obvious reasons, the chances of recovering a lizard fossil during prospection decreases with the size of the remains. It is probable that at least some specimens studied in Chapter 10 were found through surface collecting. The large size of varanid vertebrae makes them more likely to be found by this method, but smaller vertebrae (e.g. those of anguines such as *Pseudopus*) are rarely found during prospecting in localities of the Miocene of the Vallès-Penedès Basin. One can usually collect specimens without further preparation (no excavation is necessary) because the mudstones soften with water releasing the fossils on the surface. Prospection is usually the method used to find new localities, which, depending on their instrinsic characteristics, are then screen-washed and/or excavated.

4.1.2. Screen-washing and sorting

Another way to recover lizard remains is by screen-washing the sediment, searching for tooth-bearing, cranial and postcranial bones. This technique is often used to search for mammal teeth, although it can also yield remains of fishes, amphibians and reptiles. However, the remains recovered are partial or, complete at best, and rarely articulated. It is sometimes hard to attribute them at species or even genus level. Lower jaws are perhaps an exception as they have in the case of squamates, regularly been, used as holotypes. However, in recent years there has been a tendency to avoid the diagnosis of species based on this kind of material because many recent species cannot be differentiated based on lower jaw characters alone. Moreover, characters used in some specific or generic diagnoses fall within the variability of a given taxon. The process of referring isolated bones to a particular taxon can be problematic, but it is possible if the teeth have characteristic features, and/or the bones bear sculpture or distinctive facets. Despite the problems described above, screen-washing techniques offer the best chance of recovering underrepresented taxa and thus approaching the actual diversity of a given locality.

All specimens described in chapters 8, 9, and Annex I come from screen-washing of Eocene and Miocene localities. The amphisbaenian skull described in Annex I is unusual, because material recovered by screen-washing almost invariably becomes disassociated during the process, even when it was originally associated or even articulated. The small amphisbaenian skull remained articulated due to the calcitic crust covering it. Some other screen-washing specimens described in this dissertation probably represent new species, but remain unnamed because of the fragmentary nature of the recovered material (e.g. the amblyodont lacertid described in Chapter 8).

4.1.3. Excavation

The lithological characteristics of lithographic limestones such as those of La Pedrera de Meià and Las Hoyas make them less suitable to surface collecting and screen-washing. The best chances of finding specimens are obtained by the systematic splitting of slabs. The splitting sually occurs through the planes corresponding to depositional surfaces, where specimens are located. Due to the low preservation potential of complete lizard specimens, which are often delicate, the specimens provided by lithographic limestone fossil sites are very important. Unfortunately, this kind of site is rare, and usually yields only a small number of specimens. Classical Mesozoic sites such as Solnhofen (Germany, Tithonian), Cerin (France, Late Kimmeridgian), or La Pedrera de Meià (Spain, late Berriasian-Early Valanginian) or

Pietraroia (Italy, Aptian-Albian) have provided only around a dozen articulated lizards in total, and more recently discovered sites like Las Hoyas (Spain, Barremian), Tepexi de Rodriguez (Mexico, ?Aptian), and the localities of Liaoning (China) and Inner Mongolia (Lower Cretaceous) have yielded some tens more. In the Cenozoic, there are a few Eocene lithographic limestones localities in Europe (Messel and Geiseltal) and the USA (Wyoming). Specimens from lithographic limestones are special in that they are usually found in articulation, and the complicated task of finding out if some unconnected bones belong to a single taxon or even to a single specimen is avoided. They are usually well preserved, details of the bones and sometimes even soft tissues (e.g. skin impressions and cartilage), which are rarely preserved in other kind of locality. However the skeleton is often distorted (e.g. they do not maintain the shape in three dimensions but are crushed, specially the skull). Moreover, only the exposed surface of the bones can be accessed, the remaining surfaces lie inside the rock, from which they cannot easily be removed. When the density difference between the bone and the matrix is high enough, CT-scanning methods have the potential to reveal the morphology of the hidden bone surfaces (e.g. Conrad and Norell, 2006; see also Annex I and below). Another approach is Synchrotron analysis, as already reported for an Eocene lizard specimen (Edwards et al., 2012). The exceptional preservation of the bones in such localities also makes these specimens good candidates for paleohistological studies (e.g. Bailleul et al., 2011).

Among the localities included in this PhD dissertation, some have yielded fossils through more than one of the techniques described above. The best example is Can Mata, where specimens are found through surface collecting, screen-washing and systematic excavations.

4.2. Phylogenetic analyses

Cladistic phylogenetic analyses were performed when the specimens were sufficiently complete to allow the codification of at least a minimum number of characters. Analyses were run using both TNT and Paup, and resulting trees were edited with Mesquite and Adobe Illustrator CS3.

A modified version of the matrix of Conrad (2008) was used in chapters 5, 6, and 7. The options used were the same as used in Conrad (2008), with amended codings as stated in Chapter 5. The corrected version was used in subsequent analyses, adding further amendments (mainly regarding the coding of *Scandensia*, based on a new specimen) in Chapter 6, and the addition of a new genus in Chapter 7. The codings and amendments necessary in order to replicate the phylogenetic analyses were provided in the corresponding publication (and chapter), but during the editing process one mistake appeared in two of the published matrices. The correct coding is provided below.

Coding for *Pedrerasaurus latifrontalis* (amendment for Chapter 5):

1?0?000?11	02??????00	?????????0	??00?00???
???00??0?	0??1002100	000-???0??	??1?0????1
0??00000??	???????00?	????00???	??????????
??????????	??????????	???????0??	????????1?
??00??0???	???????100	??????00??	??????????
?0????????	03000000?0	1??000????	2????1????
0???0?000?	0???000??0	01??00?0?0	????0??0??
???{01}00??00	?1????????	????0-0---	?-????????
??????????	??????????	?????????	??????????
???0??????	?0		

Coding for *Jucaraseps grandipes* (amendment for Chapter 7):

000000-000	1???00??00	0??0??0000	???00000??
???00??0?	0??1000101	100-0??0??	??1?0?3??1
?01???0010	0010??????	????00???	??????????
?0????????	??????????	??????????	??????????
??00?0????	?????????0	???????0??	?0??00????
?0?000110?	?000000???	?00000???1	200??2?0??
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???1211?00 ?1???????? ????0-0--- 00????????

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4.3. CT-scans

CT-scanning techniques are becoming increasingly common in paleontology. They allow the digital isolation of bones, grant access to hidden parts of fossils, and permit reconstructions and the use of such reconstructions in additional research. It is also possible to digitally remove infilling matrix or covering crusts, a less dangerous process than physically preparing the fossil. CT-scans of two specimens from the Miocene of Catalonia were performed at the American Museum of Natural History (AMNH). One, corresponding to the first fossil skull of a Mediterranean amphisbaenian, was reported in Bolet et al., 2013a and Delfino et al., 2013, and is described in Annex I. The specimen was scanned on a GE phoenix v|tome|x s180 (GE Measurement & Control Solutions, Hanover, Germany) using a nanofocus X-ray tube with the following parameters: voltage 105 kV and current 70 mA and a magnification of 15.86723491. The raw data were imported to VG Studio Max 2.1 and exported to Avizo 7.0 for analysis, segmentation, and visualization. The covering crust and the infilling matrix present in the original fossil were deleted by considering the different densities of bone, crust and sediment in Avizo 7.0. The second specimen represents the anterior region of a skull of *Ophisaurus* still under study, and an associated portion of the trunk with the osteoderms in anatomical association. This specimen is not discussed further in this dissertation, but confirms the presence of *Ophisaurus* as a second anguine in the Iberian Miocene, together with the previously known *Pseudopus* (Bolet et al., 2013b).

4.4. Images

The images included in this work include photographs, drawings, and 3D models obtained from CT-scans. Photographs were taken either with a standard digital camera, a camera attached to a stereomicroscope, or correspond to ESEM pictures taken at the Universitat de Barcelona and University College London. Drawings were made with a camera lucida attached to a stereomicroscope, and in some cases the drawing was then finalised using Adobe Illustrator CS3.

4.5. Bibliography

A review of the available bibliography for Iberian fossil lizards was achieved during the process of writing the papers that form this dissertation. In the case of the Late Jurassic-Early Cretaceous period, the bibliography represented a good starting point for the corresponding chapters, because new material needed comparison with previously published specimens that date back to 1915. A review of previous works on Mesozoic Iberian lizards is provided in Chapter 5. Since the publication of Bolet and Evans (2010b), and apart from the additions provided in this dissertation, a few other works have been published (Narváez and Ortega, 2010; Houssaye et al., 2013a, b; Evans and Bolet, in press). In contrast, Eocene and Miocene lizard assemblages have only just begun to receive attention, and thus related bibliography is limited. For the Eocene, new Spanish material was compared to that from Silveirinha (Rage and Augé, 2003), which is the only Paleogene lizard assemblage previously described from the Iberian Peninsula. However, because this material was rather limited, comparison was extended to include European Paleogene material housed at the MNHN, and the related bibliography was also revised. Chapters 8 and 9 report results from a single late Eocene Iberian locality, but research on numerous additional assemblages from early, middle and late Eocene is in progress (see Bolet and Evans, 2010a). Miocene material is abundant in Iberian localities, but descriptions have been limited at best. Again, previous work on other European localities has served for comparison (e.g. Roček, 1984; Augé and Rage, 2000; Augé, 2003; Čerňanský, 2007, 2010, 2011, 2012; Čerňanský and Bauer, 2010; Čerňanský and Joniak, 2009; Klembara, 2008, 2012; Klembara et al., 2010; Kosma, 2004; Rage and Bailon, 2005; Böhme, 2010; Venczel, 2006; Venczel and Sanchiz, 2006; Venczel and Ştiucă, 2008). Apart from the papers that correspond to Chapter 10 and Annex I, some preliminary reports on Miocene Iberian lizards demonstrate that they are gaining attention (Bolet et al., 2013a, b; Delfino et al., 2011, 2013). Other work is in progress, including a review of the herpetofauna from the Vallès-Penedès Basin (Delfino et al., in progress). In contrast, Quaternary lizard assemblages from the Iberian Peninsula have been the subject of exhaustive descriptions. As these are known to represent a continuation of Miocene faunas, they have also been used for comparison, and extensive existing literature has been revised.

4.6. Taxonomic disclaimer

The name of the new taxon described in Annex I is not valid under the rules of the International Code of Zoological Nomenclature. The publication where it will be formally erected is in process of review, and the name proposed here will be retained if possible.

A NEW LIZARD FROM THE EARLY CRETACEOUS OF CATALONIA (SPAIN), AND THE MESOZOIC LIZARDS OF THE IBERIAN PENINSULA

5

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A new lizard from the Early Cretaceous of Catalonia (Spain), and the Mesozoic lizards of the Iberian Peninsula

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ABSTRACT

The Early Cretaceous (late Berriasian-early Valanginan) locality of La Pedrera de Meià (Montsec, Catalonia, Spain) has yielded remains of at least two genera of lizards: *Meyasaurus* (including its synonym *Ilerdaesaurus* and possibly *Rubiessaurus*) and *Eichstaettisaurus*. A new lizard specimen is described and named here as *Pedrerasaurus latifrontalis* gen. et sp. nov., being sufficiently distinct from other known genera to warrant the erection of a new taxon. The results of phylogenetic analysis are equivocal but support the placement of the new genus within Scincogekkonomorpha. The new taxon resembles *Meyasaurus*, a genus widely distributed in the Lower Cretaceous of the Iberian Peninsula, in having bicuspid teeth but differs in lacking the characteristic fusion and constriction of the frontals. *Pedrerasaurus* and *Meyasaurus* may be related, but the support for this is not strong. Recognition of a clearly distinct form with bicuspid teeth is significant in terms of attribution of fragmentary material recovered from other Jurassic-Cretaceous localities.

1. Introduction

Mesozoic lizards have been reported from a number of Jurassic and Cretaceous localities in the Iberian Peninsula (Fig. 1). The first recorded material is that representing *Meyasaurus faurai* (Vidal, 1915) from the Catalan locality of La Pedrera de Meià (Montsec, Catalonia, Late Berriasian-Early Valanginian). Further articulated material of *Meyasaurus* has been recorded from the same locality (as ‘*Ilerdaesaurus*’ Hoffstetter, 1966 [Evans and Barbadillo, 1997] and possibly ‘*Rubiessaurus*’ Gómez-Pallerola, 1979 [see Evans and Barbadillo, 1998b]) and from Las Hoyas (Cuenca, Castilla-La Mancha, Late Barremian). Disarticulated material is also recorded from Uña and Galve (Cuenca, Barremian). *Meyasaurus* is thus the most fully known Iberian Mesozoic lizard. It is characterised by marked median constriction of the fused frontals and bicuspid teeth in the marginal dentition, the latter being uncommon in other Jurassic and Early Cretaceous taxa. In consequence, fragmentary jaws containing bicuspid teeth from contemporaneous Iberian deposits have until now been attributed to *Meyasaurus*. Here we describe a new lizard specimen (Fig. 2) from La Pedrera de Meià. It resembles *Meyasaurus* in general body proportions and in having bicuspid teeth, but differs in cranial structure, demonstrating the presence of an additional bicuspid lizard taxon.

2. Geology and materials

2.1. Geology

The lithographic limestone deposits of El Montsec (Lleida, Spain) belong to an Upper Berriasian-Lower Valanginian freshwater sequence (Peybernès and Oertli, 1972; Brenner et al., 1974; Barale et al., 1984) limited by two unconformities. The one at the base separates these deposits from underlying Jurassic marine carbonates and, locally, from a Lower Berriasian marine unit. The unconformity at the top separates the freshwater sequence from Barremian coastal and shallow marine limestones. The vertebrate bearing sequence itself is composed of two lithostratigraphic units, related to each other by a lateral change of facies (Peybernès, 1976): the La Serra del Montsec Charophyte Limestones and the La Pedrera de Rúbies Lithographic Limestones, the La Pedrera de Meià site situated in the latter. The palaeoenvironment of the locality has been interpreted as a shallow, near-coastal lake, the anoxic sediments of which usually preserved complete, articulated specimens of invertebrates and fishes, and rarer material representing frogs, crocodiles, lizards and birds (Barale et al., 1994).

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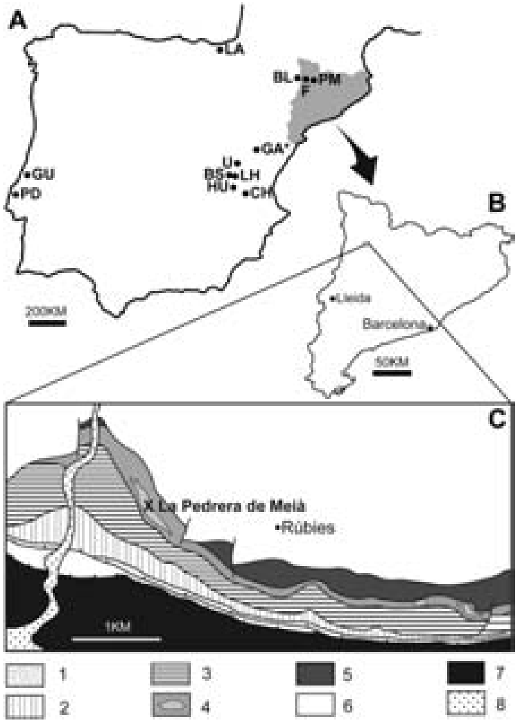

Fig. 1. Situation of La Pedrera de Meià locality; map of the Iberian Peninsula (a) with situations of the localities mentioned in the text; map of Catalonia (b) showing the Montsec de Rúbies region; geological map (c) of the Montsec de Rúbies region. 1: Triassic; 2: Lias; 3: Dogger and Malm; 4: Lower Cretaceous freshwater limestones with lithographic limestones in grey (upper Berriasian-lower Valanginian); 5: Lower Cretaceous shallow water marine limestones (upper Barremian-upper Aptian). 6: Upper Cretaceous; 7. Tertiary; 8. Quaternary. Modified from Peybernès (1976) and Mercadé (1991). BL: Blasi 2, BS: Buenache de la Sierra, CH: Chera, F: Fontllonga 6, GA*: Galve (several localities), GU: Guimarota, HU: Lo Hueco, LA: Laño, LH: Las Hoyas, PD: Porto Dinheiro (or Pinheiro), PM: La Pedrera de Meià, U: Uña.

2.2. Materials

The material described herein is a fully articulated skeleton in which the skull and postcranial bones are preserved in association and exposed in dorsal view (Fig. 2).

Institutional abbreviations: AMNH, American Museum of Natural History, New York, USA; MGB, Museu de Geologia de Barcelona, Barcelona, Spain; LH, Museo de Cuenca (Las Hoyas material), Cuenca, Spain.

3. Systematic palaeontology

Lepidosauria Haeckel, 1866
Squamata Oppel, 1811
Scincogekkonomorpha Sukhanov, 1961
Genus *Pedrerasaurus* gen. nov.
Derivation of name. From La Pedrera de Meià fossil locality and the Greek, *Sauros*, reptile.
Type and only species. *Pedrerasaurus latifrontalis sp.* nov.

Diagnosis. As for species.

P. latifrontalis sp. nov.
Type specimen. MGB 47250 (Fig. 2)
Type locality. La Pedrera de Meià (Montsec, Catalonia, Spain).

Stratigraphic horizon. La Pedrera de Rúbies Lithographic Limestones Unit (late Berriasian-early Valanginian).

Derivation of name. From the latin "lati" —meaning wide, and "frontalis" —meaning frontal, in reference to its frontal shape.

Differential diagnosis. *Pedrerasaurus* resembles *Meyasaurus* and differs from all other described Jurassic and Early Cretaceous lizards in having bicuspid posterior teeth, but differs from *Meyasaurus* in having broader, paired frontal bones (fused and very narrow in *Meyasaurus*) with the median suture showing strong interdigitations in its posterior half, rugose rather than vermiculate sculpture on the skull bones, a slender, rather than expanded squamosal, shorter postparietal processes on the parietal, and less disparity in length between the anterior and posterior dorsal ribs. *Pedrerasaurus* resembles *Ardeosaurus* from the Jurassic Solnhofen Limestone in having paired frontals with an interdigitated suture, but differs in having: shorter postparietal processes; a narrower squamosal (it is broader, dorsoventrally flattened, and restricts the upper temporal fenestra in *Ardeosaurus*); a braincase that is completely covered by the parietal (it is exposed for some distance behind it in *Ardeosaurus*): no osteoderms on the skull; and a higher number of presacral vertebrae (26 v. 23 in *Ardeosaurus*). The tooth tip morphology of *Ardeosaurus* is currently unknown.

Remarks. *Rubiessaurus* Gómez Pallerola (1979), also from La Pedrera de Meià locality, is based on a partial, poorly preserved, postcranial skeleton. The original description was inadequate and, as preserved, cannot be diagnosed to the exclusion of *Meyasaurus* (Evans and Barbadillo, 1998b).

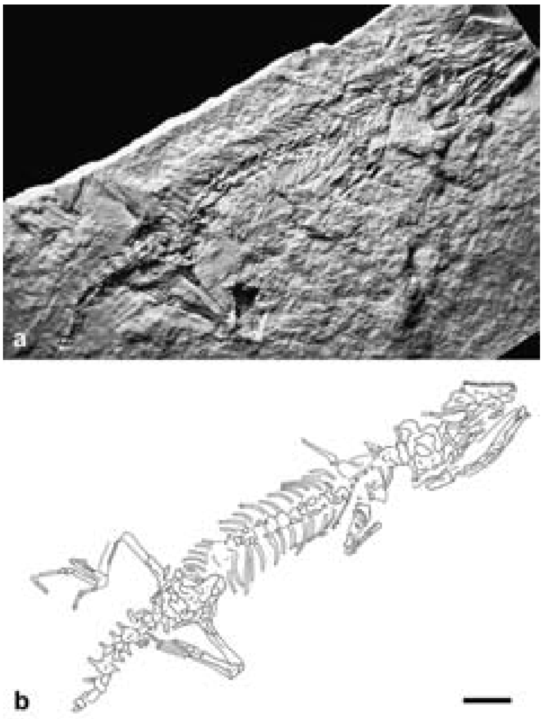

Fig. 2. *Pedrerasaurus latifrontalis* gen. et sp. nov.; type specimen, MGB 47250; photograph (a) and drawing (b) of the complete specimen in dorsal view. Scale bar = 5 mm.

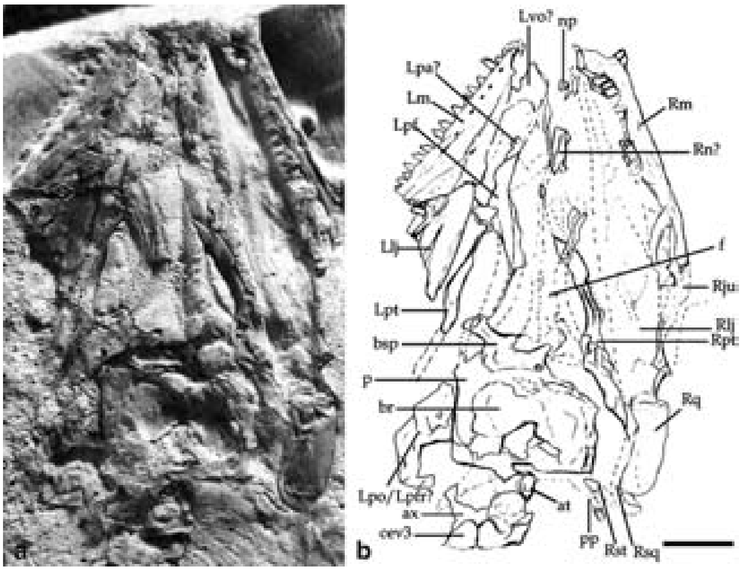

Fig. 3. *Pedrerasaurus latifrontalis* gen. et sp. nov; type specimen, MGB 47250; photograph (a) and drawing (b) of the skull. at: atlas, ax: axis, br: braincase, bsp: basisphenoid, cev3: third cervical vertebra, f: frontal, ju: jugal, L: left, lj: lower jaw, m: maxilla, n?: nasal?, np: nasal process of the premaxilla, p: parietal, pa?: palatine?, pf: prefrontal, po/pfr?: postorbital/postfrontal?, pp: postparietal process of the parietal, pt: pterygoid, q: quadrate, R: right, sq: squamosal, st: supratemporal, vo?: vomer?. Scale bar = 3 mm.

4. Description of holotype specimen MGB 47250

4.1. Introduction

The holotype of *Pedrerasaurus*, MGB 47250 (Fig. 2), comprises a fully articulated skeleton in which the skull and postcranial bones are preserved in association. Originally it was probably complete, but some bones were detached with and remained adhered to the counterpart block which was not recovered. Nevertheless, the shape of some of these elements can be reliably reconstructed from their impressions. Skin traces can be observed using a low angled light, revealing the shape and size of individual scales in the best-preserved zones. The snout-vent length (SVL), estimated as the distance from the tip of the premaxilla to the posterior end of the second caudal vertebra (Evans et al., 2004), is about 45 mm. Incomplete ossification of the ends of the limb bones, and the lack of fusion between the components of the pectoral and pelvic girdles, indicate that MGB 47250 represents an immature individual.

4.2. Skull (Fig. 3)

The skull, exposed in dorsal view, is crushed. Although it was probably originally complete, parts of the skull roof and lower jaws were removed with the counterpart and are represented by impressions. At the anteromedial tip of the skull, there are some fragments of tooth enamel, probably from the premaxillary teeth. The premaxillae were mainly lost with the counterpart, but the paired tips of the nasal processes are preserved in situ.

Compression has partially disarticulated the left maxilla so that it is preserved parallel to the bedding plane. It is complete anteriorly and broken posteriorly. The exposed labial surface (Fig. 4a) bears seven neurovascular foramina and a subtle rugose ornamentation. Fifteen teeth are visible occupying 17 loci. The right maxilla is broken and is preserved perpendicular to the bedding plane. The first two teeth can be seen in a side view of the block, within a small maxillary fragment that has been broken and slightly displaced. The remaining teeth of the right maxilla, five teeth occupying seven tooth positions, can only be seen side on. In this view, sections of the lower jaws and the maxilla or premaxilla are also visible. Little of the frontals (Fig. 3) is preserved, except for a fragment in the left anterorbital region in contact with the prefrontal and another in the same region on the right side, over the right pterygoid. However, the shape of the frontals can be determined from the well-preserved impressions left on the slab (Fig. 3). A well-defined straight median line in the impression is indicative of paired frontals. This line becomes distinctly wavy posteriorly, indicating the presence of a short area of interdigitation, a feature frequently seen in extant lizards where it strengthens the skull roof between the orbits. The frontals also have a subtle rugose ornamentation. The frontoparietal suture is not clear and it is not possible to determine the presence or absence of parietal tabs. The parietal is mostly in impression, with bone fragments remaining at the tip of the right postparietal process and at the margins where rugosities are visible. Although the bone is not well preserved, its overall shape can be reconstructed from the impressions. It is roughly square, without strong bilateral emargination from the upper temporal fenestrae, and with vertical lateral margins and rather short postparietal processes.

Of the remaining skull bones, part of the left prefrontal lies against the frontal impression, showing the same pattern of sculpture as that on the other roofing bones. The presence or absence of a lacrimal cannot be determined. The nasals are poorly preserved, but their maximum extension can be inferred from the boundaries of surrounding bones (maxillae, prefrontals and frontals). Where the parietal has been removed, the braincase and its basipterygoid processes are visible. However, crushing and the resulting loss of volume of the skull are most evident in this region, with the layers compacted into one another. The posterior part of the right jugal is preserved as an impression from which a complete

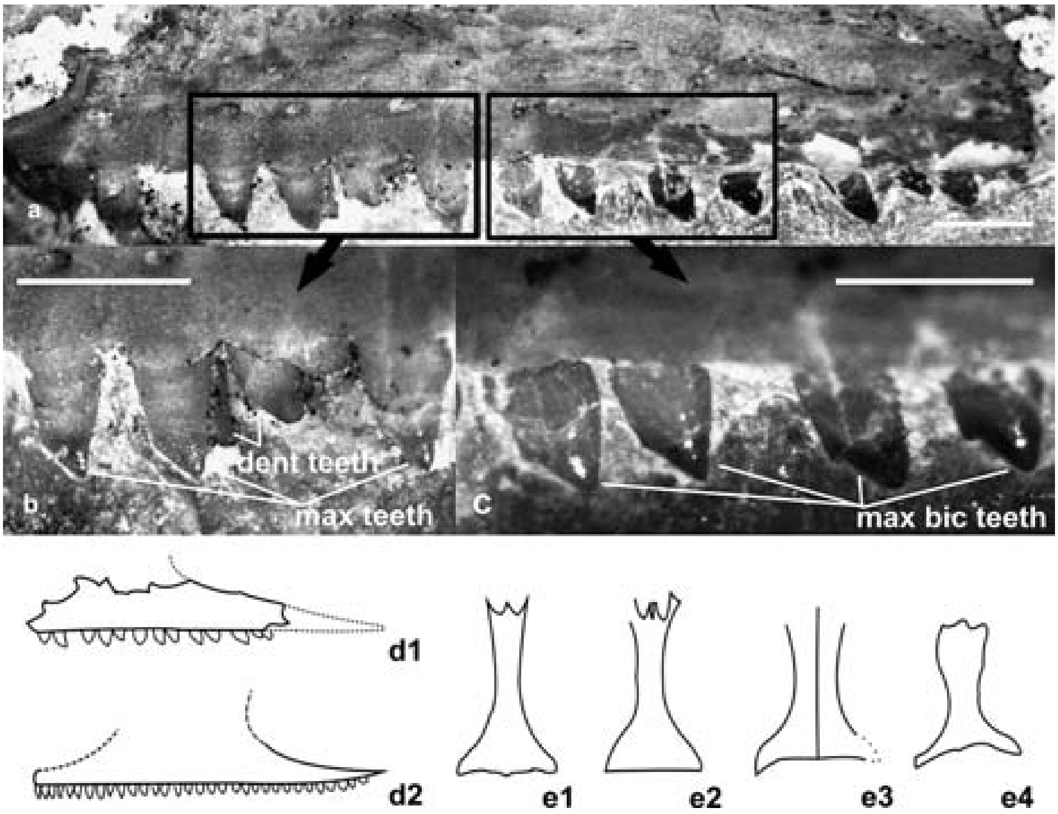

Fig. 4. Details of the skull in *Pedrerasaurus latifrontalis*; (a) detail of the maxilla, scale bar = 1 mm; (b) detail of the anterior teeth, scale bar = 1 mm; (c) detail of the posterior teeth, scale bar = 1 mm; (d) outlines of maxillae of MGB 47250 (d1) and *Meyasaurus diazromerali* (d2), reduced to the same size for comparison; (e) outlines of the frontals of *M. diazromerali* (e1), *M. crusafonti* (e2), MGB 47250 (e3) and *Eichstaettisaurus sp.* (e4), reduced to the same size for comparison. dent teeth: dentary teeth, max teeth: maxillary teeth, max bic teeth: maxillary bicuspid teeth.

jugal arch can be inferred, although it is interrupted by the impression of the right mandible. The same can be seen in the corresponding position on the left side, although the boundary between maxilla and jugal is poorly defined. Further posteriorly, the well-preserved right quadrate is visible in anterior view. It is rather slender and of simple morphology, without a strongly differentiated cephalic condyle or squamosal surface, but appears to have had a discrete pterygoid lappet. Medial to the quadrate, there is a long narrow impression that is interpreted as a slender 'hockey-stick' shaped squamosal (i.e. with a short curved ventral process but lacking a dorsal process). Between this and the parietal is a smaller impression that probably represents the supratemporal. The corresponding region on the left side is more difficult to resolve; bone fragments here may be parts of the postfrontal and/or quadrate.

The anterior region of the palate is exposed due to the removal of the frontals, nasals and most of the right maxilla. This region is also difficult to interpret but, from their position, the exposed fragments are probably parts of the left and right vomer, and right palatine. Overlying the posterior end of the right maxilla or the anterior part of the jugal there is a bone fragment that could be part of the ectopterygoid. The right pterygoid is partially preserved close to the midline, but its lateral flange, i.e. the one that would contact the ectopterygoid, is missing. The anterior part of the quadrate ramus bears a depression that could be the pit for the epipterygoid, but the state of preservation renders this uncertain. Part of the left pterygoid is visible inside the left orbit between the left maxilla and the frontal. It continues posteriorly as an impression.

4.3. *Lower jaw (Fig. 3)*

The lower jaws are represented by parts of the dentaries, a splenial, and impressions of the coronoid and retroarticular regions. The right lower jaw has left a detailed impression of its external face with some trace of sutural contacts. The dentary is represented only by a fragment of the anterior symphysis, two anterior teeth, and part of a posterior tooth. Further teeth are preserved in impression but an accurate count is not possible. An impression posterior to the dentary may represent the coronoid process, whereas the retroarticular process is partially preserved near the right quadrate. The anterior end of the left dentary is covered by the maxilla except for four small teeth. Its posterior end is exposed in lingual view, with the Meckelian canal closed by the splenial. Two mature teeth are preserved posteriorly, the penultimate one represented only by its apex. Posterolingual to the last mature tooth there is a tiny tooth crown. The post-dentary region of the left lower jaw is missing.

4.4. The dentition

The most clearly preserved teeth are those of the left maxilla, as seen in labial view (17 tooth positions). The anterior maxillary teeth are monocuspid and slightly posteriorly recurved (Fig. 4b) whereas the posterior teeth are straight and weakly bicuspid with a principal cusp and a tiny anterior accessory cuspule (Fig. 4c). The dentary teeth are mainly obscured and their number cannot be estimated. The only complete anterior tooth (left dentary) is bicuspid with weak apical striae, whereas the one complete posterior tooth is straight and appears monocuspid, although its crown may be damaged. Based on this tooth, the implantation was pleurodont. Occasional gaps in the maxillary tooth row indicate active replacement. The small tooth lying behind the last mature one at the posterior end of the left dentary is posterolingual in position, but whether this is indicative of anguimorph-type posterolingual replacement, or simply an aberration, is impossible to determine without a more complete lingual view of the tooth row.

4.5. Axial skeleton (Fig. 5)

The vertebrae and ribs are not well preserved and most of the bone was lost with the counterpart. Although the remaining impressions provide some information, there is distortion of the pectoral and cervical regions and some vertebral boundaries are difficult to determine precisely. This is compounded by the fact that the neural arches of the vertebrae may not be fully fused. Nonetheless, there were an estimated six cervical vertebrae and 20 dorsal vertebrae, giving a count of about 26 presacral vertebrae in total. The first clearly identifiable vertebral remnant is the odontoid process of the axis. The bone fragments anterior to that must therefore be part of the atlas. The first distinct cervical vertebra bearing short ribs is the fourth. The posteriormost presacral vertebrae are preserved in situ but are too damaged to provide any information concerning their morphology. Posterior to those, the two sacral vertebrae are also only partially preserved. In contrast, the first nine caudal vertebrae are nearly complete. Each bears a single pair of transverse processes that appear to be perpendicular to the tail axis or slightly anteriorly directed. The length of these transverse processes decreases gradually posteriorly along the tail. The nine anterior caudals are followed by two or three poorly preserved vertebrae, but the rest of the robust tail is missing. The preserved vertebrae seem to lack autotomy planes. This could be a preservational artefact or may indicate that autotomy planes, if present, began posterior to this point. There seems to be a change in the angle of the tail at the end of the preserved portion that could be the result of either a breakage between vertebrae or the beginning of a zone of autotomy. The ribs are simple and thin. There is only a gradual length reduction in the posterior thoracic region, but this could be a juvenile trait (see below). At least six inscriptional ribs have left partial impressions, three to the left upper and three to the lower right (Fig. 5).

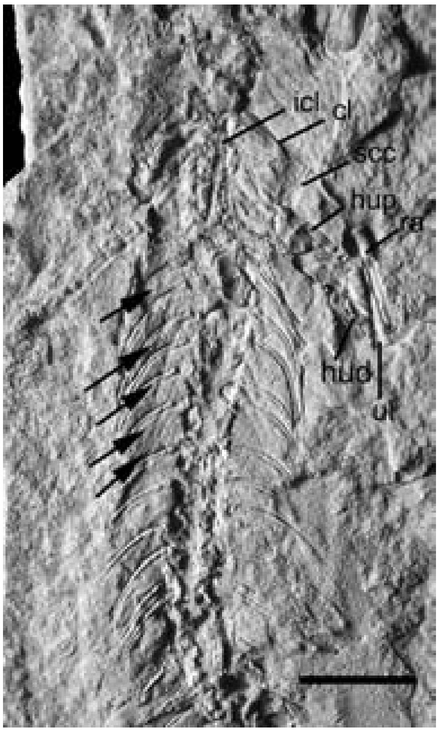

Fig. 5. *Pedrerasaurus latifrontalis* gen. et sp. nov; type specimen, MGB 47250; photograph of the trunk, arrows indicate xiphisternal rib impressions. cl: clavicle, hud: humerus distal end, hup: humerus proximal end, icl: interclavicle, ra: radius, scc: scapulocoracoid, ul: ulna. Scale bar = 5 mm.

4.6. Pectoral girdle and forelimbs (Fig. 5)

The left forelimb is represented only by an impression to the side of the left pectoral girdle that almost certainly represents the humerus. On the right side, there is a complete impression of the unfused right scapula and coracoid, the latter showing at least one anterior emargination. In the midline, there is a clear impression of a delicate cruciform interclavicle. Close to it is part of the right clavicle which seems to be unexpanded (possibly a juvenile trait given the interclavicle shape). Posterolateral to the girdle there is a bone fragment that is interpreted as the proximal end of the right humerus, bearing what may be a small nutrient foramen. If this interpretation is correct the epiphysis is not ossified. The radius and ulna are preserved in parallel. As for the humerus, the epiphyses are not ossified, this being most evident at the proximal end of the ulna which lacks an olecranon process. Under the humerus there is an elongated bone that is probably a metacarpal from the right manus. This, in turn, lies adjacent to two further probably metacarpals. The phalanges are not visible but may be embedded in the matrix.

4.7. Pelvic girdle and hindlimbs (Figs. 6 and 7)

The pelvic girdle is almost complete and is one of the better-preserved regions. Under the sacral vertebrae are the left ischium and fragments of the right ischium. Anterior to these there is a partial left pubis, the shape of which can be inferred from the fragments and the impression. It is proximally robust, perforated by an ovoid pectineal foramen, and tapers distally into a short symphysial process. The right pubis is also partially preserved, but its interpretation is more problematic because another impression overlaps it. The two ilia are broken anteriorly, but possess long slender iliac blades that extend to the transverse process of the first caudal vertebra. The elements of the pelvic girdle do not appear to be co-ossified.

The right hind limb is better preserved than the left. It includes part of the femur, and parts of the shorter tibia and fibula, all of which are robust but lack ossified epiphyses. Distal to the tibia and fibula, the astragalocalcaneum (probably not fully conjoined) bears a facet for the (unossified) tibial distal epiphysis. An indistinct distal impression probably represents distal tarsal four but, as in immature extant lizards, it may not have been fully formed. The metapodials are in

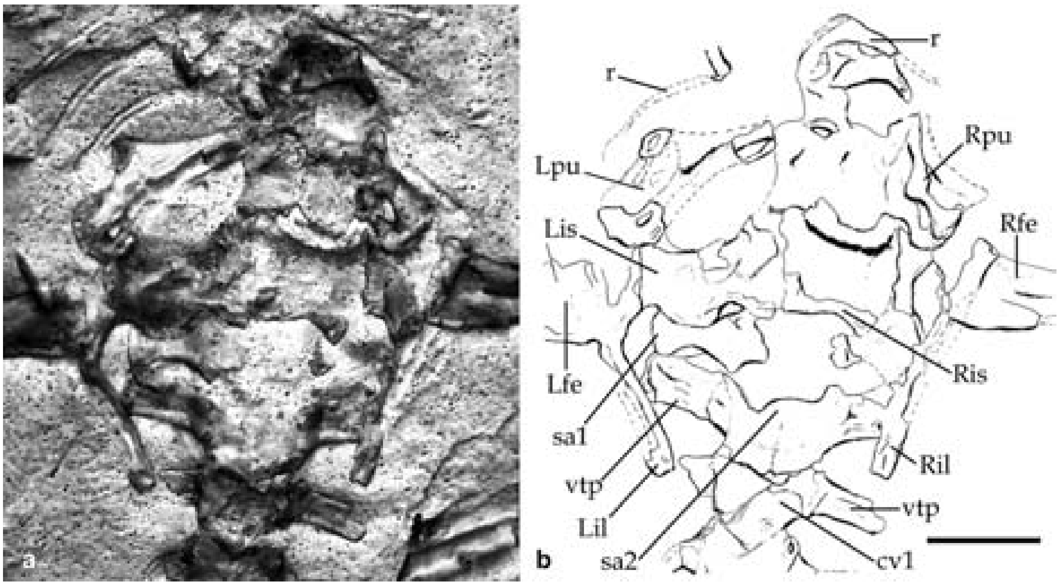

Fig. 6. *Pedrerasaurus latifrontalis* gen. et sp. nov; type specimen, MGB 47250; photograph (a) and drawing (b) of the pelvic girdle. cv1: first caudal vertebra, il: ilium, is: ischium, L: left, pu: pubis, r: rib, R: right, sa1: first sacral vertebra, sa2: second sacral vertebra, vtp: vertebral transverse process. Scale bar = 2 mm.

impression but, as preserved, were robust, and the phalanges are obscured by matrix around the tail. On the left hind limb, the dimensions of the femur, tibia and fibula can be taken from their impressions (Table 1). The astragalocalcaneum and metapodials are without clear impressions and although some phalanges are partially preserved, it is not possible to give a phalangeal formula.

4.8. Skin impressions

Subtle skin impressions can be seen under low angled light, notably in the neck and tail regions. The scales are rather rounded rhomboids in the former and more distinctly rhomboidal in the latter. A change of rock texture marks the boundary between skin impressions and unmarked matrix.

5. Discussion

5.1. Ontogenetic status of MGB 47250

Several features of MGB 47250 are indicative of immaturity (Maisano, 2002 and personal observations) including: a head that is large in proportion to the body (Fig. 2); orbits that are large in proportion to the skull (Fig. 3); thin skull bones (Fig. 3); unossified long bone epiphyses (Figs. 5–7); pectoral girdle (scapula, coracoid,

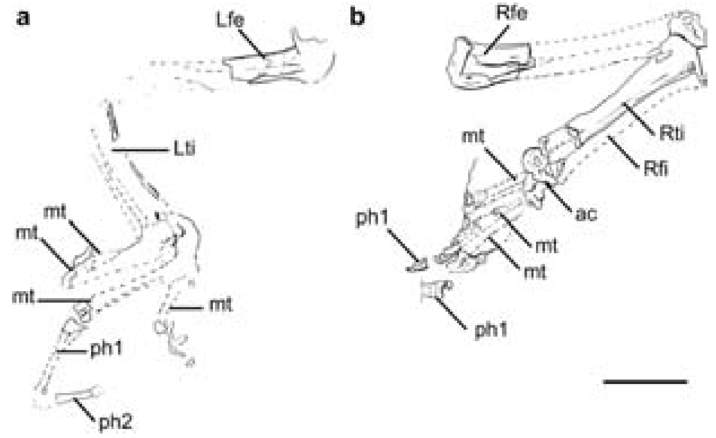

Fig. 7. *Pedrerasaurus latifrontalis* gen. et sp. nov; type specimen, MGB 47250; drawing of the left (a) and right (b) forelimbs. ac: astragalocalcaneum, fe: femur, fi: fibula, L: left, mt: metatarsal, ph1: first phalanx, ph2: second phalanx, ti: tibia.

Table 1
Measurements (in mm) and proportions of MGB 47250 and *Meyasaurus diazromerali*, for comparison. Met IV: fourth metatarsal, Orb: orbit. For other abbreviations see the caption to Fig. 7.

	Fe	Ti	Fi	Met IV	Ph[a]	Ra	Ul	SVL	Skull
MGB 47250	7.65	5.84	5.67	3.91	3.00	4.42	4.33	48.00	17.02[b]
*Meyasaurus**	7.70	5.00	5.13	4.23	2.69	4.44	4.36	36.67	12.56

	Ti/Fe	Fe/SVL	Met/Ti	Ph/Met	Ra/SVL	Skull/SVL	Orb/Skull
MGB 47250	0.76	0.16	0.67	0.77	0.09	0.35	0.33
*Meyasaurus**	0.65	0.21	0.84	0.64	0.12	0.34	0.3

* Measurements for *Meyasaurus* taken from *Meyasaurus diazromerali* holotype (LH 370).

[a] First phalanx from the same toe as Met IV.

[b] The tip of the snout is lost, total skull length is estimated.

Fig. 5) and pelvic girdle (ilium, pubis, ischium, Fig. 6) components not co-ossified; astragalus and calcaneum probably not fully co-ossified (Fig. 7); and vertebral neural arches barely fused. Although the MGB 47250 individual was clearly not a hatchling (the skull is too well formed), these features suggest that it was immature at death and could have at least doubled in size had it lived to reach maturity. The adult size would probably have been close to *Meyasaurus diazromerali* specimens from Las Hoyas (Evans and Barbadillo, 1997) but smaller than *M. faurai* (Vidal, 1915). However, *M. diazromerali* individuals of the same size as the *Pedrerasaurus* specimen (MGB 47250) are more gracile. This is particularly obvious when comparing limb bones and *Pedrerasaurus* seems to have been substantially more robust than *M. diazromerali*.

5.2. Comparison

The bicuspid dentition of MGB 47250 precludes attribution to any Late Jurassic and Early Cretaceous genus with the exception of *Meyasaurus* Vidal, 1915 and *Durotrigia* Hoffstetter, 1967 (Berriasian, England). However, the latter taxon is represented by a single eroded fragment of dentition and is here considered to be nomen dubium. *Ardeosaurus* Meyer, 1860 (Tithonian, Germany) could also be a candidate as its dentition is unknown. It differs from MGB 47250 in having a more robust skull with heavy ornamentation and a restriction of the upper temporal fenestra by the surrounding bones. Those differences could, plausibly, be ontogenetic but *Ardeosaurus* also has a lower presacral vertebral count (23 [Mateer, 1982] compared with 26 or more in MGB 47250). *Meyasaurus,* however, is broadly similar to MGB 47250 in having comparable body proportions (Table 1); no osteoderms; a heterodont dentition composed of slightly recurved, monocuspid anterior pleurodont teeth (Fig. 4) and bicuspid posterior teeth (Fig. 4). However significant differences exist.

The teeth of MGB 47250 are taller in relation to the tooth bearing bone than in described specimens of *Meyasaurus*, and the estimated tooth count (fewer than 20, Fig. 4d) seems to be lower than in *M. crusafonti* and *M. diazromerali* (30), and or *Meyasaurus unaensis* (40) (Evans and Barbadillo, 1997). The posterior teeth of *Meyasaurus*, at least in *M. crusafonti* and *M. unaensis*, are higher-crowned than the anterior ones, while in MGB 47250 there seems to be the opposite trend, at least in the maxilla. The lower jaw of MGB 47250 is more robust than that of *Meyasaurus*, and has a straighter ventral outline than that of *M. crusafonti*. The dentary of MGB 47250 is also longer than those of *Meyasaurus*. However these dental and osteological differences cannot be used to distinguish MGB 47250 unequivocally from *Meyasaurus*, as characters vary between species in the latter genus. Of greater significance is frontal morphology. The frontals of all species of *Meyasaurus* are consistent in being fused and highly constricted between the orbits so that they form a narrow interorbital bar. This characteristic morphology allows them to be identified even when disarticulated and isolated. The frontals of MGB 47250 are preserved in impression but their morphology is quite clear. As in many lizards, they are embayed by the orbits but the interorbital bar remains substantial (Fig. 4e); the cristae cranii are more weakly developed; and the frontals are generally broader at every point than the slender frontals of *Meyasaurus*. Furthermore, a clear impression of a midline suture line that is straight anteriorly but becomes strongly sinuous in the mid-orbital region shows that the frontals of MGB 47250 were paired and that they remained so in the mature animal. The interdigitation is a structural feature that develops to resist torsional stress in this area of the bone. Juvenile specimens of *Meyasaurus* have paired frontals which become fused during ontogeny (Evans and Barbadillo, 1997), leaving a midline dorsal groove that is not visible in ventral view. However, where frontals are paired in the juvenile and fuse in the adult, the midline suture is a straight abutment until it fuses.

There are other differences. As in *Meyasaurus*, and most other lizards, the parietal of MGB 47250 seems to be unpaired, but the postparietal processes are much shorter than those of *Meyasaurus*. The squamosals of MGB 47250 are slender whereas those of *Meyasaurus* broaden posteriorly and bear a slight dorsal process, even in immature specimens (Evans and Barbadillo, 1997). A subtle rugose sculpture (not vermiculate as in *Meyasaurus*) is visible on the prefrontal, the frontal and the parietal, although this difference could be ontogenetic. Tooth replacement in *Meyasaurus* is lingual; that of MGB 47250 is equivocal given the posterolingual position of the only visible replacement tooth.

Some of the differences in postcranial anatomy between *Meyasaurus* and MGB 47250 may reflect immaturity (e.g. rib proportions) or damage (e.g. the lack of obvious autotomy septa). However the transverse processes of the caudal vertebrae are long, narrow and rounded in *Meyasaurus*, but broader, more angulated, and somewhat more robust in MGB 47250, despite its immaturity. This greater robusticity is also seen in other parts of the skeleton (see above 5.1. Ontogenetic status), suggesting that the adult of *Pedrerasaurus* was more heavily built than that of *Meyasaurus*.

In summary MGB 47250 resembles *Meyasaurus* in having bicuspid teeth in its dentition, but displays several differences in its cranial morphology (notably in frontal and squamosal morphology) which preclude its attribution to that genus. Separate generic distinction therefore seems appropriate for MGB 47250 although it is not an ideal holotype giving its immaturity and incomplete preservation.

A situation where two genera are closely similar dentally and postcranially, but have distinct frontals, occurs within recent lacertids (Barahona, 1996; Barahona and Barbadillo, 1997). In *Lacerta* and *Gallotia*, for example, hatchlings and juveniles present strongly constricted frontals, but these broaden with maturity, as would be the case in *Pedrerasaurus*. The genus *Acanthodactylus*, however, maintains strongly constricted frontals in adults, as would be the case of *Meyasaurus*. Moreover, some species of *Acanthodactylus* and *Eremias* have unpaired frontals in both juveniles and adults (Arnold, 1983; El-Toubi and Soliman, 1967) while most other lacertids retain paired frontals even in adults. The first condition is seen in *Meyasaurus* and the second in *Pedrerasaurus*.

Between the Early and Late Cretaceous, squamate assemblages underwent a global transition with the gradual extinction of lineages surviving from the Jurassic, e.g. paramacellodids and eichstaettisaurs (e.g. Evans, 2003; Evans and Manabe, 2000; Evans and Wang, 2005a,b, 2010; Nydam and Cifelli, 2002, and references therein), and the appearance of early representatives of more derived lineages (e.g. Nydam et al., 2007; Evans and Manabe, 2008). Few Early Cretaceous genera persisted to the Late Cretaceous, but as some temporally extensive genera are known (e.g. *Parviraptor* which ranges from the Middle Jurassic to the Early Cretaceous [Evans, 1994]), comparison of *Pedrerasaurus* with later Cretaceous lizards could be instructive.

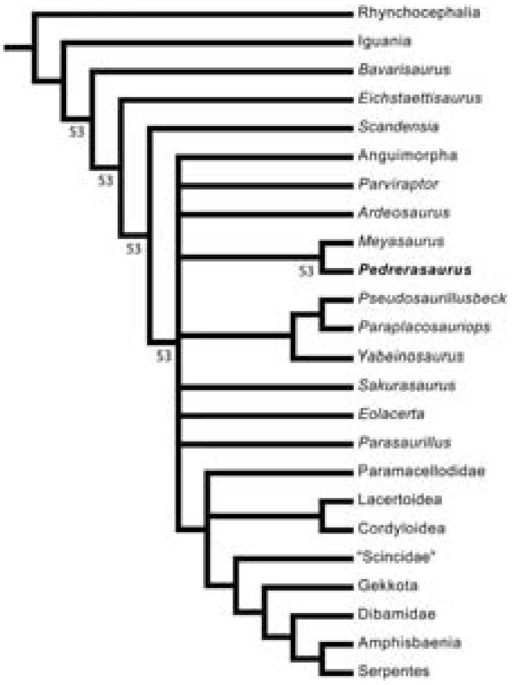

Fig. 8. 50% Majority rule tree of 2440 shortest recovered trees from the analysis described in the text. Some fossil taxa included in the analysis (AMNH Gekkonomorph, *Tepexisaurus*, *Ornatocephalus*, and *Hymenosaurus*) are not shown in the figure because they are not relevant to *Pedrerasaurus*. Major groups have been collapsed in the interest of space. *Parasaurillus* is "*Pseudosaurillus*" *sp.* of Conrad (2008) (Evans and Searle, 2002). Numbers indicate the percentage of trees that recovered the clade.

The Late Cretaceous record of lizards from the Iberian Peninsula is limited, but screen-washing of samples from some localities has yielded new material. Currently, only fragmentary material from Laño (Álava province) has been described in any detail (Rage, 1999; genus and species A in Astibia et al., 1991). This material consists of an isolated tooth and two bone fragments (lower jaw or maxilla) containing two further teeth. These teeth are pleurodont, cylindrical, and rather short. Some are conical, with an almost imperceptible second cusp; others are more obviously bicuspid with a main cusp and an additional small cuspule. The latter resemble the anterior teeth of *Pedrerasaurus*, but further comparison is limited. According to Rage (1999), the bases of the Laño teeth are surrounded by cementum, a feature not visible in *Pedrerasaurus* because only the most posterior dentary teeth are exposed in lingual view. Rage referred the Laño material to Scincomorpha, and suggested that the presence of basal cementum might indicate teiid affinities. However, the full extent of the cementum deposit cannot be determined in these specimens.

Outside the Iberian Peninsula, only a few Late Cretaceous lizards have been described with a heterodont dentition including both monocuspid and bicuspid teeth. These include: fragmentary, indeterminate 'scincomorph' remains from the Maastrichtian of Hateg, Rumania (Grigorescu et al., 1999; Codrea et al., 2002); *Estescincosaurus* (=*Sauriscus*) (Scincomorpha, Scincidae) from the Late Cretaceous of the USA (Estes, 1964; Sullivan, 1997); *Globaura venusta*, from the Santonian-Campanian of Mongolia (Borsuk-Białynicka, 1988); and *Parmeosaurus scutatus* from the Late Cretaceous of Mongolia (Gao and Norell, 1999). However, these genera differ from *Pedrerasaurus* in the general morphology of the skull, where known and, in many cases, in the presence of osteoderms on the skull or body. All of these bicuspid toothed genera have been referred to Scincomorpha (most recently by Conrad, 2008).

5.3. Phylogenetic relationships

Pedrerasaurus was coded into the largest available data matrix (that of Conrad, 2008), with the addition of nine characters and 11 species-level codings to replace the previously composite Iguanidae, Corytophanidae, Crotaphytidae, and Phrynosomatidae (Norell et al. (2007) (276 taxa, 372 characters). The methodology and ordering of Conrad (2008) was followed, with the exclusion of character 364 (biogeography). Multistate characters were treated as polymorphism, and not applicable characters (-) as missing data. The full matrix was run on T.N.T. (Goloboff et al., 2003) because it is too large for PAUP* (Swofford, 2001).

The Ratchet search of TNT resulted in 2440 trees with a length of 3828 steps (CI: 0.129, RC 0.091), as reported by PAUP. The Strict Consensus Tree shows no resolution for most Jurassic and Early Cretaceous fossil taxa, including *Meyasaurus* and *Pedrerasaurus*. In 53% of the trees (Majority Rule Consensus Tree, Fig. 8) *Pedrerasaurus* was placed as the sister taxon of *Meyasaurus*, but in the Adams Consensus Tree (Fig. 9) *Meyasaurus* lies closer to crown-group scleroglossans than does *Pedrerasaurus*. A subset of the matrix (82 taxa, one species per genus and representative mosasauroids only) was run in a heuristic search in both PAUP and TNT. The PAUP search (TL: 1977, CI: 0.239, RC: 0.147) placed a (*Yabeinosaurus (Meyasaurus* + *Pedrerasaurus*)) clade at the base of Anguimorpha, but neither the TNT heuristic search nor a subsequent PAUP 20 taxon Branch and Bound search recovered this topology, instead finding one similar to that of the Adams Consensus with the full matrix.

To explore the question further, we ran two additional analyses (PAUP, Heuristic): one with *Pedrerasaurus*, *Meyasaurus* and representative living forms from the original matrix (59 taxa) and another with *Pedrerasaurus*, *Meyasaurus* and representative fossil forms (48 taxa). Only the first analysis placed *Meyasaurus* and *Pedrerasaurus* as sister-taxa, suggesting that this grouping is an artefact of running incompletely coded fossil taxa with a large number of fully coded living taxa.

Given these inconsistencies, only tentative phylogenetic conclusions can be drawn. Most analyses placed *Pedrerasaurus* as a scincogekkonomorph (sensu Conrad, 2008, i.e. Scleroglossa and its stem taxa), but its position in relation to crown-scleroglossan clades and to *Meyasaurus* is unstable. Minor changes to the component taxa of the matrix (e.g. substituting one iguanian for another) can result in major changes in topology. Similar problems have been encountered with other Jurassic-Cretaceous lizard taxa (e.g. *Eolacerta*, *Meyasaurus*, *Parviraptor*, *Yabeinosaurus*, Evans and Barbadillo, 1997, 1999; Müller, 2001; Evans and Wang, 2005a,b, 2010; Conrad, 2008), even when known from near complete specimens. The grouping of Gekkota with scincids, dibamids, amphisbaenians and snakes in our trees differs from the more traditional one of Conrad (2008), where gekkonomorphs (Gekkota + stem) form the sister clade to the remaining non-iguanian squamates. We do not consider the topology of this part of the tree to be secure and the phylogenetic relationships of limbless squamates remain far from resolved.

5.4. The lizards of the Iberian Peninsula

Compared to other parts of Europe, the Iberian Peninsula has a relatively good, if unevenly distributed, Mesozoic squamate record

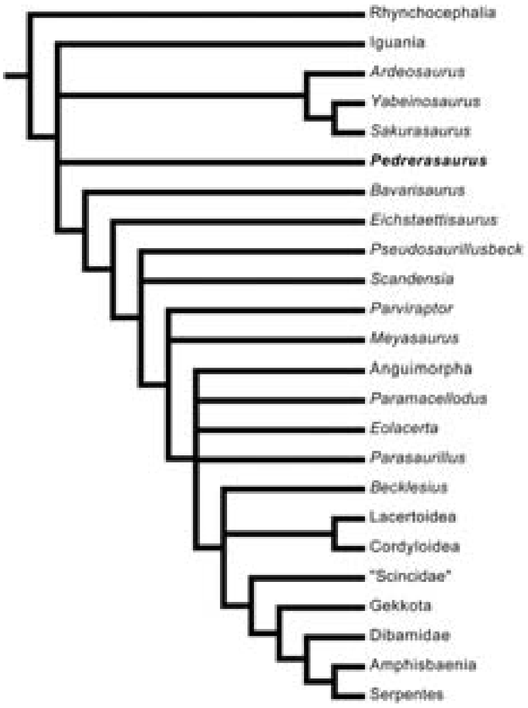

Fig. 9. Adams consensus of 2440 shortest recovered trees from the analysis described in the text. Some fossil taxa included in the analysis (AMNH Gekkonomorph, *Tepexisaurus*, *Ornatocephalus*, and *Hymenosaurus*) are not shown in the figure because they are not relevant to *Pedrerasaurus*. Major groups have been collapsed in interest of space. *Parasaurillus* is "*Pseudosarillus*" *sp.* of Conrad (2008) (Evans and Searle, 2002).

(Fig. 1). The oldest known Iberian squamates are currently those from Guimarota (Kimmeridgian, Portugal). These are mainly represented by disarticulated but well-preserved elements that have been attributed to the putative anguimorphs *Parviraptor* and *Dorsetisaurus*, the?scincoid *Saurillodon*, the paramacellodids *Becklesius* and *Paramacellodus*, and indeterminate scincomorphs (Seiffert, 1973; Broschinski, 2000). Some of these taxa were also recorded by Seiffert (1973) from the younger Portuguese locality of Porto Dinheiro (Tithonian-Berriasian [Mohr, 1989] or Berriasian [Wilson, 1979]). For the remainder of the Cretaceous, the record is entirely from Spain. In addition to *Pedrerasaurus* described here, La Pedrera de Meià has yielded several specimens of *Meyasaurus* (Vidal, 1915; Hoffstetter, 1966; Evans & Barbadillo, 1996, 1997) and a single specimen of *Eichstaettisaurus* (Evans et al., 2004). Upper Hauterivian-lower Barremian deposits at Galve and Las Hoyas, and upper Barremian deposits at Uña, and Buenache de la Sierra have also produced squamate remains. The specimens from Galve are rare and incomplete but include records of *Meyasaurus* (=*Ilerdaesaurus*) sp., Scincomorpha indet., and *Paramacellodus sp.* at the fossil sites of Herrero, Colladico Blanco, Cerrada Roya and Poca (Crusafont and Adrover, 1965, 1966; Kühne, 1966; Krebs, 1985; Estes and Sanchiz, 1982; Richter, 1991, 1994a,b). New material, as yet undescribed, has been recovered from residues obtained by screen-washing at La Cantalera and Vallipón (Ruiz-Omeñaca and Canudo, 2001), both at Galve. Las Hoyas has yielded well-preserved specimens of *M. diazromerali* (Evans and Barbadillo, 1997), *Hoyalacerta sanzi* (Evans and Barbadillo, 1999), and *Scandensia ciervensis* (Evans and Barbadillo, 1998a; Bolet and Evans, work in progress). A new genus, represented by an almost complete specimen, and fragmentary material of a paramacellodid are currently also under study by the authors. The material from Uña is partially or fully disarticulated, but includes *M. unaensis*, the paramacellodids *Paramacellodus sinusosus* and *Becklesius cataphractus*, and, based on a single partial lower jaw with teeth, a putative anguimorph, *Cuencasaurus estesi* (Richter, 1991, 1994a,b). Squamate eggs have also been reported from Galve (Kohring, 1990, 1991). In addition to the above sites Buenache de la Sierra (Cuenca) has yielded fragmentary, but indeterminate, remains of at least one lizard (Buscalioni et al., 2008).

At the abandoned Laño sand quarry (Álava province), Upper Cretaceous deposits (upper Campanian/lower Maastrichtian) have produced iguanians, scincomorphs, possible amphisbaenians and snakes (Astibia et al., 1991; Rage, 1999). Indeterminate squamates have also been reported from the localities of: Chera 0 and Chera 1c (Campanian/Maastrichtian, Valencia) (Company et al., 2009a,b); Lo Hueco (upper Campanian-lower Maastrichtian, Cuenca) (Ortega et al., 2008; Barroso-Barcenilla et al., 2009); Blasi 2 (Maastrichtian, Huesca) (López-Martínez et al., 2001); and Fontllonga 6 (Maastrichtian, Catalonia) (Álvarez-Sierra et al., 1994).

Thus, the record of Mesozoic squamates on the Iberian Peninsula ranges from the late Jurassic to the latest Cretaceous. The Upper Jurassic squamate assemblage is comparable to that of older or contemporaneous localities in North America and Britain, with the presence of paramacellodids, and the anguimorphs *Parviraptor* and *Dorsetisaurus* (Evans, 1994; Evans and Chure, 1998). In the Early Cretaceous, the composition of Iberian assemblages changed somewhat. Some Jurassic genera and lineages survived, notably *Eichstaettisaurus* (Evans et al., 1999, 2004) and paramacellodids (Richter, 1991, 1994a,b; Ruiz-Omeñaca and Canudo, 2001), but other Iberian squamates e.g *Hoyalacerta*, *Scandensia*, *Cuencasaurus*, *Pedrerasaurus* and the new taxon from Las Hoyas, appear to be more derived and more geographically restricted (Evans pers. obs.). However, this apparent endemicity may be an artefact of the record and of the difficulty of comparing articulated with dissociated material. As an illustration of this, *Meyasaurus* was, until recently, thought to be restricted to the Iberian Peninsula but has now been recorded from the Lower Cretaceous (Barremian) Wessex Formation of southern Britain (Sweetman, 2009; Evans pers. obs.). Of the Jurassic residuals, *Eichstaettisaurus* was first described from the Late Jurassic of Solnhofen, Germany (Broili, 1938) but survived into the Early Cretaceous of Spain (Evans et al., 2000) and Italy (Evans et al., 2004). Paramacellodids (sensu stricto, Evans and Chure, 1998) were more widespread. First recorded from the late Jurassic of North America and Portugal, they continued to be well represented throughout Laurasia in the Early Cretaceous of Spain and Britain (Hoffstetter, 1967; Milner and Evans, 1998; Evans and Searle, 2002), Japan (Evans and Manabe, 2000), China (Li, 1985), and Russia (Averianov and Skutchas, 1999; Leschinskiy et al., 2001). If correctly identified, they also reached Morocco (Broschinski and Sigogneau-Russell, 1996) and, questionably, Tanzania (Zils et al., 1995).

This Early Cretaceous admixture of Jurassic and more derived squamate lineages is consistent with interpretation of western Europe as a rather isolated archipelago of small landmasses (the Iberian Peninsula being one of these) having limited interchange with the larger continental blocks at this time. However, the Iberian landmass, together with the Mediterranean Tethyan Sill to its east, may have provided a dispersal route between northern Africa and Europe (Gheerbrant and Rage, 2006), permitting Laurasian paramacellodid lizards and other taxa to reach Morocco.

The Late Cretaceous record of squamates in the Iberian Pensinsula is currently poor, but the presence of iguanians, snakes, indeterminate scincomorphs and possibly amphisbaenians at Laño (see above) suggests another striking faunal change. Some of the Late Cretaceous taxa, e.g. madtsoiid snakes (Gheerbrant and Rage, 2006) probably migrated to the Iberian Peninsula from Africa, but a far greater knowledge of both European and African Cretaceous squamate assemblages is required to permit unambiguous understanding of dispersal patterns. With the description of new material from several localities, including Lo Hueco (Maastrichtian, Cuenca) (Ortega et al., 2008; Barroso-Barcenilla et al., 2009), this situation should improve over the next decade.

6. Conclusions

Based on available characters, MGB 47250 cannot be referred to any previously described Mesozoic lizard. It is therefore placed in a new genus and species, *P. latifrontalis.* Phylogenetic analyses proved inconclusive but suggest *Pedrerasaurus* is a scincogekkonomorph (a scleroglossan or stem-scleroglossan). Support for a relationship with *Meyasaurus* is weak and remains equivocal pending the recovery of further material. The recognition of a second taxon with bicuspid teeth in the Early Cretaceous of the Iberian Peninsula cautions against referral of fragmentary bicuspid jaw material to *Meyasaurus* in the absence of other corroborative elements (e.g. the characteristic frontals). In addition, the failure of either *Meyasaurus* or *Pedrerasaurus* to group with scincomorph clades cautions against the tendency to refer fossil taxa with bicuspid teeth to Scincomorpha, unless supported by additional characters.

Pedrerasaurus adds to the known diversity of the La Pedrera de Meià squamate assemblage and to the Mesozoic squamate record of the Iberian Peninsula as a whole.

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Appendix 1. Taxon coding of *Pedrerasaurus*

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The matrix and characters used are those of Conrad (2008). Changes in character codings for certain taxa are as follows: Character 212: *Meyasaurus* 4►3, *Parmeosaurus* 4►3, *Eolacerta* 0►3; Character 73: *Meyasaurus* 0►1; Character 305: *Meyasaurus* 1►0; Character 307: *Meyasaurus* 1►0.

NEW MATERIAL OF THE ENIGMATIC *SCANDENSIA*, AN EARLY CRETACEOUS LIZARD FROM THE IBERIAN PENINSULA

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NEW MATERIAL OF THE ENIGMATIC *SCANDENSIA*, AN EARLY CRETACEOUS LIZARD FROM THE IBERIAN PENINSULA

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Abstract: The Early Cretaceous Spanish locality of Las Hoyas has yielded some of the best articulated lizard fossils outside China. Five distinct taxa are known, of which the most unusual is *Scandensia ciervensis* Evans and Barbadillo, named on the basis of a single immature specimen. Here, we describe a second specimen that, although headless, provides new and important information, including the presence of osteoderms. The manus and pes of *Scandensia* are distinctive. The new specimen adds to our understanding of the pes and shows that it had an unusually robust fourth metatarsal and distinct arching of the long penultimate phalanges. The latter trait, in particular, supports the interpretation of a scansorial lifestyle for this taxon. Phylogenetic analysis places *Scandensia* in a more crownward position than originally proposed, as a scleroglossan or stem scleroglossan.

Key words: Lizard, *Scandensia*, Las Hoyas, Cretaceous, Spain.

THE Las Hoyas fossil site near Cuenca, Castilla-La Mancha, Spain, has yielded an important Early Cretaceous wetland assemblage of plants, insects, crustaceans, spiders, fish, amphibians, reptiles and birds (e.g. Ortega *et al.* 1999). It is one of the most important and complete lägerstatte of this age outside China (Yixian Formation and its lateral equivalents; Zhou *et al.* 2003), given the preponderance of articulated specimens. To date, Las Hoyas has produced five different squamate taxa. *Meyasaurus*, a lizard of fairly generalized proportions, is represented by six described (Evans and Barbadillo 1996, 1997) and several undescribed specimens (A. Bolet and S. E. Evans, pers. obs.). In contrast, the short-limbed *Hoyalacerta sanzi* (Evans and Barbadillo 1999) and the long-limbed *Scandensia ciervensis* (Evans and Barbadillo 1998) are known only from the holotypes. More recently, material of a paramacellodid lizard (a fragment of skin with characteristic rectangular keeled osteoderms; S. E. Evans, pers. obs.) and a tiny elongate skeleton representing a new fifth taxon (A. Bolet and S. E. Evans, in prep.) has been recovered.

The genus *Scandensia* is by far the most unusual of the Las Hoyas lizards in having exceptionally elongated penultimate phalanges on the manus and pes like those of scansorial pad-bearing geckos (Evans and Barbadillo 1998). These extremities are coupled with elongated and rather slender fore- and hind limbs, but also oddly robust, distally tapering ribs similar to those in crevice-dwelling lizards that are able to flatten the body against the substrate (Evans and Barbadillo 1998). Here, we describe a second, slightly larger and more mature specimen of *Scandensia ciervensis*. Although the specimen is incomplete (it lacks the skull, the anterior part of the trunk and most of the forelimbs), preparation has revealed morphological details not available from the type specimen. These include new information on the pes and the existence of thin osteoderms of a type distinct from that of paramacellodids.

Institutional abbreviation. LH, Museo de Cuenca, Castilla-La Mancha, Spain.

SYSTEMATIC PALAEONTOLOGY

LEPIDOSAURIA Haeckel, 1866
SQUAMATA Oppel, 1811

Genus SCANDENSIA Evans and Barbadillo, 1998

Scandensia ciervensis Evans and Barbadillo, 1998
Text-figures 1–5

Holotype. LH11001, a complete specimen in lateral view.

Referred specimen. LH20523c, the posterior half of a skeleton in dorsal view.

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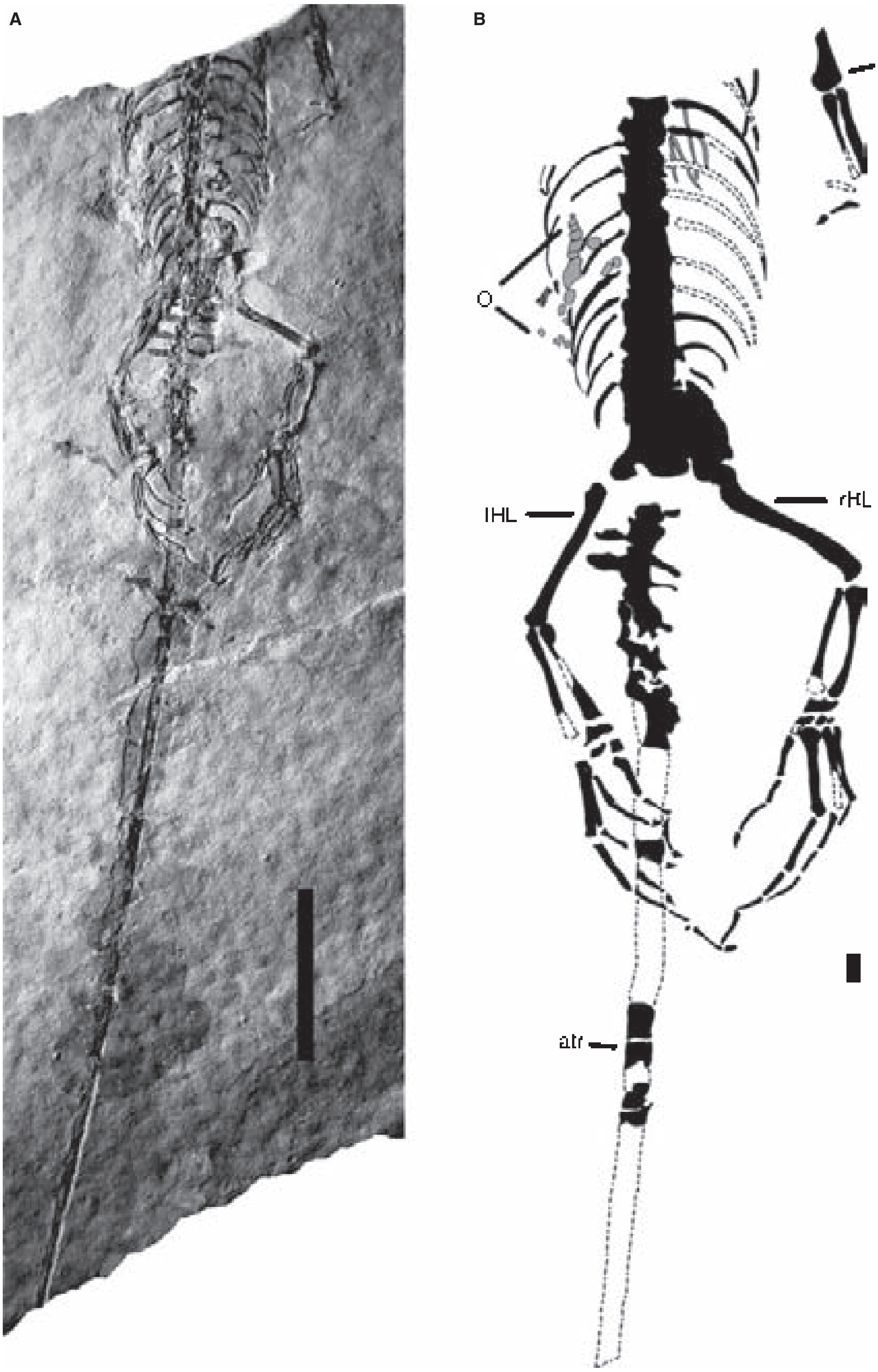
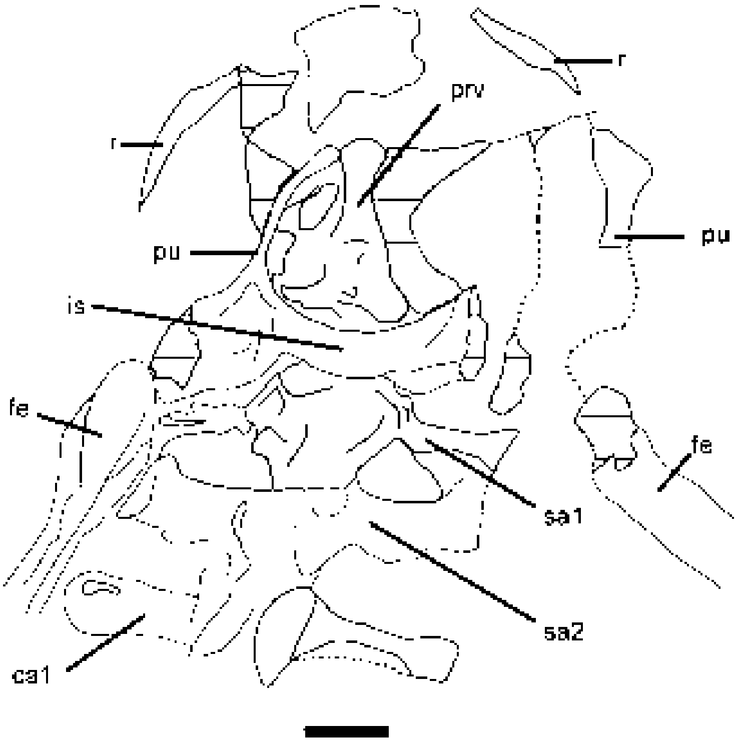


TEXT-FIG. 1. *Scandensia ciervensis* LH 20523. A, as preserved. B, interpretive figure. Abbreviations: atr, automized tail replacement; lLH, left hind limb; rFL, right forelimb; rHL, right hind limb. Scale bars represent 10 mm (A) and 1 mm (B).



TEXT-FIG. 2. *Scandensia ciervensis* LH 20523c. Details of sacrum and pelvic area. Abbreviations: ca1, caudal vertebra 1; fe, femur; is, ischium; prv, presacral vertebra; pu, pubis; r, rib; sa1 and sa2, sacrals ribs 1 and 2. Scale bar represents 1 mm.

Locality and horizon. Las Hoyas, Cuenca, Castilla-La Mancha, Spain. La Huérguina Formation (Lower Cretaceous, Barremian: Ortega *et al.* 1999).

Emended diagnosis. A small lizard showing the following unique combination of characters that differentiate it from all other known squamate taxa, fossil or modern: hyoid with two pairs of ossified ceratobranchials; amphicoelous, notochordal vertebrae; ribs proximally robust and tapering distally; body covered dorsally and ventrally by angular or rounded osteoderms, but with a sharply demarcated lateral panel of smaller, narrower elements; interclavicle rhomboid, clavicles medially expanded and fenestrate; limbs long and gracile, forelimb only slightly shorter than hind limb; in the pes, third and fourth metatarsals of similar length but fourth metatarsal markedly more robust; manus and pes characterized by the presence of elongate, slender, arched penultimate phalanges.

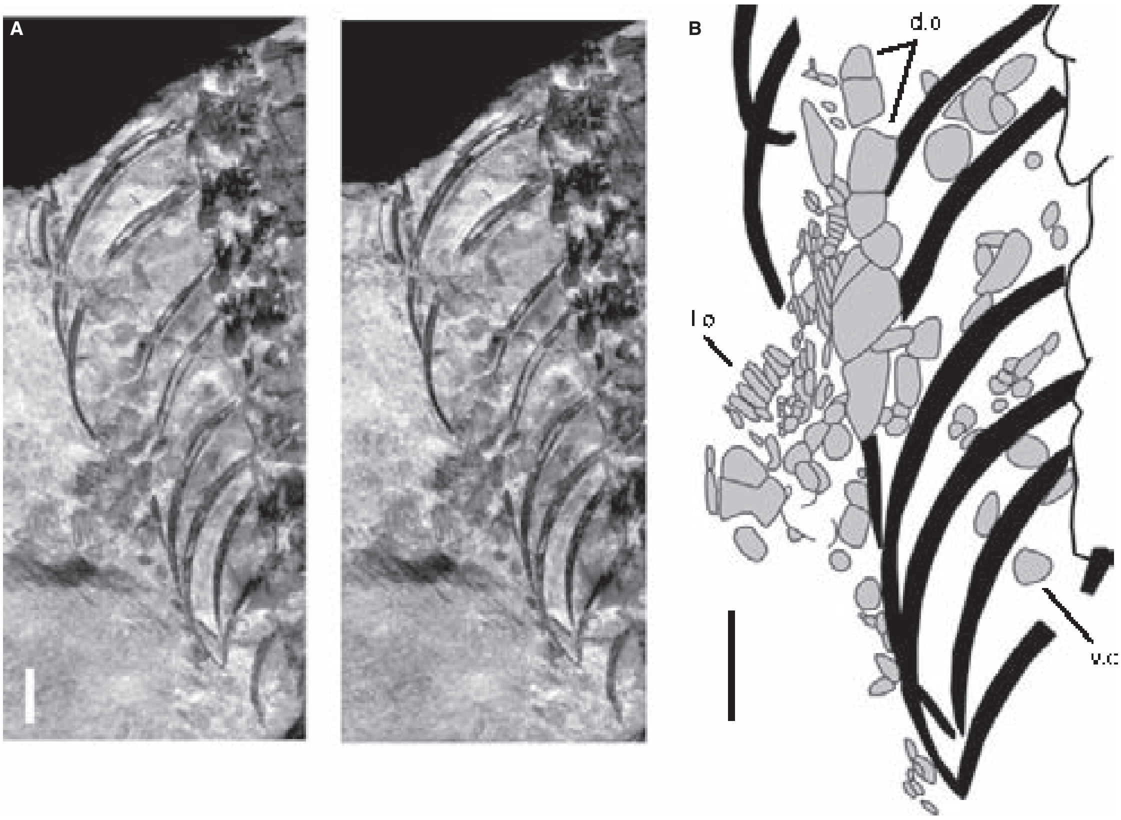
Remarks. The skull is preserved in the holotype but is crushed and yields no diagnostic characters.

Description

General. LH 20523c is a small block bearing a partial lizard skeleton represented by the posterior half of the trunk, part of the right manus, the pelvic girdle, both hind limbs and an almost complete, mostly regenerated, tail (Text-fig. 1). The preservation is irregular, because of the lost of several bones with the counterpart slab which was not recovered. The specimen is preserved in a left dorsolateral view, so that the left side of the body is more clearly seen than that of the right. Based on comparison with the holotype (LH 11001), the snout-vent length in life is estimated to have been *c.* 32–35 mm (compared to *c.* 25 mm in the holotype: Evans and Barbadillo 1998).

Vertebral column. At least eleven dorsal vertebrae are preserved, but the lack of the cervical and anterior dorsal vertebrae precludes a presacral count (25 or 26 in the holotype; Evans and Barbadillo 1998). The vertebrae are damaged but confirm that the centra are notochordal amphicoelous and without intercentra. Judging from the intervertebral articulations, the zygapophyses bore zygosphenes and zygantra.

The sacral vertebrae are clearly visible in this specimen. The first sacral rib is dorsoventrally expanded, the second anteroposteriorly so, but both widen distally and fuse to enclose a small fenestra (Text-fig. 2). The five-first caudal vertebrae bear unexpanded, single transverse processes with rounded tips. The first autotomy plane is in the fifth or sixth caudal, and the tail has broken through the seventh in the series with the rest of the tail replaced by a simple cartilaginous regrowth (Dugès 1829; Hughes and New 1959). The tip is missing because of the breakage of the slab, but we can infer that the tail was at least three times the snout-vent length. This contrasts with the holotype, which appeared to have a tail of similar length to the body (Evans and Barbadillo 1998).

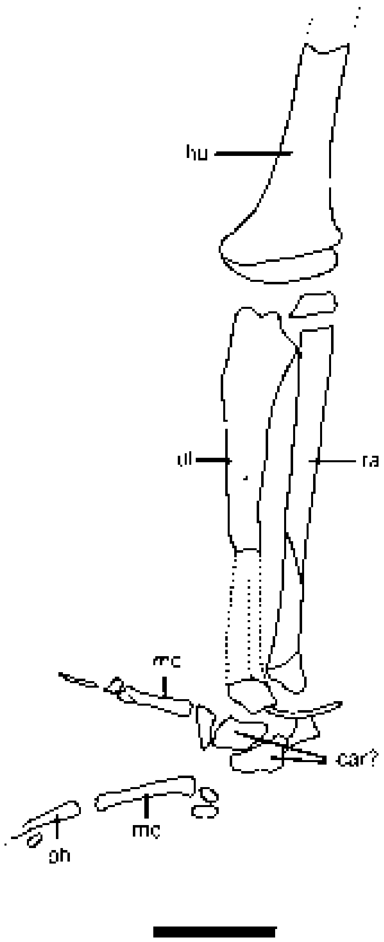


TEXT-FIG. 3. *Scandensia ciervensis* LH 20523c. Detail of left side of rib cage showing osteoderms (grey) and ribs (black). A, stereopair. B, explanatory figure. Abbreviations: d.o., dorsal osteoderms; l.o., lateral osteoderms, v.o., ventral osteoderms. Scale bars represent 1 mm.

As in the holotype, the ribs are short and strong, with a widened proximal portion and a tapering distal tip (Text-fig. 3). They shorten towards the pelvic region, but remain robust and were present on all presacral vertebrae. Costal cartilages are preserved in the anterior part of the specimen.

Osteoderms. A surprising feature of LH 20523c has been the discovery of osteoderms. Whether these were not preserved in the holotype, were inadvertently removed (they are very thin but certainly bone) or were missed because of the split into part and counterpart is not clear. In LH 20523c, these elements are most clearly seen on the left side of the specimen (very few are visible on the right) where they both overlie and, in some places, underlie, the ribs, suggesting that both dorsal and ventral series were present (Text-fig. 3A–B). The osteoderms are smooth and without pitting, sculpture or keels. In many places, they are of similar colour (though not consistency) to the matrix. This factor, added to their delicacy, overlaps, and compression makes it difficult to distinguish the boundaries of some individual elements. Text-figure 3B is therefore an approximation. The osteoderms vary in both size and shape, from large and somewhat angular dorsally to smaller and more ovoid ventrally. An overlapping series of dorsal osteoderms runs anteroposteriorly along roughly the mid-point of the ribs. However, just below this row, the osteoderms are much smaller, narrow and rectangular in shape (Text-fig. 3B). The shape change is very abrupt. This is reminiscent of the osteodermal pattern in those anguids that have a lateral body fold (e.g. *Ophisauriscus*, *Pseudopus*: Sullivan *et al.* 1999) but could also be a convergent adaptation towards body flattening.

Limbs and girdles. The right forelimb (Text-fig. 4) is incomplete proximally but preserves the distal end of the humerus, the radius and ulna, some carpals and two partially preserved metacarpals. The humeral distal epiphysis is strong, but without special features. No ectepicondylar foramen is visible but we cannot be certain it was absent. The ulna is broad proximally, tapering gently distally before broadening again at the distal epiphysis and twisting inwards. The radius is straight and slender. The carpals are not well preserved and are displaced making the region impossible to reconstruct. The radiale and ulnare are certainly present, but badly damaged, so their limits and shape are not clear. Two badly damaged metacarpals are preserved, showing only that they were not elongate. One of the metacarpals



TEXT-FIG. 4. *Scandensia ciervensis* LH 20523c. Right forelimb as preserved. Abbreviations: car, carpals; hu, humerus; mc, metacarpals; ph, phalanx; ra, radius; ul, ulna. Scale bar represents 1 mm.

nearly connects to a short, damaged, phalanx. On the left side, there is one long and extremely slender penultimate phalanx and its ungual, as well as the remains of other phalanges, but these have not been identified to position.

The pelvic girdle (Text-fig. 2) is difficult to interpret because some bones have been lost and others are overlain or hidden inside the matrix. The ilium is not preserved (but is known from the holotype: Evans and Barbadillo 1998). The left pubis is long and slender, tapering distally rather than being expanded. The ischium is short and presents a dorsal tubercle that is broken on the left side but well preserved on the right. The pelvic bones were already co-ossified.

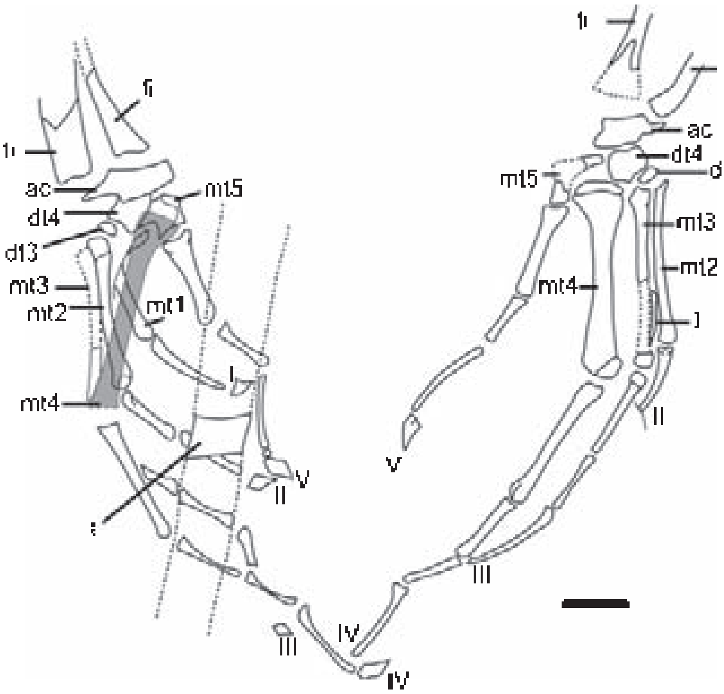
The hind limbs (Text-figs 1, 5) are the best-preserved parts of the specimen. The right femur is long, strong and slightly sigmoid. The tibia and fibula are much better preserved and exposed on the right side than the left. They are shorter than the femur and less robust. The pedes (Text-fig. 5) are more complete than those of the holotype, allowing a more accurate description and a more precise phalangeal count.

The left pes was preserved under the proximal end of the tail, but the removal of much of the latter with the counterpart left the pes exposed. The astragalocalcaneum is single and robust, and there are two distal tarsals, a small third and a large fourth. The fifth metatarsal (MT) is represented by bone and impression. It was clearly hooked, as in all lepidosaurs, but its more detailed shape (e.g. position of the plantar tubercles) cannot be reconstructed. The first digit is complete and has a slender, slightly arched penultimate phalanx with a small, pulley-like tip bearing an ungual. The second digit is also almost complete, with a short proximal phalanx, a slightly longer and more slender penultimate phalanx, and a strong, well-preserved ungual. The third digit is partly hidden in the matrix under the fourth digit but exposes a strong ungual, part of the penultimate phalanx (which disappears under the fourth digit), and a more proximal phalanx. There is probably only one phalanx missing, giving a total count of four phalanges. The fourth digit is the longest. MT4 originally crossed MT 1–3, but it has disappeared, leaving only a subtle impression and some pieces of bone close to the fifth metatarsal. The proximal phalanx of this digit is strong and long, followed by two shorter and delicate elements, a longer and more arched penultimate phalanx and, as for the other digits, a robust ungual. The fifth digit has a strong but short proximal phalanx followed by a shorter more slender second element, a long, slender, arched penultimate phalanx and the ungual.

The right pes is not as well preserved as the left, but it adds information on parts hidden in the former. The astragalocalcaneum appears more delicate, but this probably results from a different exposure. It is in its original position, articulating proximally with the distal epiphysis of the tibia and the fibula, and distally with the broken MT5, a large fourth distal tarsal, and a smaller distal tarsal three. The first digit is almost completely hidden inside the matrix, except for part of the delicate penultimate phalanx. The second digit preserves a slightly shorter metatarsal and the proximal half of a delicate first phalanx, but the rest is hidden. The third digit shows three slender phalanges (as suggested by the left foot), with the ungual hidden inside the matrix under digit four. The most remarkable digit is the fourth, which is fully exposed on this side and shows an exceptionally robust metatarsal that is broader than the fibula, but shorter. All the phalanges of the fourth and fifth toe are preserved and confirm observations made on the left foot. The pedal phalangeal count was originally described as 2:3:4:5:3/4 (Evans and Barbadillo 1998) and can now be confirmed as 2:3:4:5:4.

Ontogenetic status of the specimen

Owing to the absence of the skull in this specimen, any discussion of its ontogenetic age must be based on features of the postcranial bones. The strong ossification of most elements, including the carpals and tarsals, and the co-ossification of the pelvic bones and of the astragalus and calcaneum all suggest sexual maturity (Maisano 2002), although the detached epiphyses



TEXT-FIG. 5. *Scandensia ciervensis* LH 20523c. Right and left pes. Abbreviations: ac, astragalocalcaneum; dt3,4, distal tarsals; fi, fibula; mt1–5, metatarsals; ti, tibia; I–V, digits one to five. Grey element on left pes represents impression of fourth metatarsal. Scale bar represents 1 mm.

on some limb bones (e.g. the proximal epiphyses of radius and ulna and the proximal epiphysis of MT4) suggest that the animal had not completely stopped growing. LH 20523c was probably not fully mature skeletally but was more so than the holotype and was *c.* 20 per cent larger. Thus, some differences between the two specimens could be age (or sex) related (see the Discussion below).

DISCUSSION

The attribution of LH 20523c to Scandensia

The holotype of *Scandensia* (LH 11001) has a distinctive rib and vertebral morphology and an unusual manus and pes (Evans and Barbadillo 1998). The arrangement and proportions of the pedal bones (and of the lesser known manus) in LH 20523c match those of the holotype, as does the rib morphology, and we refer it to the same taxon. There are only three apparent differences between the two specimens, and these may be due to preservation or to ontogenetic or intraspecific variation. The right MT4 of LH 20523c is strikingly more robust than that reconstructed for the holotype, but this region of the holotype is not well preserved. Furthermore, slight differences in the size of the metatarsal could be age and/or sex related. A second apparent difference is in tail length, with the tail of LH 20523c roughly three times longer than that of the holotype. This could simply be because the tail was incomplete in the latter. Alternatively, the length difference could be sex related (males of many species have longer tails than similar-sized females; Barbadillo and Bawens 1997) or due to regeneration. In recent lizards, regenerated tails can be longer than the originals (e.g. 30% longer in *Eumeces gilberti*, 125% longer in *Eumeces skiltonianus*: Vitt *et al.* 1977). In Mesozoic squamates, regenerated tails have previously been reported for *Meyasaurus* (Evans and Barbadillo 1997), *Huehuecuetzpalli* (Reynoso 1998) and *Tepexisaurus* (Reynoso and Callison 2000). Finally, the third, and most important, difference is the presence of osteoderms in the new specimen, but the osteoderms were not evident before preparation and are extremely thin and easily removed with overlying matrix. The apparent absence of osteoderms in well-preserved fossils (i.e. articulated specimens from lithographic limestones) should therefore be treated with caution. The process by which the skin (and thus osteoderms) is lost after the death of the animal is poorly known (but see Richter 1994), and the retention of osteoderms may be dependent on their size, thickness, number, shape and mode of attachment, as well as the taphonomic conditions under which the skeleton was preserved.

The phylogenetic position of Scandensia

The original description of *Scandensia* (Evans and Barbadillo 1998) established that it was a squamate (e.g. jaw and tooth morphology, emarginated scapulocoracoid,

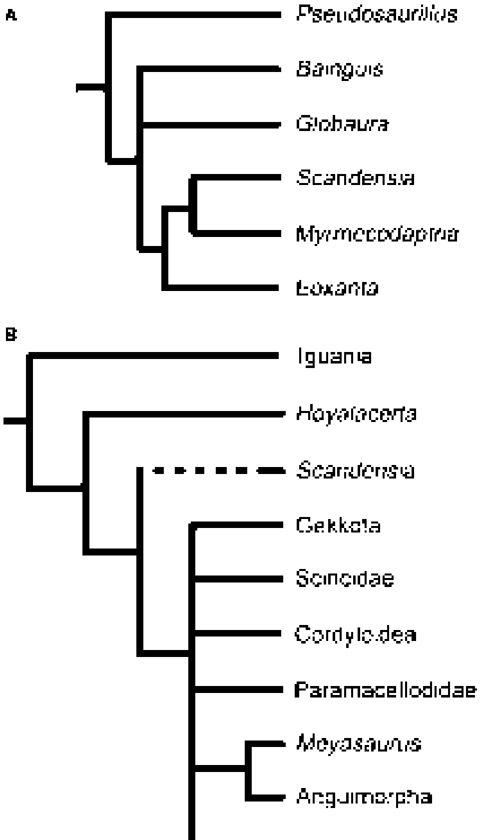
TABLE 1. Changes made to the Conrad (2008) data matrix.*

Eolacerta	305, 1►0; 306, ? ►–; 307, ? ►0; 308, ? ►–; 309, 0►–; 310, 0►–; 312, ? ►–
Ardeosaurus	305, ? 0; 306, ? ►–; 307, ? ►0; 308, ? ►–; 309, ? ►0; 310, 0►–; 311, ? ►0; 312, ? ►–
Scandensia	10, 1►0; 12, 1►?; 16, 0►?; 17, 0►?; 18, 0►?; 28, 1►?; 34, 0►?; 47, 0►1; 48, 0►?; 49, 1►?; 50, 0►?; 54, 1►?; 66, 1►?; 67, 0►?; 190, ? ►1; 203, 0►?; 204, –►?; 213, ? ►0; 215, ? ►0; 217, 0►?; 218, 0►?; 219, 0►2; 220, 0►?; 234, 0►–; 235, 0►1; 237, 1►?; 244, 0►1; 257, ? ►0; 259, 0►?; 264, 0►?; 276, 0►?; 277, 0►?; 284, 1►0; 285, 0►?; 286, 0►?; 288, 0►?; 292, 0►1; 304, ? ►1; 305, ? ►1; 306, ? ►0; 307, ? ►1; 309, ? ►–; 310, ? ►0; 311, ? ►0; 312, ? ►0; 372, ? ►0
Meyasaurus	306, ? ►–; 308, ? ►–; 309, –►0; 311, 1►0
Globaura	212, 0►3

*Additional to those in Bolet and Evans (2010).

fenestrate clavicle, absence of gastralia) and this is confirmed by the new specimen (e.g. co-ossification of the pelvic bones, pubic morphology). The first phylogenetic analysis (Evans and Barbadillo 1998), using PAUP and a modified version of the Estes *et al.* (1988) matrix, put *Scandensia* in a basal position on the squamate stem. Conrad (2008), using the computer programme TNT (Goloboff *et al.* 2003) and a new, more extensive matrix, placed *Scandensia* as a stem scleroglossan (within his larger group Evansauria). To reanalyse *Scandensia* on the basis of the new data, we used the matrix of Conrad (2008) enlarged by Norell *et al.* (2008) and amended by Bolet and Evans (2010). The codings of *Scandensia* were modified according to the new specimen, and the codings for other genera (see Table 1) were also changed where necessary. For the analysis, the methodology of Conrad (2008) was followed and the character on biogeography (364 of Conrad (2008)) was excluded. Because the matrix is extensive (276 taxa, 372 characters), use of the programme PAUP* (Swofford 2001) to analyse the full matrix is not possible as it requires too much processing time and memory. Hovenkamp (2004) recommends TNT (Goloboff *et al.* 2003) for the analysis of such large matrices. A smaller matrix (using only one representative of any one genus and removing many of the mosasauroid taxa) was run on PAUP* using heuristic search mode. Finally, a PAUP* Branch and Bound search was run with *Scandensia* and 17 other taxa representing major squamate groups and key fossils.

The Ratchet search of TNT resulted in 2187 trees with a length of 3825 steps (CI: 0.129, RC: 0.091), as reported by PAUP. In all trees, *Scandensia* grouped with bainguids (as defined by Conrad (2008), comprising *Bainguis* Borsuk-Białynicka, 1984, *Myrmecodaptria* Gao and Norell, 2000, *Eoxanta* Borsuk-Białynicka, 1988, *Globaura* Borsuk-Białynicka, 1988) and *Pseudosaurillus becklesi* Hoffstetter, 1967 (Text-fig. 6A). This clade was placed as the sister group of Scleroglossa (= gekkotans, anguimorphs and scincomorphs *sensu* Estes *et al.* 1988). However, an analysis of the character state distribution between the six 'bainguid' taxa shows that the grouping is an artefact of



TEXT-FIG. 6. Phylogenetic position of *Scandensia*. A, clade incorporating *Scandensia* as found by TNT (but see text for critique). B, simplified tree drawn from Strict Consensus showing the two alternative placements of *Scandensia* and that of other Las Hoyas lizards in relation to major squamate clades (from TNT and PAUP). Paramacellodidae is marked with an asterisk as the two best known genera, *Paramacellodus* and *Becklesius*, were placed separately in the TNT analysis – the former with anguimorphs, the latter with scincomorphs + gekkotans.

missing data. With the exception of *Globaura* (47.3% missing data), all of these taxa have more than 50 per cent missing data (*Pseudosaurillus* 86%, *Bainguis* 68.3%, *Myrmecodaptria* 58.1%, *Scandensia* 70.9%). Moreover, whereas the postcranial skeleton of *Scandensia* is well preserved but the skull is very poorly known (representing most of the missing data), the reverse is true of the other taxa, all of which are represented only by a skull or by isolated skull components. No derived character state is shared by all six taxa. Five taxa (except *Pseudosaurillus*) potentially share four character states (47 (1) jugal with little angulation; 55 (1) fused frontals; 61 (1) deep subolfactory crests on the frontal; 86 (1) adductor muscles attach ventral to parietal), but these character states are found in other squamates and two (55, 86) are uncertain in *Scandensia* because of the crushing of the only existing skull (holotype).

At a less detailed level, the results of the TNT analysis largely agree with Conrad's (2008) placement of *Scandensia* on the stem of Scleroglossa (in his Evansauria; Text-fig. 6B). In the largest PAUP heuristic analysis (139 included taxa), the Strict and Semistrict consensus of 51 447 equally parsimonious trees (EPT; TL = 3111; CI = 0.248; RI = 0.651; RC = 0.162) also places *Scandensia* as a stem Scleroglossan, but a 70 per cent majority rule tree (MRT) and the Adams consensus nests it in an unresolved position within Scleroglossa. In fact, this is the general pattern in both PAUP and TNT analyses, with the Adams consensus and the 70 per cent MRT placing *Scandensia* crownward of the Strict and Semistrict trees. A more crownward placement is supported by the presence of overlapping dorsal and ventral osteoderms, a feature today restricted to scincoids (cordylids, gerrhosaurids and scincids) and anguimorphs. However, none of these taxa has both overlapping osteoderms and amphicoelous vertebrae. This combination has previously been described only in the Early Cretaceous *Huehuecuetzpalli* from Mexico (Reynoso 1998) although, unlike *Scandensia*, its osteoderms are restricted to a dorsal row. A few gekkotans possess osteoderms (e.g. *Geckonia chazaliae*; Evans, pers. obs.) but not a covering of overlapping plates. It is possible that overlapping osteoderms were once present in the ancestor of scleroglossans and were lost in the ancestry of Gekkota as a result of skeletal paedomorphosis, but this can only be verified by a more complete fossil record with articulated specimens.

The sharp lateral transition in the shape of the osteoderms seen in the new *Scandensia* specimen is unique for a Mesozoic lizard, but a similar pattern is preserved in the Messel (Eocene) anguimorph *Ophisauriscus* (Sullivan *et al.* 1999) as well as living anguid lizards like *Pseudopus* and at least hints at the presence of a lateral fold. We ran analyses with this character (304) coded as either present (1) or (?), but the resulting tree was exactly the same (although 2 steps shorter using the (?) coding).

Functional morphology and lifestyle

In the original description of *Scandensia* (Evans and Barbadillo 1998), the discussion of lifestyle focused on two unusual features: the robust thoracic ribs, resembling those of living lizards that flatten the body dorsoventrally, and the long delicate penultimate phalanges. LH 20523c confirms the rib morphology, adding the presence of osteoderms (the abrupt change into smaller osteoderms laterally may aid body flattening), and provides more details of pedal anatomy.

The pes of *Scandensia* does not show the marked asymmetry that is found in cursorial lizards like *Iguana* where there is a strong increase in length from MT1 to MT4. The metatarsals are held together in a common skin sheath and function as a unit (Russell 1975; Russell *et al.* 1997). Instead, in *Scandensia*, MT4 is similar in length to MT3, and MT2 is only slightly shorter. The foot is therefore relatively symmetrical and more like that of gekkotans, though proportionally somewhat longer. Russell *et al.* (1997) reported that the shaft of the fourth metatarsal in *Gekko* is much more robust than that of the preceding three. They correlated this with the increased capacity of the fourth digit to diverge from the others, allowing the digits a greater spread as the first four metatarsals are not bound in a common sheath. This may provide at least a partial explanation for the robusticity of the fourth metatarsal of *Scandensia* and would be also be consistent with the more symmetrical foot.

The foot of *Scandensia* further resembles that of gekkotans in the morphology of the penultimate phalanges. Their unusual length has been discussed elsewhere (Evans and Barbadillo 1998), but the new specimen also shows that the distinct arching of these phalanges is not a taphonomic artefact. According to Russell (1975), the arching of the penultimate phalanges in *Gekko* ensures that the claw has a steep angle of attack in relation to the substrate. In conjunction with the action of a strong digital flexor muscle and distal condyles that limit claw movements to the vertical plane, this morphology allows the claws to grip strongly. The arching of the penultimate phalanges also causes the digit to hyperextend when the dorsal interosseal muscles contract, drawing the scansorial pad away from the substrate (Russell 1975). In the absence of soft tissue impressions, we do not know whether *Scandensia* had toe pads, but given the morphology of the digits and the fact that toe pads have arisen several times in specialized lizard climbers (Irschick *et al.* 1996), it is a distinct possibility.

In most lizards, the pes is adapted to provide thrust during walking and running. In climbing geckoes, however, its principal role is to enable the animal to grip the substrate, allowing the body to be pulled over the feet during vertical climbing (Russell 1975; Russell *et al.* 1997). One foot may support the full weight of the body. To prevent itself falling outwards, the lizard also flattens its body against the substrate. Taken together with small size, these specializations allow geckos (and similarly adapted anoles and scincids; Irschick *et al.* 1996) to run up and down vertically. The adaptations found in *Scandensia* are suggestive of a similar lifestyle.

CONCLUSIONS

The new specimen of *Scandensia* reveals important features of this genus not evident in the type specimen. A more complete knowledge of the pes, in conjunction with the unusual rib morphology, provides further support for the reconstruction of a scansorial lifestyle, with the manus and pes adapted primarily to grip the substrate and thus perhaps allow vertical movement on tree trunks and branches. The presence of dorsal and ventral osteoderms, and perhaps a lateral fold series (although this may be related to flattening), supports a phylogenetically more crownward position than previously proposed (Evans and Barbadillo 1998), either on the stem of Scleroglossa (Conrad 2008) or within it. The lack of good skull material still limits placement of this morphologically distinctive lizard.

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A TINY LIZARD (LEPIDOSAURIA, SQUAMATA) FROM THE LOWER CRETACEOUS OF SPAIN

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Abstract: The smallest living amniotes are all lizards, but the fossil history of this size trait in Squamata is difficult to follow because small skeletons have low preservation potential and are often hard to detect in the field. A new squamate taxon, *Jucaraseps grandipes* gen. et sp. nov., is here described on the basis of an articulated skeleton from the Early Cretaceous Spanish lagerstätten of Las Hoyas. It differs from other known Mesozoic lizards in combining very small body size with a short rostrum, low maxillary tooth count, a relatively slender and elongated body, and short limbs with large hind feet. Phylogenetic analysis using TNT places it on the stem of a clade encompassing scincomorphs, gekkotans, snakes, amphisbaenians and anguimorphs. Comparison with modern lizards suggests it was probably a cryptic surface or subsurface ground dweller but not a burrower.

Key words: Squamata, Lower Cretaceous, Las Hoyas, Spain, fossil lizard, small size.

FOR terrestrial animals, small body size confers a number of advantages, including shorter maturation times, increased agility and ease of concealment, and lower energy requirements (Blanckenhorn 2000). These, in turn, can allow for a higher population density in a given area and thereby a larger gene pool (Rodda *et al.* 2001). Amongst living amniotes, the smallest recorded taxa are all lizards, most notably species of the gekkotan *Sphaerodactylus* (e.g. *S. parthenopion*, mean snout-vent length (SVL) 16 mm, Hedges and Thomas 2001; Daza *et al.* 2008) and of the Malagasy Leaf Chamaeleon, *Brookesia* (e.g. *B. minima*, mean snout-vent length (SVL) 17 mm; Blanckenhorn 2000). Very small lizards are rarely preserved as fossils, but here we describe a tiny articulated lizard skeleton from the Lower Cretaceous of Spain.

GEOLOGICAL BACKGROUND

The Las Hoyas fossil site is located in the Serranía de Cuenca (south-western Iberian Ranges, Spain). It is a lagerstätte, the fine-grained laminated limestone of which belong to the late Barremian La Huérguina Formation (Buscalioni and Fregenal-Martinez 2010) and have produced a diverse assemblage of plants (e.g. charophytes, ferns, gymnosperms, angiosperms), invertebrates (crustaceans, diverse insects) and vertebrates (sarcopterygian and actinopterygian fish; anuran, caudate and albanerpetontid amphibians; turtles, lizards, crocodiles, pterosaurs, dinosaurs, birds: Ortega *et al.* 1999; Vullo *et al.* 2009) that lived in a seasonal subtropical wetland ecosystem (Buscalioni and Fregenal-Martinez 2010). Las Hoyas is one of only two Mesozoic localities on the Iberian Peninsula yielding fully articulated lizard remains, the other being La Pedrera de Meià (Late Berriasian–Early Valanginian, Catalonia, e.g. Bolet and Evans 2010). The Las Hoyas fossil site is the more productive of the two, although lizard material is still relatively rare. The locality has yielded six described (and further undescribed) specimens of *Meyasaurus diazromerali* (Evans and Barbadillo 1997); one of *Hoyalacerta sanzi* (Evans and Barbadillo 1999); two of *Scandensia ciervensis* (Evans and Barbadillo 1998; Bolet and Evans 2011); a partial paramacellodid (Evans and Bolet in press); and the new genus and species described herein.

MATERIAL

The new specimen, Museo de Cuenca, LH 18505, consists of a main block bearing most of the skull and skeleton of a small lizard and a small partial counterpart bearing impressions and fragments of the skull and neck.

Institutional abbreviations. IPPS, Instituto Provincial de Palaeontologia, Sabadell, Spain; LH, Museo de Cuenca, Las Hoyas Collection, Cuenca, Spain.

Anatomical abbreviations. ac, astragalocalcaneum; *acf*, anterior coracoid fenestra; *an*, angular; *ar*, articular; *br*, braincase; *c*,

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carpals; *cl*, clavicle; *co*, coronoid; *co*, coracoid; *d*, dentary; *dt3,4*, distal tarsals 3,4; *f*, frontal; *fi*, fibula; *h*, humerus; *j*, jugal; *lf*, left femur; *lil*, left ilium; *lpu*, left pubis; *m*, maxilla; *mt5*, fifth metatarsal; *n*, nasal; *o*, olecranon epiphysis; *p*, parietal; *pa*, palatine; *pf*, postfrontal; *pi*, pisiform; *pm*, premaxilla; *po*, postorbital; *pra*, prearticular; *prf*, prefrontal; *pt*, pterygoid; *q*, quadrate; *r*, radius; *rap*, retroarticular process; *rf*, femur; *ril*, right ilium; *rpu*, right pubis; *s1*, *s2*, sacrals 1–2; *sa*, surangular; *sc*, scapula; *scf*, scapulocoracoid fenestra; *sco*, scleral ossicles; *sp*, splenial; *sq*, squamosal; *st*, supratemporal; *ti*, tibia; *u*, ulna; *v*, vomer; *1–5*, digits 1–5.

SYSTEMATIC PALAEONTOLOGY

LEPIDOSAURIA Haeckel, 1866
SQUAMATA Oppel, 1811

Genus JUCARASEPS gen. nov.

Type and only species. Jucaraseps grandipes sp. nov.

Derivation of name. From the Jucar River of Cuenca, and (Latin) *seps*, a lizard or snake.

Diagnosis. As for species.

Jucaraseps grandipes sp. nov.
Figures 1–3

Derivation of name. Latin, *grandis*, large; *pes*, foot, in reference to the proportionally large feet of this lizard.

Holotype. LH 18505 (Fig. 1A), Museo de Cuenca, Cuenca, Spain.

Locality and horizon. Las Hoyas (Cuenca, Spain). Calizas de la Huérguina Formation (Limestone Unit III, Ortega *et al.* 1999); Early Cretaceous (Late Barremian).

Differential diagnosis. A small lizard characterised by the combination of small adult size, a low tooth count, an expanded retroarticular process on the lower jaw, an increased number of presacral vertebrae (31), deep cristae cranii (subolfactory crests) on the frontals and short limbs with large feet (pes 52 per cent of total limb length, 20 per cent of snout-vent length (SVL)).

It differs from other Las Hoyas lizards except *Hoyalacerta* in the combination of an extended presacral vertebral column and relatively short limbs; differs from *Hoyalacerta* in having a smaller number (8–10) of relatively large maxillary teeth (40 + small teeth in *Hoyalacerta*), 31 presacral vertebrae (27–28 in *Hoyalacerta*) and frontal morphology (shallow cristae cranii in *Hoyalacerta*); differs from all other described skeletons of Jurassic–Early Cretaceous lizards in the combination of small size, a short rostrum, a shallow lower jaw with unicuspid teeth, a low coronoid and a large expanded retroarticular process, a long body and tail, the absence of osteoderms or cranial sculpture, and the relatively short limbs (forelimb 26.6 per cent SVL; hind limb 39 per cent SVL) with large hind feet (pes 52 per cent of total hind limb length, 20 per cent SVL).

Remarks. The Japanese *Kaganaias* (Evans *et al.* 2006) resembles *Jucaraseps* in being long-bodied, but differs in being much larger, having more presacral vertebrae (36–46 dorsals, neck unknown) and having hind limbs that are much shorter in relation to the body.

Jucaraseps resembles the Upper Jurassic Guimarota genera *Saurillodon* Seiffert, 1973 and *Chalcidosaurus* Kosma, 2004 in having a relatively short dentary, although the latter taxon has a higher tooth count (21–23) than the former (9–16, Kosma 2004). However, with the exception of one partially associated skeleton of *Saurillodon* (Broschinski 2000), these taxa are represented only by isolated jaws and their body proportions and skull morphology remain unknown, precluding further comparison with *Jucaraseps*. A similar problem exists for other Jurassic and Early Cretaceous lizard taxa known only from jaw material (e.g. Seiffert 1973; Evans 1998; Nydam and Cifelli, 2002).

Comparative description

The type and only specimen of *Jucaraseps* is an almost complete skeleton preserved in dorsal view. It has an estimated snout-vent length (SVL) of 27 mm and is interpreted as a subadult individual based on skeletal development (see Discussion: *Ontogenetic status*). The skull is compressed and some bones are poorly preserved making their boundaries difficult to reconstruct. Postcranially, the specimen is well preserved except for the right forelimb and includes a long but incompletely preserved tail (Fig. 1).

Skull. The skull of LH 18505 is small (total length, premaxilla to posterior edge of skull, 5.8 mm) and narrow (3.4 mm width posteriorly), with a short snout and large orbits that contain remnants of the scleral ossicles (Fig. 2). None of the skull bones shows any trace of sculpture. The premaxillae are fused, but the ascending nasal process is broken. Only three small unicuspid premaxillary teeth are visible. The left maxilla bears about eight small, slightly recurved and relatively well-spaced unicuspid teeth. The tooth bases are visible through the bone of the maxilla and show that the implantation was pleurodont. A triangular maxillary facial process is visible on the left side, and a narrow posterior process extends below the orbit. The paired nasals border small nares anteriorly and meet the maxillae and the frontals posteriorly. They are separated from the prefrontals by a maxilla-frontal contact. The frontals are split between the part and counterpart blocks, but they can be reconstructed as long and paired, almost parallel-sided anteriorly, but increasing in width

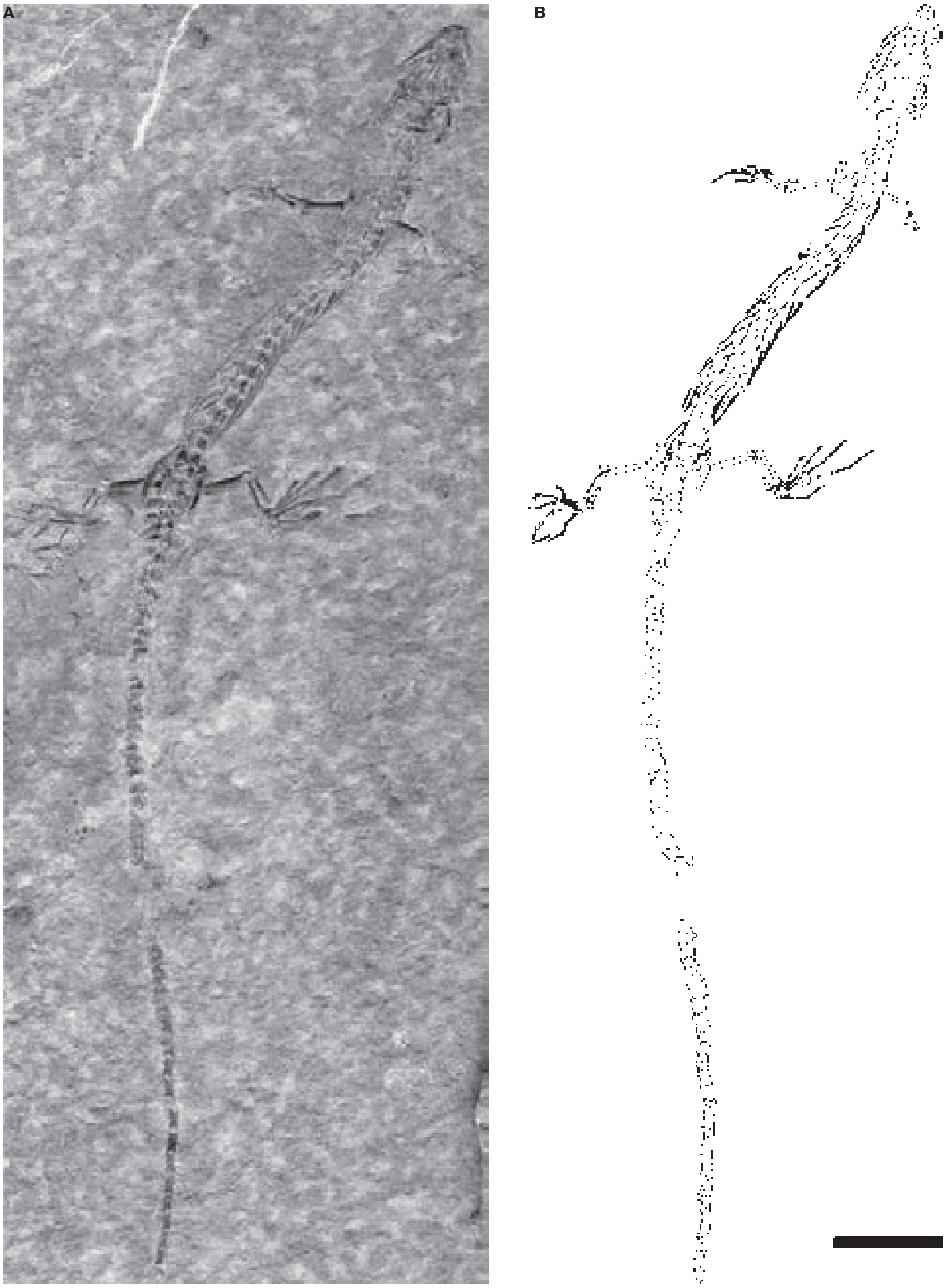

FIG. 1. *Jucaraseps grandipes* LH 18505, holotype. A, dorsal view. B, interpretive drawing. Scale bar represents 5 mm.

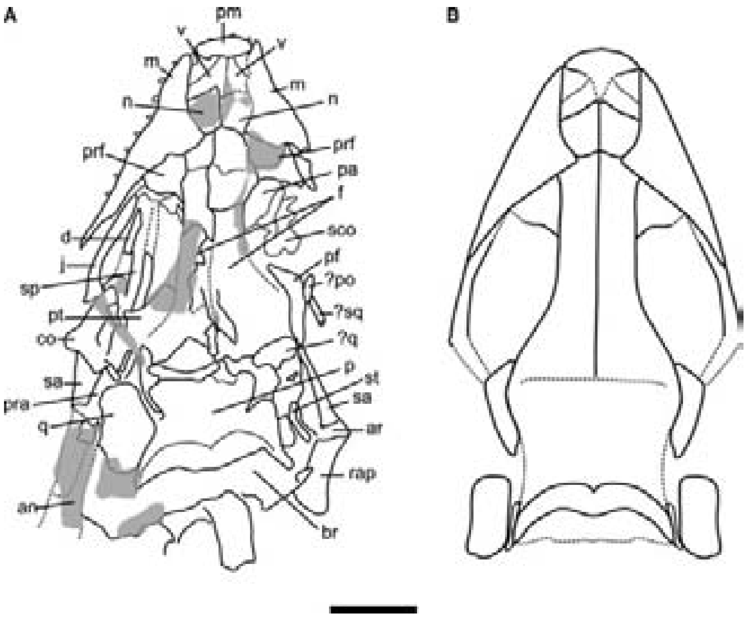

FIG. 2. Skull of *Jucaraseps grandipes*, LH 18505. A, as preserved, grey shaded areas represent bone on the counterpart block. B, reconstruction. Scale bar represents 1 mm.

posterolaterally (Fig. 2B). Ventrally, the cristae cranii (subolfactory processes) are deep and partially enclose the olfactory tracts. The single parietal is crushed and some of the more ventral bones of the skull have been pushed through it. There is no obvious parietal foramen but given the damage, we cannot be certain it was absent. The lateral border of the parietal is obscured on the left by a displaced quadrate and other elements and on the right by damage, but there is no indication that the adductor muscles extended onto the dorsal surface. Short divergent postparietal (supratemporal) processes are separated by a gently curved posterior border with shallow nuchal fossae. The prefrontals are small, and the presence or absence of a free lacrimal is uncertain. The maxillary ramus of the jugal is preserved on the left. Its slender postorbital ramus is broken but bone fragments and impressions suggest it formed a complete orbital rim. An elongate, weakly concave right postfrontal straddles the frontoparietal suture. Lateral to it are narrow bars of bone that may be parts of the right postorbital and squamosal. Further posteriorly, a slender bone lateral to the parietal is probably the right supratemporal. On the left side, these elements may be represented by bone fragments between the quadrate and parietal. The left quadrate lies beside the parietal and has a rather ovoid outline. The right quadrate lies under the parietal but has broken through it posteromedial to the postfrontal.

The palate is mostly obscured by the dorsal skull elements. Paired vomers can be seen through the narial openings, and parts of the palatines and left pterygoid are visible through the orbits.

Poor preservation precludes description of the braincase, but it appears to be relatively large, a trait common amongst small lizards (Rieppel 1984).

Lower jaw. The posterior part of the left lower jaw is partially exposed in lingual view, with its postcoronoid region preserved in impression. Overall, the jaw is long, straight and slender. The articular-prearticular, surangular, angular, coronoid and splenial are all separate. The dentary is almost completely hidden, but its posterior end did not extend beyond the posterior margin of the coronoid process. The coronoid is rather elongated with a concave ventral margin and a low dorsal process. The dentition is largely hidden by the overlying skull bones, but those teeth visible through the jugal are similar in size and shape to those of the maxilla. The right mandible is again mostly hidden below the skull but the surangular, the short wide articular surface for the quadrate, and a large, medially deflected, retroarticular process are exposed posteriorly.

Axial skeleton. There are at least 31 presacral vertebrae, two sacrals and more than 40 caudals (the end of the tail is not preserved). The vertebrae are procoelous and bear low neural spines. In general, the vertebrae are rather large in proportion to the corresponding ribs. The cervical vertebrae are shorter than the dorsals, and although some short cervical ribs are in articulation, it is difficult to determine at what level they began. The first vertebra with long, probably sternal, ribs preserved is the ninth, but the cervical vertebral count could be between six and eight. Ribs are visible on all dorsal vertebrae except the last. They are relatively long, thin and posteriorly directed, giving the body a slender outline (trunk width 2.4 mm). Their proximal heads are mostly obscured by the adjacent vertebrae but where visible, are somewhat expanded and grooved posterolaterally. The tail is long (143 per cent SVL as preserved, *c.* 180 per cent SVL in life allowing for the missing part) and autotomous. The first few caudal vertebrae bear single transverse processes that quickly decrease in size. The anterior fracture planes pass through the transverse process, but the precise level at which they begin is difficult to identify.

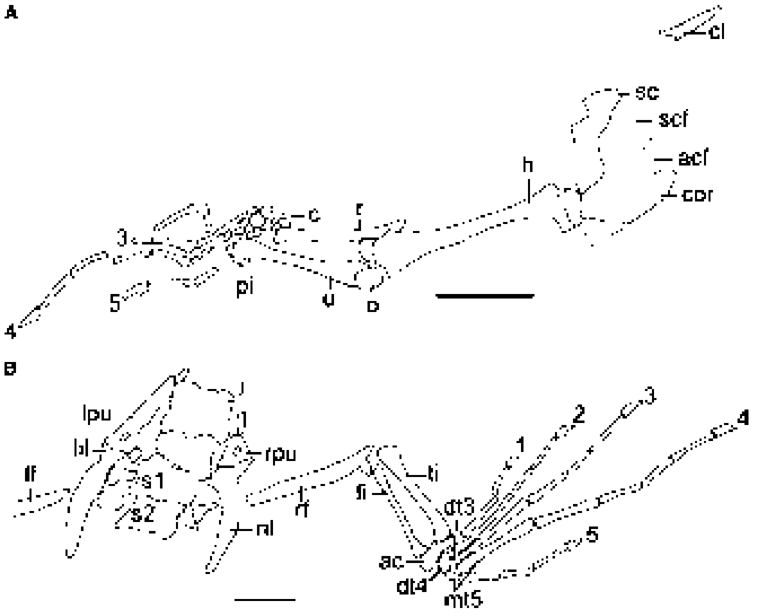

FIG. 3. *Jucaraseps grandipes*, LH 18505, limb skeleton. A, left forelimb and B, right hind limb. Scale bars represent 1 mm

Pectoral girdle and forelimbs. The left pectoral girdle is partially preserved, with the scapula and coracoid in articulation but not completely co-ossified (Fig. 3A). There are two emarginations: one between the scapula and coracoid and one (anterior coracoid fenestra) within the coracoid. As preserved, the clavicle is narrow proximally and expands distally but this region is preserved only in impression and is incomplete. The left forelimb is more complete than the right. It is short (7.2 mm, 26 per cent SVL), slender and delicate, with a short humerus (2.4 mm) bearing well-ossified proximal and distal epiphyses. The radius and ulna are even shorter (1.8 mm), but the olecranon process of the latter is not completely fused to the shaft. Because of the very small size, it is difficult to differentiate between the carpals and the detached proximal epiphyses of the metacarpals, but several ossified carpals, including a large pisiform, are visible. The rest of the hand is irregularly preserved, one of the digits being lost (or hidden inside the matrix), and only digit four is complete. This complete digit is longer than the humerus (estimated manus length 3 mm).

Pelvic girdle and hindlimbs. The pelvic bones are not co-ossified (Fig. 3B). The ilium has a long, tapering blade without an anterior tubercle. The pubis is slender with a long, anteriorly directed, symphysial component and a large proximal obturator foramen but no pectineal process. The ischium is hidden by the sacrum except for a small fragment close to the left pubis. The width of the body across the pelvis is approximately 2.8 mm. The hind limbs are gracile (10.55 mm, 39 per cent SVL) and are comprised of a short straight femur (3.2 mm), a shorter tibia and fibula (1.9 mm), and a long foot (5.45 mm, 52 per cent of total hind limb length; 20 per cent SVL). The left tibia has a clearly visible proximal epiphysis that is attached but not fully co-ossified with the shaft and is at least partially ossified. The astragalocalcaneum shows no remnant of a suture and bears articular surfaces for the tibia and the fibula. There are two distal tarsals (dt4 and dt3). The pes is almost complete, but the fifth metatarsal is partly hidden below the fourth. The phalangeal formula is 2:3:4:5:4, the fourth digit being the longest. In total, the pes is almost three times the length of the tibia.

PHYLOGENETIC RELATIONSHIPS

We performed a cladistic analysis using the matrix of Conrad (2008), modified by Norell *et al.* (2008) and Bolet and Evans (2010, 2011). The matrix is too large (254 taxa, 372 characters) to be run with PAUP (Swofford 2002), and we therefore used the programme TNT (Goloboff *et al.* 2003, 2008). Character ordering (additive characters) followed Conrad (2008). *Jucaraseps* can be scored for 124 of 372 characters (Table 1), but this is comparable with many fossil taxa because soft-tissue characters cannot be scored. Kuehneosauridae was the designated outgroup taxon.

The analysis was first performed using the Traditional search facility of TNT (1000 replicates, TBR branch swapping). This yielded 10 equally parsimonious trees of Length (L) 3952 (consistency index (CI) = 0.136; rescaled CI (RC) = 0.096; retention index (RI) = 0.704, as reported after import into PAUP, Swofford 2002). In all trees, *Jucaraseps* was placed on the stem of Scleroglossa (scincomorphs, gekkotans, snakes, amphisbaenians and anguimorphs, but see Townsend *et al.* 2004; Vidal and Hedges 2005 for an alternative molecular squamate phy-

TABLE 1. Coding of 372 characters for *Jucaraseps* in the matrix of Conrad (2008) as extended in Norell *et al.* (2008).

000000-000	1???00??00	0??0??0000	???00000??	????00??0?	0??1000101
100-0??0??	??1?0?3??1	?01???0010	0010??????	?????00???	??????????
?0????????	??????????	??????????	??????????	??00?0????	?????????0
???????0??	?0??00????	?0?000110?	?000000???	?00000???1	200??2?0??
0???0?0000	00?0??0??0	?10?00????	????00?00?	???1211?00	?1????????
????0-0-	00????????	??????????	??????????	??????????	??????????
??????????	??				

logeny), nested within a subset of Jurassic–Cretaceous fossil taxa (Fig. 4): the Upper Jurassic *Eichstaettisaurus*, *Ardeosaurus* and *Bavarisaurus* (Solnhofen, Germany; Hoffstetter 1964; Evans 1994*a*); the Middle Jurassic to Early Cretaceous *Parviraptor* (Britain, Portugal; Evans 1994*b*); and the Early Cretaceous *Yabeinosaurus* (China, Evans *et al.* 2005) and *Sakurasaurus* (Japan, Evans and Manabe 2009). The matrix is too large for calculation of Bootstrap or Bremer support so we reran the analysis using the TNT New Technology search with Ratchet (100 iterations; 1000 Random Addition (RAM) sequences). A second Traditional Search (1000 repetitions, TBR branch swapping) was then run using the three ratchet trees (L, 3946; CI, RC, RI as above) as starting trees. In this Traditional search, the saved trees exceeded the available computer memory (at 90 000), but the Strict, Adams (Combinable components) and Majority Rule consensus of these 90 000 trees were each well resolved with respect to the position of *Jucaraseps*. Although the full search found some shorter overall trees (L, 3943), the position of *Jucaraseps* was unchanged from that in the Traditional search.

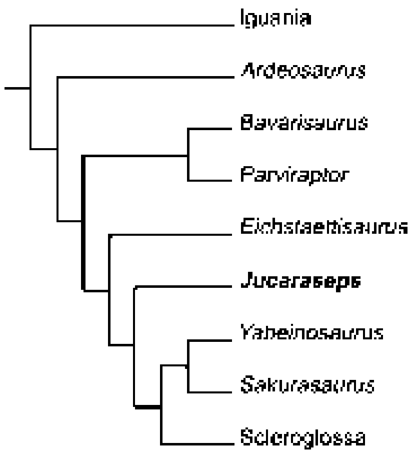

FIG. 4. Condensed cladogram showing the position of *Jucaraseps* and several other Jurassic–Early Cretaceous squamate taxa, based on an analysis of the matrix of Conrad (2008) run using TNT (Goloboff *et al.* 2003). The analysis included 254 taxa, the remainder of which fall into either Iguania or Scleroglossa.

DISCUSSION

Ontogenetic status

Jucaraseps is the smallest of the Las Hoyas squamates (Table 2). Its very small size raises the question of its ontogenetic age. Age estimation for a fossil lepidosaur has to be based on indicators of skeletal maturity, notably terminal fusions of the braincase, vertebrae, limb girdles, and limb epiphyses (Maisano 2001, 2002). These fusions (particularly of the limb bone epiphyses) are generally indicative of the end of growth, but there is considerable variation in the timing and sequence of these events (Maisano 2002). In the *Jucaraseps* specimen, the pectoral and pelvic components are sutured but not fused, as in immature lizards. Against this, the co-ossification of the astragalus and calcaneum, the triangular rather than rounded shape of the fourth distal tarsal, the attachment (but not complete fusion) and mineralisation (at least partial ossification) of the limb and digital epiphyses and, to a lesser degree, the closure of the vertebral sutures suggest an animal approaching maturity, and this is supported by the complete formation and articulation of the skull bones (although these are thin). The open girdle sutures do not necessarily conflict with this. Body size reduction can be correlated with apparent skeletal immaturity, so an adult may show features that appear juvenile (e.g. small adults of the scincid *Eumeces*, Griffiths 1990). LH18505 is therefore interpreted as a subadult animal at perhaps 70–80 per cent of adult size (*c.* 30–33 mm estimated adult SVL, 7–9 mm estimated adult skull length). This is at the lower end of the size range of living lizards, especially given the presacral elongation, although not at the extreme represented by the miniaturised gecko *Sphaerodactylus parthenopion* (Hedges and Thomas 2001; Daza *et al.* 2008).

Comparison

Although Mesozoic terrestrial/freshwater squamates with long bodies and reduced limbs are rare (e.g. *Kaganaias*, from the Early Cretaceous of Japan; Evans *et al.* 2006), there are many fossil taxa for which the postcranial skele-

TABLE 2. Las Hoyas lizard taxa.

Genus	Max SVL mm	Skull mm	PS No.	FL/SVL per cent	HL/SVL per cent	Foot/HL per cent
*Meyasaurus**	52	18	25	41	58	50
Scandensia	35	12†	25–26	47	53	45
Hoyalacerta	34	10	27–28	23.5	32.5	35
Jucaraseps	24–33†	7–9†	31	26	34	54

SVL, snout-vent length; PS, presacral vertebral number; FL, forelimb length; HL, hind limb length. *Based on the largest available specimen of *Meyasaurus diazromerali*, but *M. faurai* from Montsec (IPPS 10) is larger (SVL *c.* 139 mm). †Estimate (incomplete skull in *Scandensia*; for *Jucaraseps* up to possible adult size).

ton is unknown or incomplete. A short-jawed, long-bodied lizard was described from the Middle Jurassic of England (Evans 1998), but this reptile differs markedly from *Jucaraseps* in having very elongate vertebrae with fused osteoderms. The genus *Saurillodon* from the Late Jurassic of Portugal (Seiffert 1973) is also short-jawed but a partial association (jaws, frontals, parietal) included humeri of relatively normal length (Broschinski 2000), with no indication of limb reduction. In a later study, Kosma (2004) described several additional species of *Saurillodon* from Guimarota, all based on isolated dentaries, as well as a second short-jawed taxon, *Chalcidosaurus*. He reconstructed these lizards (Kosma 2004, p. 156, fig. 138) with varying degrees of elongation and limb reduction, but this is conjectural pending recovery of postcranial material. *Tarratosaurus* (Broschinski and Sigogneau-Russell 1996) from the Early Cretaceous of Morocco is equally problematic. It was interpreted as a burrower on the basis of the short lower jaw (and hence short rostrum), but again the postcranial skeleton is unknown. Perhaps most relevant to *Jucaraseps*, the Las Hoyas genus *Hoyalacerta* (Evans and Barbadillo 1999) is also somewhat elongated (28–29 presacrals) and short-limbed but it differs cranially and dentally (frontal morphology, tooth number and size) from *Jucaraseps*, and its feet are relatively smaller (Table 2).

Phylogenetic relationships

The results of the phylogenetic analysis place *Jucaraseps* on the stem of Scleroglossa (*sensu* Estes *et al.* 1988; Conrad 2008) with several other Jurassic/Cretaceous taxa (Fig. 4). It thus falls within Conrad's (2008) more inclusive Scincogekkonomorpha. However, this phylogenetic placement must be considered provisional for two reasons. The first is that the skull of *Jucaraseps* is incompletely known, limiting the number of characters that can be coded, most notably those of the palate, braincase and jaws. As skull characters make up a large proportion of the data matrix, future finds with more complete cranial material may change the topology of the tree.

The second reason is that the phylogenetic relationships of even extant squamates remain incompletely resolved. The first comprehensive phylogenetic analysis of Squamata was that of Estes *et al.* (1988). They recovered a tree with a primary dichotomy into Iguania (then Iguanidae, Agamidae and Chamaeleontidae) and Scleroglossa (all other squamates). Subsequent morphological analyses, including most of those involving fossil taxa, have obtained broadly similar results (reviewed *in* Conrad 2008). However, phylogenetic analyses using molecular characters (e.g. Townsend *et al.* 2004; Vidal and Hedges 2005) and those using a combined molecular/morphological data set (e.g. Wiens *et al.* 2010; Müller *et al.* 2011) consistently obtain a markedly different topology in which Iguania lies closer to anguimorphs and snakes. In these trees, Gekkota (Townsend *et al.* 2004), Dibamidae (Vidal and Hedges 2005; Wiens *et al.* 2010; Müller *et al.* 2011) or a combination of the two (Bayesian trees of Wiens *et al.* 2010) form the sister group to the remaining squamates rendering Scleroglossa paraphyletic. There are therefore major issues to be resolved with respect to squamate relationships but these are outside the scope of the current work.

Lifestyle

The Las Hoyas wetland supported both an aquatic community (water plants, arthropods, fish, frogs, salamanders, turtles and crocodiles) and a terrestrial one (Buscalioni and Fregenal-Martinez 2010). The latter comprised a diversity of plants and insects, spiders and terrestrial vertebrates including albanerpetontid amphibians, terrestrial crocodiles, pterosaurs, dinosaurs, birds and lizards (Buscalioni and Fregenal-Martinez 2010).

Compared to the other Las Hoyas lizards (*Meyasaurus*, *Scandensia*, *Hoyalacerta*, and a paramacellodid, Evans and Bolet in press), *Jucaraseps* is characterised by small size, a narrow somewhat elongated body, relatively short forelimbs, longer hind limbs (but with short pro- and epipodials and a long pes) and a long tail (145–180 per cent SVL allowing for the missing part) (Fig. 5). On the basis of living lizards of similar size and proportions (e.g. the scincid *Lerista elegans*, SVL 21–37 mm, 0.597 g; Benesch and Withers 2002), *Jucaraseps* is estimated to have weighed less than one gram.

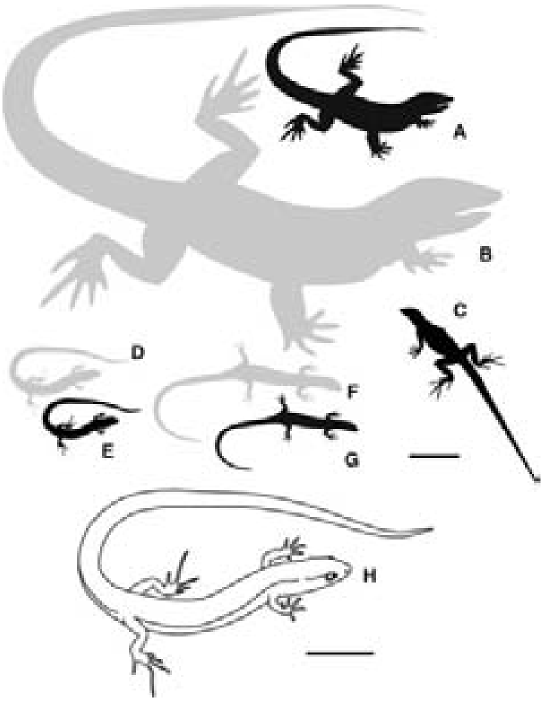

FIG. 5. Las Hoyas lizards. A–D, scaled silhouettes of: A, B, *Meyasaurus*, A, holotype of *Meyasaurus diazromerali* (LH 370, subadult); B, possible maximum size of *Meyasaurus* based on adult of *Meyasaurus faurai* Vidal 1915 (IPPS 10, Montsec). C, *Scandensia ciervensis* (LH 11001, adult). D, E, *Jucaraseps grandipes*; D, subadult holotype specimen (LH 18505); E, estimate of adult size. F, G, *Hoyalacerta sanzi*; F, holotype specimen (LH 11000, subadult); G, estimate of adult size. H, life reconstruction of *Jucaraseps grandipes*. Scale bars represent 20 mm (A–G) and 10 mm (H).

The smallest living lizards are *Brookesia* chamaeleons and sphaerodactylid geckos, but both have relatively short bodies and tails. Presacral elongation is found primarily in modern Anguidae, Gymnophthalmidae and Scincidae (e.g. Wiens and Slingluff 2001; Brandley *et al.* 2008), but only in the latter group is body elongation commonly combined with small size (e.g. Greer 1989, 2001; Melville and Swain 2000; Greer and Wadsworth 2003). Greer (2001) examined representatives of 1206 living scincid species and recorded a modal SVL of 55 mm, with 24 species having a SVL of 34 mm or less (mostly members of the lygosomine genus *Menetia*). Small scincids seem therefore to provide the most appropriate eco-analogue for *Jucaraseps*, and studies examining the relationship between body proportions and lifestyle provide potentially useful insights into its lifestyle.

Given its size and shape, *Jucaraseps* seems to best fit the ecological model of small cryptic surface to subsurface dwelling scincids with moderately elongated bodies and short limbs (Greer and Wadsworth 2003), but with long feet that may have been used to aid balance and grip in a very small animal moving on uneven surfaces (Melville and Swain 2000). *Jucaraseps* is unlikely to have been a burrower, as lizards weighing less than one gram reportedly lack the power to force their heads through the substrate (Benesch and Withers 2002). Moreover, burrowers generally do not have the long tails of surface dwellers (Brandley *et al.* 2008). Many small scincids are associated with leaf litter or the uppermost layers of soil, and Greer (1989) links this to body elongation and limb reduction. There are also small gymnophthalmids (e.g. *Gymnophthalmus pleii*, Turk *et al.* 2010) with a similar morphology and lifestyle.

A long tail coupled with an increase in presacral numbers enhances body flexibility especially if combined with shortened limbs. Elongated lizards that retain limbs tend to use a mixed locomotor pattern – lateral undulation when moving through vegetation or soft substrate and limbs when moving quickly over the ground (e.g. *Eremiascincus*, some *Lerista*, some *Niveoscincus*: Greer 1989; Greer *et al.* 1998; Melville and Swain 2000). Ground cover at Las Hoyas would have varied between the wetter and drier areas of the ecosystem, but fossil remains of fern fragments (pinnae and pinnulae), and both gymnosperm and angiosperm leaf types (Buscalioni and Fregenal-Martinez 2010) suggest there could have been a carpet of loose plant material (equivalent to modern leaf litter) in which *Jucaraseps* lived and moved. However, its slender body would also have been well adapted to sliding into crevices or under rocks to escape heat, rain, fire or predators – all of which are likely to have been a threat in the Las Hoyas ecosystem (Buscalioni and Fregenal-Martinez 2010). Lengthening the body may have had additional advantages. Within the scincid genus *Eumeces*, individuals of larger species (e.g. *E. fasciatus*) have fewer presacral vertebrae (26–27) than those of the smallest species (30–32, *E. brevirostris*, *E. lynxe*; Griffiths 1990). A similar pattern is found in other scincids (e.g. *Chalcides*, *Scelotes*, *Lerista*; Griffiths 1990) and it has been suggested that by increasing the relative volume of the abdomen, presacral elongation may compensate for the overall reduction in size, and thus clutch space, in small females.

On the basis of the gut contents, the most common Las Hoyas lizard, *Meyasaurus*, apparently fed in and around the water and this may explain its relative abundance at the locality (Evans and Barbadillo 1997, Evans and Bolet in press). The other Las Hoyas squamates are rarer and probably lived on drier ground, further from the water. *Scandensia* was a specialised climber (Evans and Barbadillo 1998; Bolet and Evans 2011), either on rocks or vegetation, whereas *Hoyalacerta* and the paramacellodid, like *Jucaraseps*, are interpreted as ground-living (Evans and Bolet in press). *Jucaraseps* had short jaws (*c.* 3–4 mm) with 8–10 relatively large teeth. Given its small size, its gape, and therefore prey size, would have been limited. Most of the adult insects and spiders recovered from Las Hoyas would have been too large for *Jucaraseps* to eat (and may even have posed a threat; Greer 1989), but small larvae and spiderlings would have been within its range.

CONCLUSIONS

Jucaraseps lies at the lower end of the modern lizard size range and demonstrates that very small-bodied lizards existed in the Early Cretaceous. Its slender, elongated body is reminiscent of many small living scincid lizards and some gymnophthalmids, and *Jucaraseps* is likely to have had a similar lifestyle. By comparison with living ecomorphs, its size, shape and large feet are suggestive of a secretive ground-living lizard that is likely to have hunted for small insects in and around loose vegetation but would itself have been a target for other small vertebrates and, possibly, large invertebrates. *Jucaraseps* thus increases our understanding of the Las Hoyas assemblage as a whole.

Phylogenetic analysis places *Jucaraseps* on the stem of a traditional monophyletic Scleroglossa (*sensu* Estes *et al.* 1988 and Conrad 2008; *contra* Townsend *et al.* 2004 and Vidal and Hedges 2005), which would be consistent with the frequency of body elongation/limb reduction within this group. However, further material (especially of the skull) may lead to a refinement of this position, as may more global molecular/morphological analyses of Squamata as a whole.

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LIZARDS AND AMPHISBAENIANS (REPTILIA, SQUAMATA) FROM THE LATE EOCENE OF SOSSÍS (CATALONIA, SPAIN)

8

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Lizards and amphisbaenians (Reptilia, Squamata) from the late Eocene of Sossís (Catalonia, Spain)

Arnau Bolet and Susan E. Evans

ABSTRACT

A new diverse late Eocene lizard and amphisbaenian assemblage from the classical mammal locality of Sossís (Catalonia, Spain) is described. It represents the first Paleogene lizard assemblage from Spain and the first late Eocene lizard locality from the Iberian Peninsula. The family-level composition of the assemblage replicates that of other contemporaneous European localities, with the presence of iguanians, geckos, lacertids, scincids, cordyliforms, amphisbaenians, anguines, and glyptosaurines. Many of these families still occur in Catalonia, but the presence of thermophilic taxa like iguanians and cordyliforms are indicative of warmer conditions during the Eocene. The closest faunal match is with the contemporaneous French localities of the Phosphorites du Quercy. Sossís and other newly recovered Paleogene Spanish squamate assemblages have the potential to contribute to an understanding of patterns of faunal interchange between different Paleogene bioprovinces, complementing existing data on mammals.

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Keywords: Squamata; lizards; amphisbaenians; Eocene; Iberian Peninsula; Spain

INTRODUCTION

Eocene European lizard faunas are relatively well known from France, Germany, Switzerland, and England (Figure 1; e.g., Augé, 2005; Rage and Augé, 2010; Klembara and Green, 2010). However, the Iberian record has been limited to the early Eocene (MP7) Portuguese assemblage of Silveirinha (Rage and Augé, 2003), which is also the only described Paleogene herpetofauna from southern Europe. The late Eocene Sossís fossil-site (Graus-Tremp basin, Catalonia) has been known since the 1940s (see Casanovas et al., 1998 and Checa and Casanovas, 1990 for historical background) and contains one of the best known mammal assemblages of the continental late Eocene of the Iberian Peninsula (see Cuesta et al., 2006 for artiodactyls, and López-Martínez et al., 1998 for a revision of the remaining mammal fauna). Despite mention of indeterminate croco-

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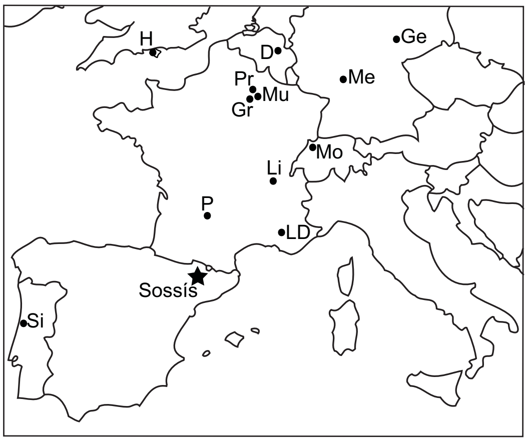

FIGURE 1. Map of southwestern Europe showing the main Eocene and Oligocene localities cited in the text. Abbreviations correspond to D: Dormaal; Ge: Geiseltal; Gr: Grisolles; H: Headon Hill; LD: La Débruge; Li: Lissieu; Me: Messel; Mo: Mormont-Entreroches; Mu: Mutigny; P: Phosphorites du Quercy (comprising the following localities, among others: Escamps, Lavergne, La Bouffie, Le Bretou, Les Pradigues, Malpérié, Perrière, Pech-du-Fraysse, Rosières and St. Néboule); Pr: Prémontré; Si: Silveirinha. For the exact age of each locality see the text.

diles (e.g., Berg and Crusafont, 1970) and turtles, the herpetofauna of the site has never been described in detail. In the 1990s, screen-washing efforts in the search for primates (currently under study [Marigó et al., in press]) yielded an important herpetofauna represented by thousands of isolated elements (tooth-bearing bones, skull bones, vertebrae, and osteoderms). In addition to the lizards, described here for the first time, the collection contains amphibians (frogs and salamanders), crocodiles, turtles, and snakes, which will be described elsewhere. This is the first Eocene lizard assemblage described from Spain, and the first late Eocene lizard assemblage from southern Europe.

GEOLOGICAL SETTING

Sossís is located in the Pobla de Segur subbasin, within the Graus-Tremp basin, which is one of the two Southern Pyrenean Basins (Cuesta et al., 2006). The Sossís lacustrine basin contains several fossiliferous levels at three localities: Roc de Santa, Sossís, and Claverol (Cuenca-Bescós, 1998). These levels have been correlated with Headonian levels from Montmartre (France, MP17a; Sigé, 1997), based on the presence of the rodent *Theridomys euzetensis* (Peláez-Campomanes, 1998).

MATERIAL AND METHODS

The material described here comes from a screen-washing concentrate obtained by researchers from the former Institut de Paleontologia de Sabadell (now Institut Català de Paleontologia Miquel Crusafont). The initial work focused on mammals, particularly small primates that had previously been reported by Crusafont (1965, 1967) and Crusafont and Golpe-Posse (1974). Consequently, the concentrate had only partially been processed and the herpetological material was not picked out or described. The restudy of the concentrates has revealed abundant herpetological remains, most of which are disarticulated except for some snake vertebrae. As the specimens come exclusively from screen-washing, the material is more fragmentary than if it had been surface collected or quarried, but it provides a better representation of the high diversity of small vertebrates, most of which are very small. The following isolated elements are described: frontals, parietals, premaxillae, maxillae, dentaries, vertebrae, and osteoderms. We have followed established criteria, recently formalised by Smith (2009a), in order to associate specimens: the specimens were secondarily associated with one another (considered to represent the same species) on the basis of size, abundance, apomorphies, complementarity of articulation, and other more or less direct data, such as surface ornamentation. These criteria have to be combined, as far as possible, in order to avoid the misassociation of elements of different taxa. In a well-sampled site such as Sossís, the represented taxa will each have a common size range, but the relative size of the morphotypes will not be always decisive on its own. Relative abundance can be used, with caution, to associate two common morphotypes or, on the contrary, two poorly represented morphotypes. Although complementarity of articular surfaces can provide relatively direct evidence for association of two elements, well-preserved articulation surfaces are rare in the Sossís collection. The strongest evidence for association comes from the similarity of dermal sculpture. Photographs were taken with an Environmental Scanning Electron Microscope. The material described herein is housed at the Institut Català de Paleontologia Miquel Crusafont, labelled IPS followed by the corresponding number.

Institutional and Other Abbreviations

IPS, Institut de Paleontologia de Sabadell (now Institut Català de Paleontologia Miquel Crusafont); QU, Phosphorites de Quercy, Muséum national d'Histoire naturelle; USTL, Université des Sciences et Techniques du Languedoc; MP, Mammal Paleogene reference level

SYSTEMATIC PALEONTOLOGY

Squamata Oppel, 1811

Higher-level relationships within squamates are still not resolved, with a conflict between morphology based trees (e.g., Estes et al., 1988; Conrad, 2008; Gauthier et al., 2012) and those based on molecular or combined data sets (e.g., Townsend et al., 2004; Vidal and Hedges, 2005; Wiens et al., 2006, 2010, 2012; Conrad et al., 2010; Müller et al., 2011). However, most of these analyses support the monophyly of the same major squamate groups: Iguania, Gekkota, Dibamidae, Scincoidea, Anguimorpha, Serpentes, and Lacertiformes, the latter clade encompassing Amphisbaenia in molecular (e.g., Townsend et al., 2004; Wiens et al., 2012) and combined evidence (Wiens et al., 2006, 2010; Müller et al., 2011) trees, but not those derived from morphology alone (e.g., Estes et al., 1988; Conrad, 2008; Gauthier et al., 2012). Gauthier et al. (2012) use the alternative name Lacertoidea for this clade but previous authors (e.g., Estes et al., 1988; Conrad, 2008) applied Lacertoidea to a larger clade that included xantusiids, a group now more often placed with scincoids (e.g., Vicario et al., 2003; Gauthier et al., 2012; Wiens et al., 2012). Vidal and Hedges (2005) also grouped amphisbaenians with lacertids, teiids, and gymnophthalmids, but unnecessarily erected a new clade name, Laterata. The monophyly of Scleroglossa (all squamates except Iguania), Scincomorpha (lacertiforms and scincoids) and Autarchoglossa (non-gekkotan, non-iguanian squamates) is not generally supported in molecular trees. We have therefore avoided these higher clade names until the relationships are clarified and a consensus is reached. In some cases, and because the European record is reasonably well known, comparisons have been focused on European taxa, and identifications are thus subject to geographic restrictions.

Iguania Cuvier, 1817
Iguanidae Gray, 1827

Three pleurodont iguanian genera, *Carduciguana* (Augé, 1987; MP16-19, France), *Geiseltaliellus* (Kuhn, 1944; MP7, Belgium, Portugal; Augé, 2005; Augé and Pouit, 2012; MP8-10, MP16-19, MP28, France; Rossmann, 2000a; MP11-12, Germany) and *Pseudolacerta* (De Stefano, 1903, MP16-19, France) have been reported from the European Paleogene. All of these taxa have tricuspid teeth, a characteristic shared by several of the Sossís specimens. Among extant lizards, tricuspidy is also found in lacertids and teiids, but teiids usually have cementum at the base of the tooth and among Eocene lacertids, tricuspid teeth are found only in *Plesiolacerta lydekkeri*. In that species, a weak third cusp results in an asymmetric tooth shape, and the grooves separating the main cusp from the accessory cusps are developed lingually but not labially (Augé, 2005). This morphology does not match any of the tricuspid jaw fragments from Sossís which more closely resemble those of *Geiseltaliellus* and *Pseudolacerta*.

Genus *Geiseltaliellus* Kuhn, 1944
Geiseltaliellus pradiguensis Augé, 2007

Material: IPS 56093 (Figure 2.1), partial right dentary with four preserved teeth; IPS 56094, partial right maxilla with one broken and three complete teeth; IPS 59521, fragment of ?dentary with five teeth (Figure 2.2); less certainly IPS 59523, five fragments of ?dentaries with teeth.

Description: The identified elements have exceptionally tall pleurodont tricuspid teeth, projecting only slightly above the parapet of the dentary. The teeth are slightly posteriorly inclined, but due to the deformation of the specimens this feature is of doubtful value. A mesiodistal constriction of the crown seems to characterize most teeth.

Remarks: *Geiseltaliellus* is known from the early to late Eocene (MP7-19; Augé, 2007) of Europe, with a single post-Grande Coupure record at Pech-du-Fraysse (France, Phosphorites du Quercy, MP28; Augé and Pouit, 2012). *Geiseltaliellus pradiguensis* (France, Les Pradigues, MP17) differs from other *G.* species in having tall, slender teeth that project only one fifth of their height above the jaw parapet (one third in the other *Geiseltaliellus* species, Augé, 2007). The teeth of the Sossís material are straight and slightly posteriorly inclined, and the exceptionally tall teeth are clearly reminiscent of *Geiseltaliellus* species.

Geiseltaliellus sp.

Material: IPS 56090 (Figure 2.3), partial left dentary with eight complete and four broken teeth.

Description: This well-preserved specimen (IPS 56090) is a partial left dentary broken into two

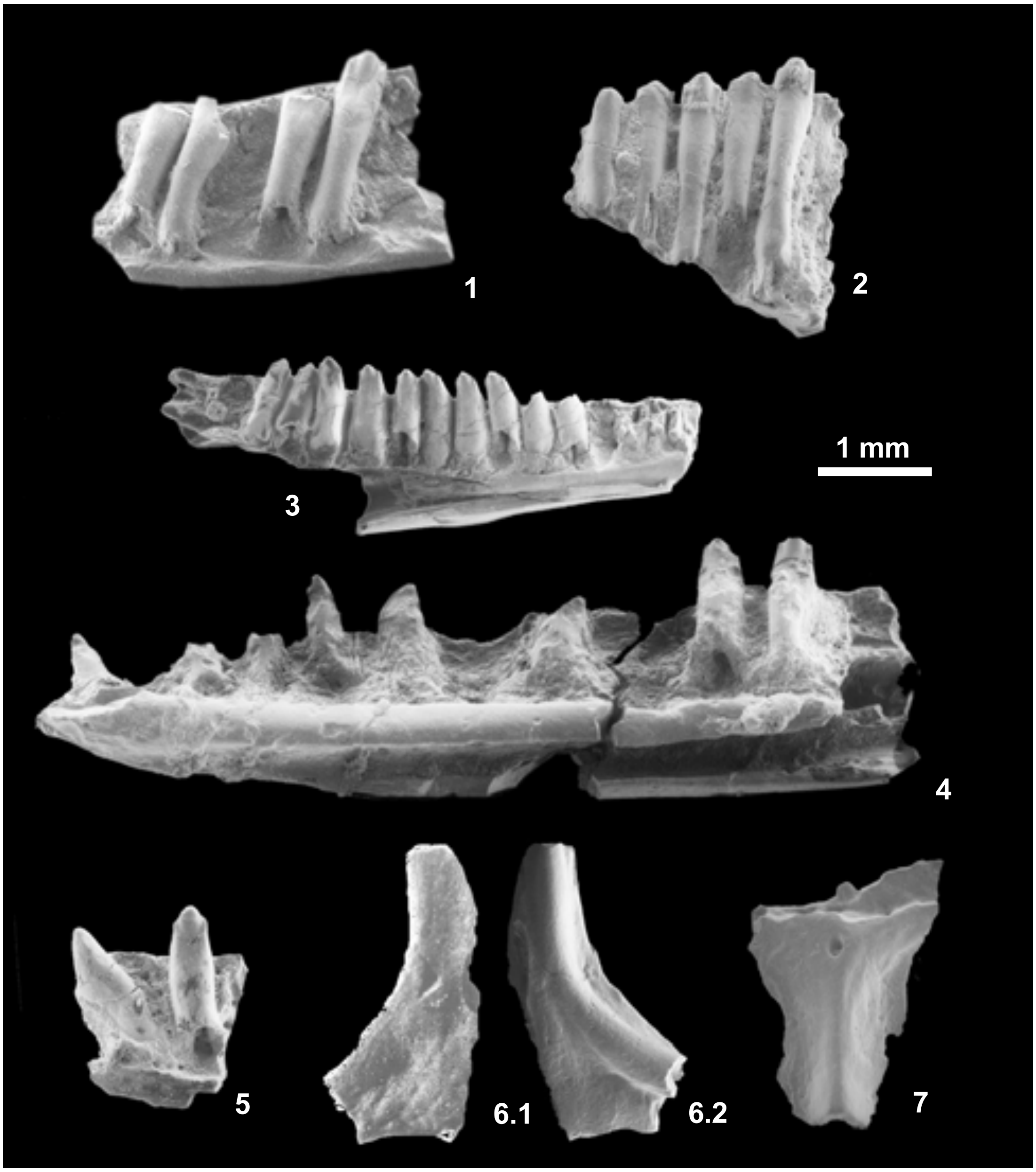

FIGURE 2. Pleurodont iguanians from the Sossís locality. 1, 2: *Geiseltaliellus pradiguensis.* 1- fragment of right dentary in lingual view (IPS 56093); 2- fragment of ?dentary in lingual view (IPS 59521). 3: *Geiseltaliellus* sp. Partial left dentary in lingual view (IPS 56090). 4, 5: *Pseudolacerta* sp. 4- Partial right dentary in lingual view (IPS 56164); 5- fragment of right dentary in lingual view (IPS 56165). 6-7: ?Iguanidae indet. 6- partial frontal in dorsal (6.1) and ventral (6.2) views (IPS 56109); 7- partial parietal in dorsal view (IPS 56091).

pieces and lacking the symphysial region. The ventral margin of the bone is straight. The Meckelian canal is wide open posteriorly, but becomes narrow with converging margins anteriorly. The splenial obscures this region and it is difficult to assess whether the two margins make contact, but fusion of the bone is certainly absent. The subdental shelf is moderately developed, with a rather rounded lingual surface and lacking a sulcus dentalis. The dentary presents a short posterolingual facet for the anterior process of the coronoid, and preserves eight complete teeth, with two additional broken bases, and three empty positions at the back and front of the bone. The implantation is pleurodont and the teeth are high-crowned, with one-third of their height projecting above the parapet. The crowns are clearly tricuspid, with a strong central cusp flanked by smaller cusps. As preserved, the teeth are slightly recurved, with tapered tips and somewhat enlarged bases. The teeth are perpendicular to the long axis of the bone in the middle part of the tooth row but have a tendency to incline slightly posteriorly in the anterior part of the tooth row and slightly anteriorly in posterior tooth positions. There is a large labial foramen at the middle height of the dentary, at the level of the first broken tooth.

Remarks: This material is referable to *Geiseltaliellus* on the basis of the dentary morphology: the Meckelian canal is closed and fused in *Cadurciguana* and has parallel borders in *Pseudolacerta*. IPS 56090 also lacks the enlarged anterior caniniform teeth typical of *Pseudolacerta*. It is clearly different from the *G. pradiguensis* specimen described above in having much shorter teeth. If the specimen is adult, the species would lie at the lower end of the size range of the genus. The presence of two species of *Geiseltaliellus* in the same deposit is common in European Eocene sites (e.g., at the French localities of Grisolles, Malpérié and Les Pradigues; Augé, 2005).

Genus *Pseudolacerta* De Stefano, 1903
Pseudolacerta sp.

Material: IPS 56164 (Figure 2.4), a partial right dentary with five complete and three broken teeth; IPS 56165, a fragment of dentary with two teeth (Figure 2.5); and less certainly, IPS 56152, anterior part of a right dentary with 5 broken teeth.

Description: IPS 56164 is a right dentary lacking only its posterior end. The bone is straight and rather slender. The subdental shelf is rounded and there is no sulcus dentalis. The Meckelian canal has parallel margins, but the opening extends from posterolingual to anteroventral. The dentition is heterodont, with enlarged anterior caniniform teeth, and slender posterior tricuspid teeth. IPS 56165 is interpreted as bearing the last caniniform and the first tricuspid teeth of a smaller specimen of the same taxon. IPS 56152 is an anterior part of dentary presenting large, probably, caniniform teeth (mostly broken). All three specimens are tentatively referred to *Pseudolacerta*.

Remarks: Among Eocene iguanians, a heterodont dentition, with large anterior caniniform teeth and slender posterior tricuspid teeth, is only known for *Pseudolacerta*. Both known species (*Pseudolacerta mucronata* and *Pseudolacerta quercyini*) are known from MP17 horizons at Les Pradigues, France (Augé, 2005), but the Sossís material more closely resembles *P. quercyini* in its smaller size, its weaker anterior caniniform teeth, its straight dentary margin and dental platform (parallel margins of Meckelian canal), and the more slender anterior dentary. *Pseudolacerta lamandini* (Filhol, 1877; MP17-19, France) was recently transferred to the genus *Geiseltaliellus* (Augé, 2005). This species has a dentary morphology reminiscent of *Pseudolacerta*, although the caniniform shape of the anterior teeth is less marked. Moreover, the transfer of *P. lamandini* to *Geiseltaliellus* remains unsettled (Smith, 2009b). We tentatively refer the Sossís material to *Pseudolacerta* sp., but *P. mucronata* can be eliminated due to its massive caniniform teeth. Dentaries of the other recorded European iguanian, *Cadurciguana*, combine a closed and fused Meckelian canal with tricuspid teeth. Such dentaries are absent at Sossís.

Additional Pleurodont Iguanian Material

The remaining specimens are difficult to assign as they lack diagnostic characters and could belong to either *Geiseltaliellus* or *Pseudolacerta* or to an additional taxon.

Material: IPS 49853, IPS 56092, IPS 56138-56144, IPS 56230, IPS 56232, IPS 59481, IPS 59501, IPS 59506, IPS 59522, tooth-bearing bone fragments; ?IPS 56109, partial frontal (Figure 2.6); ?IPS 56091, partial parietal (Figure 2.7).

Remarks: With the exception of anterior dentary specimens and more or less complete dentaries, most tooth-bearing bones with tricuspid teeth cannot be referred to a discrete pleurodont iguanian taxon. They probably belong to *Pseudolacerta* and *Geiseltaliellus*, but the presence of additional taxa cannot be discounted. IPS 56109 is a partial fused frontal resembling that of *Geiseltaliellus*, but its fragmentary nature precludes precise attribution. The cristae cranii are weakly developed and do not meet each other ventrally. A subtle ornamentation is present on the dorsal surface of the bone.

IPS 56091 is the anterior part of a small parietal that can be referred tentatively to Iguania. It is clearly different from the known parietals of *Geiseltaliellus* in that the parietal foramen is close to the frontoparietal suture but still within the parietal. It also differs from *Cadurciguana*, in which the parietal foramen lies at the frontoparietal suture. The

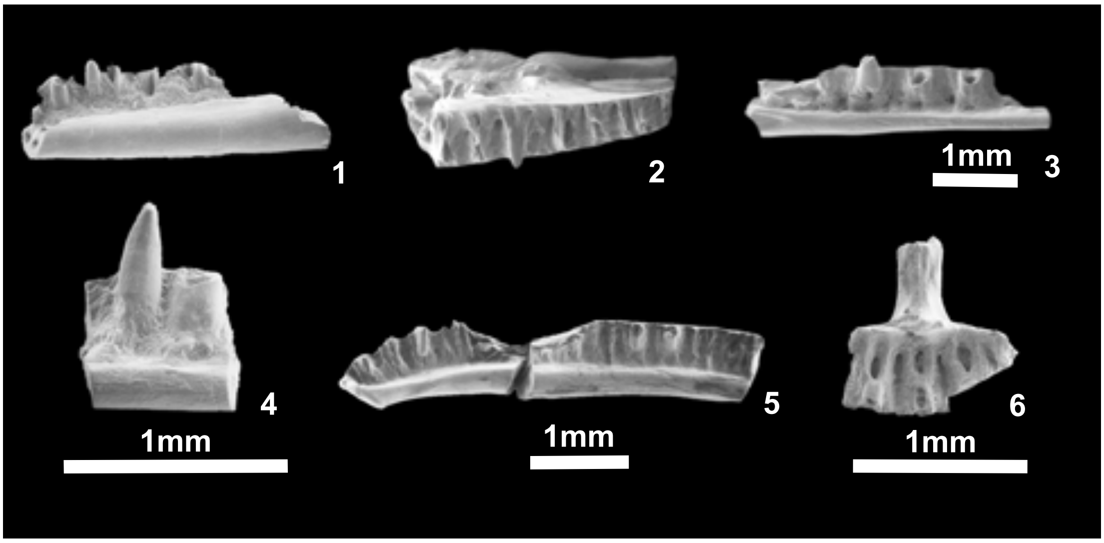

FIGURE 3. Gekkotan material from the Sossís locality. 1, 2: Gekkota indet. Form A. 1- partial right dentary in lingual view (IPS 56178); 2- partial right maxilla in lingual view (IPS 56065). 3, 4: Gekkota indet. Form B. 3- partial left dentary in lingual view (IPS 56132); 4- fragment of right dentary in lingual view (IPS 56116). 5: Gekkota indet. Form C. Partial right dentary in lingual view (IPS 56173). 6: Gekkota indet. Premaxilla in lingual view (IPS 59478).

parietal of *Pseudolacerta* is unknown. The occurence of the parietal foramen within the parietal is the common condition in non-iguanian lizards but it is rare in iguanians, with the exception of some polychrotines (Evans, 2008). Comparison of IPS 56091 with the parietal of *Geiseltaliellus* (e.g., Smith, 2009b) and its living relatives, the corytophanines (e.g., Smith, 2011), highlights marked differences, and therefore the identification of this bone as iguanian is only tentative.

Gekkota Cuvier, 1817

The presence of three clearly different types of slender dentary with a closed and fused Meckelian canal and numerous teeth has allowed the identification of three different, but currently indeterminate, gekkotans. Gekkotan remains are relatively rare in the fossil record as these lizards are generally gracile with thin bones. In the Paleogene of Europe, the following genera are recognized: *Laonogekko* (Augé, 2003; France: Prémontré, MP10), *Cadurcogekko* (Hoffstetter, 1946; France: many localities, MP 16-19), *Rhodanogekko* (Hoffstetter, 1946; Rage and Augé, 2010; France: Lissieu, MP14). Indeterminate gekkotan material has been reported from the early and late Eocene of France and Belgium (Augé, 2005). The absence of gekkotans from most middle Eocene localities is probably linked to the fact that levels at Geiseltal and Messel (Germany) usually yield large lizards (Augé, 2005). The few Middle Eocene gekkotans known are from localities that have yielded lizard remains through screen-washing (e.g., Lissieu, MP14 and Le Bretou, MP16; Augé, 2005; Rage and Augé, 2010).

Gekkota indet. Form A

Material: IPS 56176, partial right dentary with one preserved tooth; IPS 56178, partial right dentary with one preserved tooth (Figure 3.1); IPS 56065, partial right maxilla with one preserved tooth (Figure 3.2).

Description: Small unicuspid, cylindrical, and closely spaced teeth unite the maxilla and partial dentaries associated in this form. These dentaries are a little more robust than those of the other gekkotans from the site. The dentaries are also characterized by a well-developed subdental shelf that becomes shallower anteriorly. The Meckelian canal is completely closed and fused, and a sulcus dentalis is present and anteriorly deep. The teeth are smaller and much more closely packed, cylindrical and slender than those in Form B. Note that the presence of a second transversely positioned cusp cannot be evaluated in these specimens because preserved tooth crowns are worn.

Gekkota indet. Form B.

Material: IPS 56132, partial left dentary with one preserved tooth (Figure 3.3); IPS 56116, fragment of right dentary with one preserved tooth (Figure 3.4); IPS 56133, fragment of left dentary; IPS 56172, partial right dentary with three broken teeth; IPS 56182, fragment of right dentary; IPS 56183, anterior portion of right dentary with one preserved tooth; IPS 56184, fragment of right dentary with two broken teeth; IPS 56185, anterior portion of right dentary; IPS 56186, fragment of ?right dentary with two broken teeth; IPS 56187, fragment of right dentary with two broken teeth; IPS 56188, fragment of ?right dentary; IPS 56192, anterior portion of right dentary with three broken teeth; IPS 59499, fragment of dentary with one broken tooth; IPS 59511, partial dentaries and fragments of dentaries.

Description: This second form is characterized by teeth that are more robust, slightly labiolingually compressed, and more widely spaced. The internal face of the crown is flat, without any striations, and the tip bears a second cusp situated in a lingual position, resulting in two parallel crests. Although none of the dentaries is complete, the tooth count would presumably have been much lower in Form B than in Forms A and C. The dentaries are also extremely slender, with a relatively shallow, rounded subdental shelf, the dorsal and ventral surfaces of which are almost parallel. The Meckelian canal is closed and fused. There is a short facet for the articulation of the splenial, but this is restricted to the posterior part of the dentary. A sulcus dentalis is absent.

Gekkota indet. Form C.

Material: IPS 56117, fragment of right dentary with one preserved tooth; IPS 56173, partial right dentary (Figure 3.5) with five broken teeth; IPS 56174, fragment of right dentary with two teeth; IPS 56175, anterior region of a right dentary with six broken teeth; IPS 56177, partial right dentary with one preserved tooth; IPS 56180, fragment of ?left dentary with five broken teeth; IPS 56190, anterior portion of left dentary with three broken teeth.

Description: This form shares characters with Forms A and B, but it is clearly different from both. The dentaries are long and slender, with a subdental shelf that has parallel dorsal and ventral surfaces (as in Form B), but teeth that are conical, small, numerous and closely packed as in Form A.

Additional Gekkotan Material

Material: IPS 59478, partial fused premaxilla (Figure 3.6); IPS-56114, left dentary fragment with two preserved teeth; IPS 56115, left dentary fragment with two teeth; IPS 56120, fragments of dentaries; IPS 56179, fragment of right dentary with four broken teeth; IPS 56181, fragment of right dentary with four broken teeth; IPS 56189, fragment of dentary with two broken teeth; IPS 56191, fragments of dentaries; IPS 59520, fragments of dentaries.

Description: This small unpaired premaxilla shows the typical gekkotan T-shape. Its dorsal process appears rather slender. The lateral processes are straight and at 90º to the nasal process. The tips of the lateral processes are broken, but a minimum of nine tooth positions is interpreted. The tooth crowns are all broken, so their morphology cannot be observed. This material cannot be attributed to any one of the gekkotan 'forms' outlined above.

Remarks: Diagnostic character states of fossil gekkotans are largely restricted to maxillae, premaxillae, and frontals. Unfortunately, only one partial maxilla, one partial premaxilla, and several partial dentaries are preserved among the Sossís material. Although this material demonstrates the presence of gekkotans at Sossís, the material is too fragmentary to make a more precise referral. Dentaries are the most abundant and recognisable Paleogene gekkotan bones, but they have not been characterized at generic level and the most useful elements are maxillae (Augé, 2005). *Rhodanogekko* is known only from a distinctive frontal from Lissieu, France (MP14; Hoffstetter, 1946), obviating comparison with the Sossís gekkotans as no frontal material is available. The overall shape of the maxilla and dentaries of Form A are similar to those of *Laonogekko* from Prémontré, France (MP10; Augé, 2005), but important comparative characters are missing. Based on dentaries, three different gekkotans can be recognized at Sossís. The extremely slender subdental shelf, absence of a sulcus dentalis, and tooth shape of Form B seems to differentiate it not only from Sossís Forms A and C, but also from the other described Eocene gekkotans *Laonogekko* (Prémontré, MP10) and *Cadurcogekko* (Hoffstetter, 1946, from the Phosphorites du Quercy, France, MP16-19; Augé, 2005). The dentary of *Rhodanogekko* is unknown. The premaxilla, IPS 59478, differs from that of an indeterminate gekkotan described from Prémontré (Augé, 2005, figure 69) in having a more slender nasal process and a lower tooth count (9 v. 11+ in the Prémontré specimen, Augé, 2005).

Lacertiformes Estes et al., 1988
Lacertidae Bonaparte, 1831

Lacertids are a constant component of the Cenozoic European faunas, and are known from most

Eocene localities. The following characters are considered as suggestive of lacertid affinity (Augé, 2005): heterodont dentition with pleurodont anterior unicuspid and posterior bicuspid teeth; dentary ventral margin and subdental shelf ventrally arched; a Meckelian canal that is wide posteriorly but narrows towards the symphysis; and a splenial facet that almost reaches the symphysis. In many squamates, including lacertiforms, the coronoid has a lateral lappet that overlies the postero-labial surface of the dentary. Its presence in lacertiforms differentiates them from most scincoids, in which a postero-labial process of the dentary overlaps the coronoid (Augé, 2005). A number of the Sossís small dentaries can be attributed to Lacertidae based on this combination of characters. Only five species of Eocene lacertids fall in a similar size range: *Gracilicerta sindexi* (France, MP16-19, Augé, 2005); *Dormaalisaurus girardoti* (France and Belgium, MP7-16, Augé and Smith, 2002); *Dormaalisaurus rossmanni* (France and Belgium, MP7-10, Augé and Smith, 2002); *Succinilacerta succinea* (Baltic amber, Lithuania and Poland, MP13, Boulenger, 1917; Borsuk-Białynicka et al., 1999); and *Escampcerta amblyodonta* (France: La Bouffie, MP17; Escamps, MP19; Augé, 2005). Of these, *Succinilacerta succinea* (Boulenger, 1917) is known only from amber specimens and cannot be compared directly with the other taxa. In comparing the small Sossís lacertids to *Dormaalisaurus* and *Gracilicerta,* two characters, the presence or absence of striae and the degree of development of the small second cusp, were most useful in differentiating between genera and species in fragmentary specimens. *Escampcerta amblyodonta* differs in having a posterior amblyodont dentition, as do the larger *Pseudeumeces, Cernaycerta, Dracaenosaurus* and *Quercycerta* (Augé, 2005).

Genus *Dormaalisaurus* Augé and Smith, 2002

Dormaalisaurus rossmanni Augé and Smith, 2002

Material: IPS 59524, partial left dentary with four preserved teeth (Figure 4.1); IPS 56048 (Figure 4.2), partial right maxilla with six preserved teeth; IPS 56049, partial right maxilla with four preserved teeth; IPS 56060, four fragments of dentary with few preserved teeth; IPS 56089 partial right maxilla with three preserved teeth + partial left dentary with five broken teeth; IPS 56097, right dentary fragment with one tooth; IPS 56127, posterior fragment of left dentary with two preserved teeth.

Description: None of the specimens is complete, but tooth-bearing bones are united by the presence of labiolingually compressed teeth in which the second cusp is barely developed. The subdental shelf and the ventral margin of the dentary are only weakly curved (almost straight), and a deep sulcus dentalis is present. The maxilla lacks ornamentation at least on the preserved part of the labial surface, and the single preserved labial foramen is very large. The sulcus dentalis is narrow but rather deep.

Remarks: These elements are referred to Lacertidae on the basis of the tooth and dentary characters listed above. Among other characters, the presence of striae on the lingual surface of the crowns and a less developed second cusp differentiates *Dormaalisaurus* from *Gracilicerta*. *Dormaalisaurus girardoti* has a moderately developed second cusp, whereas in *D. rossmanni* the crowns are labiolingually compressed and there is no true second cusp. The presence and degree of development of striae on the lingual side of the crowns is variable, but is probably related to the degree of preservation.

Dormaalisaurus girardoti Augé and Smith, 2002

Material: IPS 56056, partial right dentary with two teeth (Figure 4.3); IPS 56051, fragment of left maxilla with four teeth; IPS 56054, fragment of right dentary with three preserved teeth; IPS 56059, anterior end of maxilla with two preserved teeth; IPS 59525, dentary and maxilla fragments.

Description: The subdental shelf and the ventral margin of the dentary are only weakly curved. The lingual surface of the subdental shelf is rounded. The crowns bear moderately developed cusps situated anterior to the main cusp. The crowns are lingually striated.

Remarks: The specimens referred to *Dormaalisaurus girardoti* differ from those of *Gracilicerta sindexi* (see below) in that the subdental shelf and the ventral margin of the dentary are less arched, and lingual striations are present on the crowns. They differ from specimens referred to *D. rossmanni* in the presence of a better developed second cusp. Some of these characters could be influenced by ontogeny, but until this is investigated in the better-known material from France, we prefer to maintain the original taxonomic units and to refer our material on the basis of the characters previously described.

Genus *Gracilicerta* Augé, 2005

Gracilicerta sindexi Augé, 2005

Material: IPS 56171, partial left dentary with eight preserved teeth (Figure 4.4); IPS 49854, fragment of left dentary with three preserved teeth; IPS 49856, fragment of left dentary with one preserved

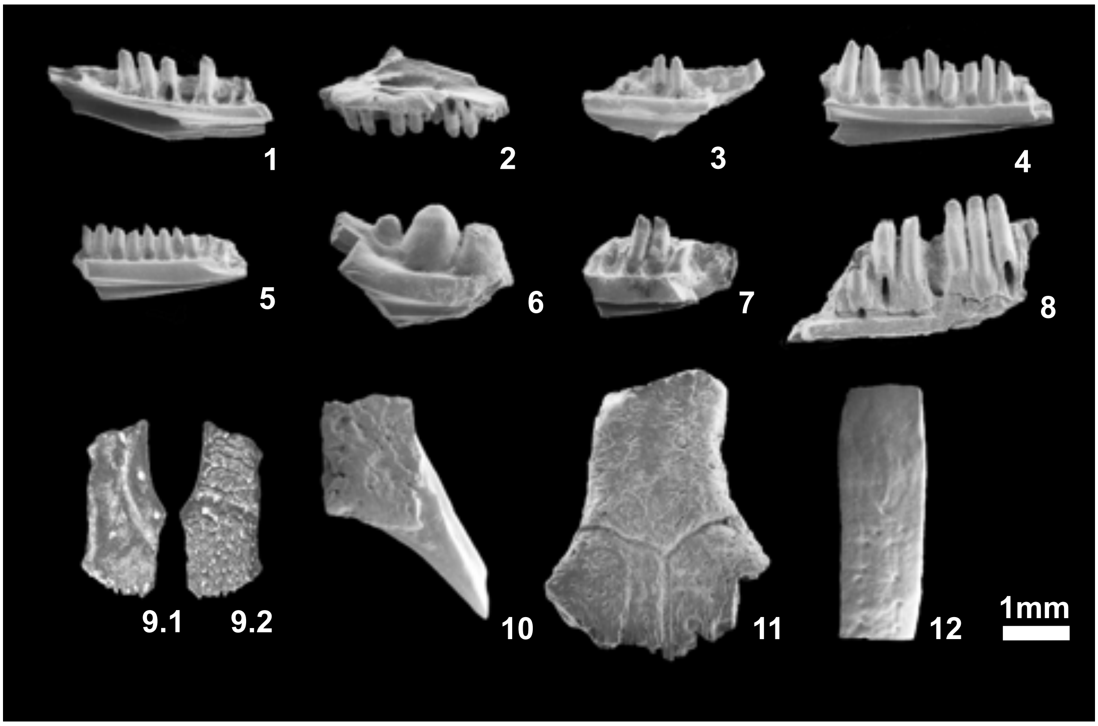

FIGURE 4. Lacertiforms and scincoids from the Sossís locality. 1, 2: *Dormaalisaurus rossmanni*. 1- partial left dentary in lingual view (IPS 59524); 2- partial right maxilla in lingual view (IPS 56048). 3: *Dormaalisaurus girardoti*, partial right dentary in lingual view (IPS 56056). 4: *Gracilicerta sindexi*, partial left dentary in lingual view (IPS 56171); 5: Lacertidae indet., fragment of left dentary in lingual view (IPS 56066); 6: ?Lacertidae (amblyodont form), fragment of left dentary in lingual view (IPS 56169); 7: ?Cordyliformes, fragment of left dentary in lingual view (IPS 56195); 8: ?Scincidae, fragment of dentary (IPS 56193); 9: Lacertidae indet. (IPS 56043). 9.1- left frontal in ventral view. 9.2- left frontal in dorsal view; 10: Lacertidae indet., posterior fragment of parietal in dorsal view (IPS 56046). 11: ?Lacertidae indet., fused frontal in dorsal view (IPS 56166). 12: Cordyliformes indet., body osteoderm in external view (IPS 49848a).

tooth; IPS 56050, fragment of left maxilla with two preserved teeth.

Description: The lingual face of the subdental shelf is flat all along the preserved portion. The ventral margin of the dentary is arched. The crowns bear a pointed, well-developed, and anteriorly positioned second cusp. A deep sulcus dentalis is present.

Remarks: As noted above, the dentary of *Gracilicerta sindexi* is differentiated from that of *Dormaalisaurus* species by the absence of striations on the tooth crowns, as well as the anteroventrally open Meckelian canal and a generally smaller size. The presence of a deep subdental shelf that leaves the Meckelian canal exposed only ventrally in the anterior part of the dentary, and the more arched general shape of the dentary supports attribution of IPS 56171 to this species. Compared to it, the dentary of *Dormaalisaurus* shows a weaker bicuspidy and a less arched shape.

?Lacertidae indet. (amblyodont form)

Material: IPS 56169, fragment of left dentary with three preserved teeth (Figure 4.6); and, less certainly: IPS 56102, posterior left dentary fragment with two preserved teeth; ?IPS 56036, posterior left dentary fragment with two worn teeth; IPS 49913, right dentary fragment with two preserved teeth; IPS 56067, anterior portion of left maxilla with three preserved teeth; and IPS 56170, anterior portion of right maxilla with three preserved teeth.

Description: None of the tooth-bearing bones is complete but they certainly belonged to a short-jawed lizard. IPS 56169 (Figure 4.6) preserves the posteriormost three dentary teeth which are swollen and molariform (amblyodont) with well-defined lingual and labial striations. The subdental shelf is deep, but not prominent, and the lingual margin is flat. There is no sulcus dentalis, and small resorption pits are situated lingual to the base of each tooth. IPS 56102 and IPS 56036 (not figured) are smaller dentary fragments showing the same overall morphology: a deep subdental shelf, an enlarged amblyodont penultimate tooth, and a reduced last tooth. One right dentary fragment (IPS 49913, not figured) represents a more anterior jaw region and bears two labiolingually compressed but still amblyodont teeth, with highly worn crowns and small, lingually positioned, basal resorption pits. Two additional maxillary fragments (IPS 56067 and IPS 56170, not figured) are tentatively referred to the same taxon on the basis of tooth similarity.

Remarks: The tooth morphology of IPS 56169 is intermediate between that of moderately amblyodont lacertids such as *Pseudeumeces* Hoffstetter, 1944 and the much stronger amblyodonty of *Dracaenosaurus* Pomel, 1846. *Dracaenosaurus* ranges from MP28 to MP30 in France (Augé, 2005; Augé and Hervet, 2009), although there is one specimen (MNHN 1903-20), precise locality and age unknown, from old collections of the Phosphorites du Quercy. This latter specimen, the holotype of *D. sauvagei* (Filhol, 1882) but synonymised with *D. croizeti* (Augé, 2005), is from the late Eocene or, probably, the Oligocene (Augé, 2005). Hoffstetter (1944) used the presence of a small tooth posterior to the last molariform to differentiate *D. sauvagei* from *D. croizeti*, but Augé (2005) interpreted this as ontogenetic variation. The Sossís material shows some resemblance to *Dracaenosaurus*, but its smaller size and the weaker degree of amblyodonty suggest it is generically distinct. However, the available material is too poor to permit the erection of a new genus. Two additional amblyodont lacertids (*Escampcerta amblyodonta* and *Quercycerta maxima*) are known from the late Eocene of France (Augé, 2005), but the Sossís material differs from them in its much stronger amblyodonty, and the enlarged penultimate tooth. The amblyodont Sossís dentary fragments IPS 56036 and IPS 56102 are less amblyodont than IPS 56169, and also much smaller, but they show the same tendency towards an enlargement of the penultimate tooth. They are interpreted as juveniles of the same taxon as IPS 56169. They also resemble an unidentified left dentary (USTL Mal 606) from the MP17 level at Malpérie (France) (Augé, 2005, figure 206), although the latter's amblyodonty is less obvious due to wear. The small Sossís specimens and that from Malpérié may belong to the same taxon. IPS 49913, IPS 56067, and IPS 56170 are also amblyodont, but they correspond to regions (one dentary mid-section and two maxilla fragments) that cannot be directly compared to the other specimens, and they are less clearly related to them.

Additional Lacertid Material

Material: IPS 49855, eleven dentary fragments; IPS 56043, partial left frontal (Figure 4.9); IPS 56044, IPS 56045, ?IPS 56047, fragments of right frontal; ?IPS 56166 (Figure 4.11), partial fused frontal; IPS 59479, fragment of frontal; IPS 56046 (Figure 4.10), fragment of parietal; IPS 56053, fragment of right maxilla with three preserved teeth; IPS 56055, fragment of right dentary with two broken teeth; IPS-56058, fragment of right dentary with one preserved tooth; IPS 56066, anterior region of left dentary with eight preserved teeth.

Apart from dentary and maxillary fragments, a small number of dermal skull elements have been recognized. The frontals and parietals, with the typical lacertid ornamentation, are particularly interesting, and show more than one morphology. Although the bones cannot be referred to a particular taxon with confidence, they do show some potentially significant features. IPS 56043 (Figure 4.9) is a small frontal that was clearly one of a pair because of the medial sutural surface. It is relatively wide and has a concave lateral margin. The ornamentation is vermiculate anteriorly, gradually becoming pitted posteriorly. A transverse ridge marks the boundary between the frontal and frontoparietal scales. The posterior margin shows that the frontoparietal suture was strongly interdigitated. The crista cranii is not strongly developed (at least the preserved part), and is pierced by two large foramina. The ornamentation differs from that of the *Dormaalisaurus* sp. frontal figured in Augé and Smith (2002), which is more uniform and less dense. It is possible, then, that IPS 56043 represents a *Gracilicerta* frontal, although this cannot be assured. Other more poorly preserved specimens (IPS 56044, IPS 56045, not figured) may represent the same taxon. IPS 56166 (Figure 4.11) is a much larger unpaired frontal. The ornamentation is more uniformly vermiculate than in the smaller frontals, and the bone is much more robust. A transverse groove across the middle of the bone represents the boundary between frontal and frontoparietal scales. Although paired frontals are typical for lacertids, fused frontals occur in several extant taxa where they may be strongly constricted between the orbits (e.g., *Acanthodactylus*, SE pers. obs.) or broad (e.g., *Gallotia galloti*, Barahona and Barbadillo, 1998: figure 4). Arnold (1989) interpreted frontal fusion in lacertids as resulting from an extension of cranial ontogeny beyond that of primitive taxa. IPS 56166 is very similar to two undescribed specimens from the old collections of the Phosphorites du Quercy (QU 17677, AB pers. obs.) and may represent an additional, large lacertid taxon at Sossís, possibly conspecific with the similar-sized amblyodont dentary (IPS 56169) described above. IPS 56046 (figure 4.10) is a small partial lacertid parietal, which cannot be assigned to one or another taxon. The ornamentation present on this bone is of lacertid type, but as the parietal has not been described for *Dormaalisaurus* or for *Gracilicerta*, it is not possible to make a definite referral.

Scincoidea Oppel, 1811
Cordyliformes Fitzinger, 1826

Although several Paleogene specimens have tentatively been referred to Cordylidae (e.g., Van Dyck, 1983), the presence of cordyliforms (cordylids and gerrhosaurids) in the European Paleogene remains controversial (Augé, 2005). *Pseudolacerta*, once attributed to Cordylidae (Hecht and Hoffstetter, 1962; Augé, 1990) has now been referred to Iguania (Augé, 2005). A partial postcranial skeleton from the Upper Oligocene of Germany (Rott, MP30, Kempf et al., 1997), initially named '*Lacerta*' *rottensis* (von Meyer, 1856), was attributed to Cordyloidea (=Cordyliformes) by Böhme and Lang (1991), but the specimen is apparently lost (Augé, 2005). However, the middle Eocene *Eocordyla mathisi* from France is still tentatively referred to the Cordylidae (Augé, 2005), and is of interest as it occurs at levels MP16 and 17 (overlapping in time with Sossís). European Neogene cordylids are recorded from the Miocene of the Czech Republic (*Palaeocordylus bohemicus*, Dolnice, MN4, Roček, 1984; Merkur-North, MN3, Čerňanský, 2012), Austria (Cordylidae indet., Obergänserndorf 2, MN5; Böhme, 2002), and Germany (*Bavaricordylus ornatus*, Petersbuch 2, MN4a; Kosma, 2004; Cordylidae indet., Puttenhausen, MN5; Abdul-Aziz et al., 2008; *Bavaricordylus molassicus* and Cordylidae indet., Sandelzhausen; Böhme, 2010). Although the dental morphology of *Bavaricordylus* is not conclusively cordyloid, Kosma (2004) based his attribution on the presence of rugosities on the lower jaw related to a covering of osteoderms. Outside Europe, *Konkasaurus* (Madagascar, latest Cretaceous) has tentatively been referred to Cordylidae, and would represent the earliest known cordyliform (Krause et al., 2003).

Cordyliformes indet.

Material: IPS 49848, more than 300 body osteoderms (Figure 4.12); and less certainly IPS 56195, anterior (symphyseal region) fragment of left dentary (Figure 4.7) with two preserved teeth.

Description: The osteoderms are rectangular, with an anterior overlapping surface, thin tapering lateral edges, and numerous foramina in the external and internal surfaces. The largest complete osteoderm is 4 mm long, although some of the broken ones may have been longer. Their width never exceeds 2 mm, but some reach 0.5 mm in thickness. A small number bear a low, oblique keel. IPS 56195 is an anterior portion of dentary. The preserved teeth have distinct labial and lingual cusps (cuspis labialis and cuspis lingualis, sensu Richter, 1994), and the cuspis lingualis is formed by two apically converging main striae (the stria dominans anterior and posterior, sensu Richter, 1994) at their point of intersection. The lingual surface of the tooth is concave, and bears numerous well-developed striae, some of which seem to bifurcate apically.

Remarks: The osteoderms described herein represent the earliest and most extensive collection available of cordyliform osteoderms from the entire European record. Interestingly, despite the attribution of dental remains from several European localities to cordyliforms, osteoderms are recorded only on two specimens, the lost Oligocene specimen from Rott, Germany, and Miocene material from Obergänserndorf 2, Austria (Böhme, 2010). Given the high preservational potential of osteoderms, due to their numbers and robusticity, the absence of these elements in most Eocene deposits is intriguing. Their small size may render them less likely to be recovered unless the site is intensively screen-washed using fine sieves. The osteoderms of *Cordylus* and advanced cordylids tend to be spiny, unlike the rectangular elements of the Malagasy *Konkasaurus* (Krause et al., 2003) or those from Sossís. Richter (1994) gave a detailed review of scincid, gerrhosaurid, and cordylid osteoderms, in relation to those of Mesozoic paramacellodids, concluding that the latter group has compound ventral osteoderms like those of scincids and gerrhosaurids. Those of *Konkasaurus*, however, showed no evidence of compound structures and the same applies to the Sossís material.

The tooth morphology of IPS 56195 is suggestive of scincoid attribution, but it lacks an antrum intercristatum. In most scincids (and also some lacertids, Kosma, 2004), the cuspis lingualis is not formed by the striae dominantes, but instead by a second system of apically converging cutting edges, the crista lingualis anterior and posterior (sensu Kosma, 2004). In these taxa, a sulcus, the antrum intercristatum, may be present between a well-developed cristae lingualis and the labial crista mesialis and distalis. According to Kosma (2004), many cordyliforms and paramacellodids lack an antrum intercristatum, but as it is also missing in some scincids (e.g., *Tropidophorus bavaricus* from the Miocene of Germany; Böhme, 2010), the character is of restricted value in differentiating members of each group. It is possible that the osteoderms tentatively referred to Cordyliformes (see above) belong to the same taxon as this dentary, but this cannot be demonstrated with the available material. IPS 56195 differs from *Eocordyla* (Augé, 2005) and also from taxa referred to the Scincidae (Augé, 2005). Had this dentary been found in Mesozoic sediments, it would have probably been attributed to a paramacellodid, supported by the co-occurring rectangular osteoderms, and this highlights a wider problem regarding the status of paramacellodids as a distinct group.

Scincidae Gray, 1825
?Scincidae indet.

Material: IPS 56193, ?dentary fragment with five preserved teeth (Figure 4.8); ?IPS 56052, fragment of tooth-bearing bone with one tooth.

Description: The teeth are columnar and very tall, with a slight posterior increase in diameter. A deep antrum intercristatum (sensu Kosma, 2004) is present.

Remarks: The teeth of this second scincoid jaw type differ from those of IPS 56195 described above in having a deep antrum intercristatum, and in lacking lingual striations. The teeth of IPS 56193 are reminiscent of the Paleocene Belgian *Scincoideus* (Folie et al., 2005), but this taxon has a relatively plesiomorphic dentition.

?Scincoidea Incertae Sedis., Unnamed New Genus and Species

Two further specimens from Sossís, IPS 56061 (a partial left dentary with two teeth) and IPS 56168 (a fragment of right dentary with one preserved tooth) represent another small taxon with possible scincoid affinities. This will be described and named elsewhere together with similar French material (AB, pers. obs.).

Amphisbaenia Gray, 1844

Relatively little is known of the fossil history of amphisbaenians in Europe (Augé, 2012). References to the presence of the family Amphisbaenidae in the European Paleogene (e.g., Hecht and Hoffstetter, 1962; Augé, 2005) are based mainly on the resemblance of some fossils to the recent genus *Blanus*, or on the fact that they cannot easily be attributed to any group of 'non-amphisbaenid' amphisbaenians. However, *Blanus* is now placed in its own family (Blanidae, Kearney, 2003) rather than Amphisbaenidae. Of currently recorded European Paleogene amphisbaenians, the genus *Omoiotyphlops* from the Phosphorites du Quercy (exact fossil-site unknown, estimated age between latest early Eocene and early Miocene) is a nomen dubium (Estes, 1983: Augé, 2005), and the genus *Campinosaurus* (Augé, 1992) from Belgium (Dormaal, MP7) is problematic. It is characterized by the presence of striae at the base of the teeth (Augé, 2005), but the only known specimen is a partial dentary with seven preserved tooth positions, making a tooth count of fewer than 10 unlikely. Moreover, with the exception of the striae, the dentary resembles that of the possible scincoid *Foliesaurus* Augé and Smith, 2009, from the Oligocene of Belgium. Attribution of this material to Amphisbaenia is therefore uncertain. A form close to *Blanus* has been reported for several Paleogene European sites (e.g., Augé, 2005; Rossmann, 2000b), but uncertainty regarding the relationships of the living genus complicates referral of the Paleogene remains (Augé, 2005). The German *Palaeoblanus*, described from the lower Miocene of Weisenau (MN2)(Schleich, 1988) and more tentatively from Gaimersheim (?MP27-28) and Ehrenstein (MP30)(Augé, 2005) is distinguished from the extant *Blanus* only in the presence of well-developed foramina over the labial surface of the dentary (Augé, 2005), and by the presence of an enlarged first tooth, subtle differences that possibly do not justify its referral to a separate genus. Similarly, the recently described *Louisamphisbaena* from Grisolles (France, MP16), tentatively referred to Blanidae (Augé, 2012), is difficult to distinguish from *Blanus*. Indeterminate blanids have been also recently reported from Escamps, St. Néboule (MP18) and Malpérié (Phosphorites du Quercy, France; Augé, 2012). Rossmann (2000b) reported a new amphisbaenian from France (Le Bretou, MP16), but as yet this is unnamed and undescribed. The tentative recognition of the Eocene American genus *Anniealexandria* in France (Mutigny, MP8-9, Augé, 2012) is problematic. The main diagnostic character is the presence of nine dentary teeth, rather than a maximum of eight as in other amphisbaenians (Smith, 2009a). However, at

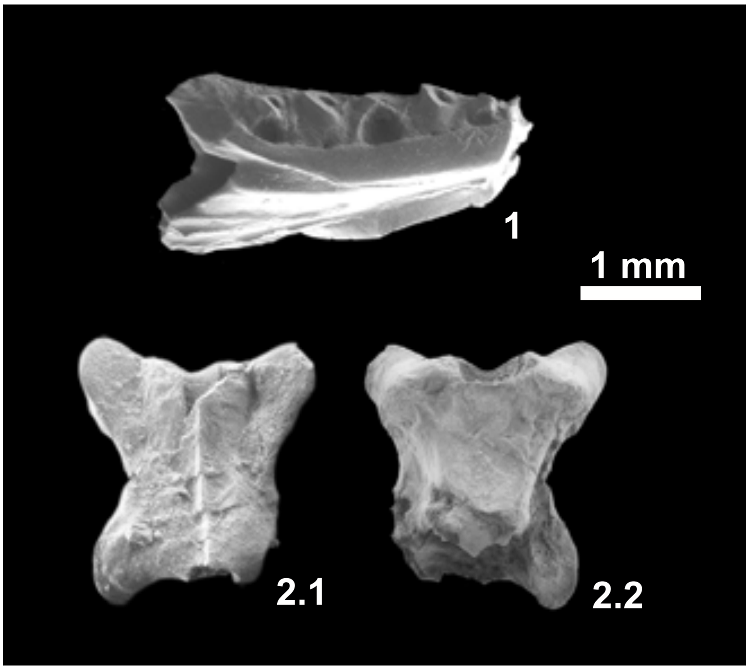

FIGURE 5. Amphisbaenians from the Sossís locality. 1, 2: cf. Blanidae indet. 1- partial left dentary in lingual view (IPS 56062); 2- dorsal vertebra (IPS 56063) in dorsal (2.1) and ventral (2.2) views.

least one specimen of *Amphisbaena alba* from Bolivia also has nine dentary teeth (Figure 11, p. 1774 in Daza et al., 2011), and the original description of *Anniealexandria* (Smith, 2009a) noted similarities with *Amphisbaena*.

cf. Blanidae indet.

Material: IPS 56062, partial left dentary with five broken teeth (Figure 5.1); IPS 56063, almost complete dorsal vertebra (Figure 5.2); IPS 56064, almost complete dorsal vertebra; IPS 56155, partial dorsal vertebra.

Description: IPS 56062 is lacking its symphyseal region but it is unlikely that more than three or four additional teeth were originally present (tooth count of eight or nine). An intramandibular septum is well-developed, fused to the ventral margin of the dentary, and its posterior edge extends beyond that of the last tooth. Two marked depressions on the dorsolingual and ventrolingual surface of the dentary are interpreted facets for the anterolingual process of the coronoid and the splenial, respectively. Labially (not shown), only the last, particularly large, neurovascular foramen is preserved. Two vertebrae clearly belong to Amphisbaenia. One (IPS 56063) is small and almost complete and the other (IPS 56155) is more poorly preserved. They are strongly dorso-ventrally compressed, lack a neural spine, and have a flat ventral surface to the condyle (preserved only in IPS 56063). Both the condyle and cotyle are widest transversely.

Remarks: As preserved, IPS 56062 is indistinguishable from that of *Blanus* but given the limited nature of the material, it is possible that it represents a different but closely related genus. We tentatively refer the Sossís material to Blanidae, pending the recovery of more material and the study of additional undescribed amphisbaenian material from Spain (AB pers. obs.) and France. Augé (2012) similarly attributed new material from France to Blanidae based on the strong resemblance of the material to that of the extant genus. The Sossís vertebrae are not diagnostic beyond the level of Amphisbaenia, but they differ from those of Rhineuridae, mainly in the lack of striae over the neural arch.

Anguimorpha Fürbringer, 1900

Anguimorphs are relatively well-represented in the European Paleogene, mainly by anguids referred to the subfamilies Glyptosaurinae and Anguinae (e.g., Estes, 1983). The extinct Holarctic subfamily Glyptosaurinae is represented in Europe by the glyptosaurin genus *Placosaurus* from the

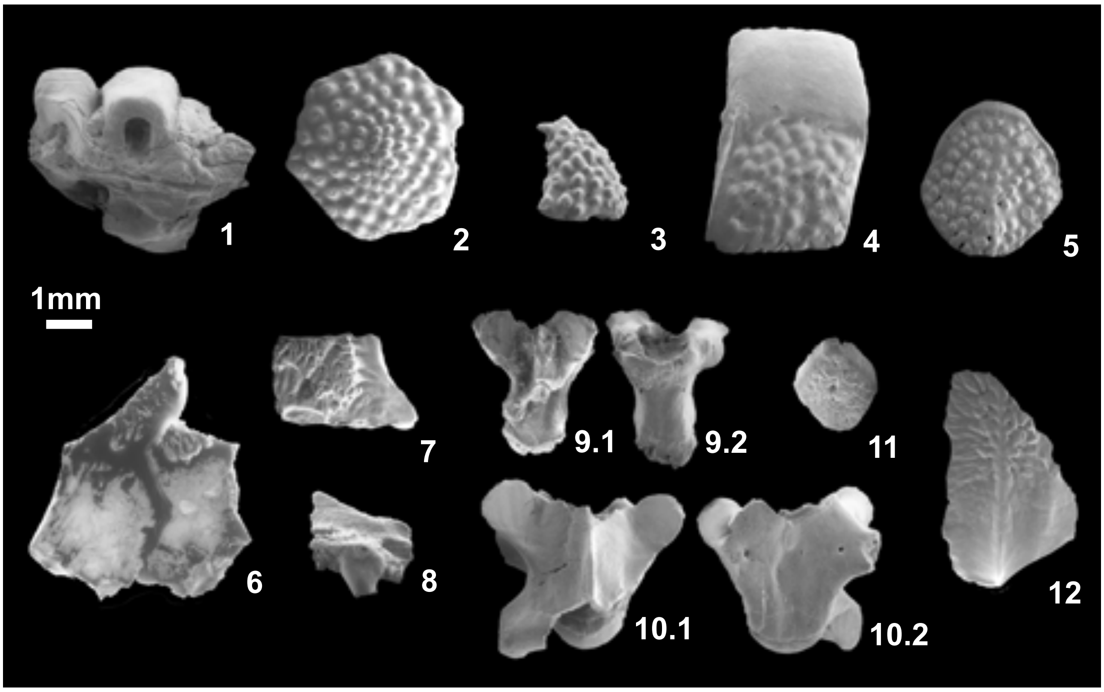

FIGURE 6. Anguimorph specimens from the Sossís locality. 1: Glyptosaurinae indet., fragment of ?dentary (IPS 56167); 2-5: Glyptosaurini indet. 2- hexagonal skull osteoderm in external view (IPS 49845a); 3- skull osteoderm of unusual shape (IPS 49845b). 4- rectangular body osteoderm in external view (IPS 59528); 5- rounded body osteoderm in external view (IPS 49846d); 6-8, 11, 12: Anguinae indet. 6- partial parietal in dorsal view (IPS 56085); 7- posterior region of a right frontal in dorsal view (IPS 56086); 8- fragment of right ?maxilla in lingual view (IPS 56129); 9: Anguinae indet. Form A, vertebra (IPS 56082) in dorsal (9.1) ventral (9.2) views; 10: Anguinae indet. Form B, caudal vertebra (IPS 56080) in dorsal (10.1) and ventral (10.2) views; 11- rounded body osteoderm, in external view (IPS 49851a); 12- elongated body osteoderm, in external view (IPS 49847a).

Eocene of France (La Débruge, MP18; Phosphorites du Quercy, MP 16-19: Sullivan and Augé, 2006) and probably Belgium (Dormaal, MP7: Sullivan et al., 2012), and by the 'melanosaurin' *Placosauriops* Kuhn, 1940 (France, ?Prémontré, MP10; Germany, Messel and Geiseltal MP11-12), *Paraxestops* Hoffstetter, 1962 (Switzerland, Mormont-Entreroches, MP19) and *Paraplacosauriops* Augé and Sullivan, 2006 (France, Phosphorites du Quercy, unknown locality, middle or late Eocene, and Lavergne, MP16: Augé and Sullivan, 2006). Indeterminate specimens of Glyptosaurini (Belgium, England, France, Portugal, and Switzerland; MP8+9 to MP20) and 'Melanosaurini' (France and Portugal, MP7-13) are also recorded from numerous localities across Europe (Augé, 2005). For Anguinae, complete skeletons of *Ophisauriscus* are known from the middle Eocene of Germany (Kuhn, 1940; Klembara, 1981; Sullivan et al., 1999), whereas *Helvetisaurus* and *Headonhillia* are based on disarticulated remains from the late Eocene of Switzerland and France (Augé, 2005), and from England (Headon Hill, Klembara and Green, 2010), respectively. Disarticulated and fragmentary remains from the Eocene and Oligocene have been referred to the extant genera *Anguis* (France, MP8+9 to MP30; Augé, 2005) and *Ophisaurus* (Belgium, England, France, and Switzerland ?MP1-5, MP7-30)(Hecht and Hoffstetter, 1962; Augé, 1992; Augé and Smith, 2009; Klembara and Green, 2010). *Anguis* and *Ophisaurus* are also recorded from the Neogene, as are representatives of the living *Pseudopus*, but the latter currently has no Paleogene record (Klembara et al., 2010). Klembara et al. (2010) considered *Dopasia* to be a synoym of *Ophisaurus,* as suggested by Sullivan et al. (1999), but later (Klembara and Green, 2010) maintained *Dopasia* for some Oligocene species. Conrad et al. (2010) also separated *Dopasia harti* and *Pseudopus apodus* from *Ophisaurus*. Anguine relationships thus remain incompletely resolved, and this complicates referral of new fossil material.

Anguidae Gray, 1825
Glyptosaurinae Marsh, 1872
Glyptosaurini Sullivan, 1979
Glyptosaurini indet.

Material: IPS 49845a, hexagonal skull osteoderm (Figure 6.2); IPS 49845b, skull osteoderm with unusual shape (Figure 6.3); IPS 49845c, 25 skull osteoderms with unusual shapes; IPS 49845d, >600 hexagonal skull osteoderms; IPS 49845e skull osteoderm; 59477, seven skull osteoderms; IPS 59497, two hexagonal skull osteoderms; IPS 59468, hexagonal skull osteoderm; IPS 59485, 28 skull osteoderms; IPS 59508, two skull osteoderms; IPS 59527, 22 worn skull osteoderms. IPS 49846a, body osteoderm; IPS 49846b, >700 body osteoderms; IPS 49846c, >1300 fragments of osteoderm; IPS 49846d, rounded body osteoderm (Figure 6.5); IPS 49846e, rounded body osteoderm; IPS 49846f, 50 rounded body osteoderms; IPS 56068, skull bone fragment with two fused osteoderms; IPS 56069, skull bone fragment with one fused osteoderm; IPS 56070, skull bone fragment with two fused osteoderms; IPS 56071, skull bone fragment with one fused osteoderm; IPS 56072, skull bone with one fused osteoderm; IPS 56073, skull bone with one fused osteoderm; IPS 56075, skull bone with one fused osteoderm; IPS 59526, skull osteoderm; IPS 59528, body osteoderm.

Description: Thick, tuberculate hexagonal to polygonal skull osteoderms are abundant at Sossís. Irregular osteoderms (with an angular ventral surface or a horn shape) probably represent marginal positions on the skull. Some have worn surfaces so that the typical tubercles have partially or totally disappeared. Body osteoderms are always tuberculate and typically rectangular, with a maximum length of 6 mm. They are bevelled and although they sometimes bear a protuberance formed by tubercles, they are not truly keeled. A few smaller and more rounded (ovoid) osteoderms probably represent osteoderms from the limbs as observed, for example, in *Helodermoides* (Sullivan, 1979). In these ovoid or rounded osteoderms, the overlap surface is not restricted to the anterior margin but also extends on to the lateral margin.

Remarks: Glyptosaur osteoderms, with the typical tuberculate ornamentation, are the most abundant type within the Sossís osteoderm collection. The hexagonal shape of the skull osteoderms is characteristic of the Glyptosaurini (contra plate-like, non-hexagonal, sub-rectangular to polygonal osteoderms in 'Melanosaurini'; Sullivan, 1979). The Sossís skull osteoderms cannot be differentiated from those of the typical European glyptosaurine *Placosaurus*, but the attribution of other less diagnostic elements, such as skull bones and body osteoderms, is more tentative. However, nothing points to the presence of a second glyptosaurine (i.e., a 'Melanosaurini').

Glyptosaurinae indet.

Material: IPS 56167, fragment of ?dentary with two preserved teeth (Figure 6.1); IPS 56149, fragment of ?maxilla with one preserved tooth; IPS 56150, fragment of maxilla with one preserved tooth.

Description: These jaw fragments bear teeth with labiolingually expanded crowns, that have truncated, almost horizontal occlusal surfaces.

Remarks: These jaw fragments are referred to the Glyptosaurinae on the basis of tooth morphology (robust, labiolingually expanded and square-off tips). A heterodont dentition would be indicative of the presence of 'Melanosaurini' (e.g., *Paraplacosauriops*), whereas an homodont dentition would suggest Glyptosaurini (e.g., *Placosaurus*), but the preserved remains are too fragmentary to determine this.

Anguinae Gray, 1825
Anguinae indet.

Material: IPS 49847a, elongated body osteoderm (Figure 6.12); IPS 49847b, thousands of elongated body osteoderms; IPS 49851a, rounded body osteoderm (Figure 6.11); IPS 49851b, more than 100 rounded body osteoderms; IPS 56082, partial dorsal vertebra (Figure 6.9); IPS 56162, two body osteoderms; IPS 56234, two partial vertebrae; IPS 56085, posterior fragment of parietal (Figure 6.6); IPS 56086, posterior fragment of a right frontal (Figure 6.7); IPS 56080, dorsal vertebra (Figure 6.10); IPS 56081, 37 partial vertebral centra, condyles showing tendency to be triangular in ventral view; IPS 56083, multiple vertebral condyles; IPS 59486, 30 body osteoderms; IPS 56159, body osteoderm; IPS 56231, three body osteoderms; IPS 59490, four fragments of vertebrae; IPS 59504, vertebra condyle; IPS 59509, three body osteoderms; IPS 59487, two vertebral condyles; and less certainly: IPS 59473, vertebral centrum; IPS 59496, four partial vertebrae; IPS 56128, tooth-bearing bone with one broken tooth; 56129, maxilla fragment with one broken tooth; IPS 56130, anterior fragment of left maxilla; IPS 56136, fragment of left dentary with one broken tooth.

Description: The osteoderms are typically elongated and keeled, with an ornamentation of pits and ridges. They have an irregular margin but lack a gliding surface. Smaller, ovoid, bevelled osteoderms with the same ornamentation are referred to the same taxon, and represent regional variation on the body. Similar variation occurs in the glyptosaur material. A partial parietal (IPS 56085) is referred to the same taxon, based on the presence of the typical anguine ornamentation consisting of pits and anastomosing grooves. The parietal is small and has a long smooth dorsal surface between the posterior margin of the ornamented surface and the posterior margin of the parietal table (area levis sensu Klembara and Green, 2010). IPS 56128, IPS 56129, IPS 56130, and IPS 56136 are very fragmentary tooth-bearing bones with what seem to be (broken) recurved teeth.

Remarks: The attribution of isolated fragmentary remains of anguines is complicated by the fact that many taxa are represented by isolated material. With the exception of the partial parietal, which shows similarities to that of *Headonhillia* Klembara and Green, 2010 in the long area levis, the rest of material (including tooth-bearing bones) cannot be identified beyond Anguinae indet. At least two types of anguine osteoderms are present, but as they vary in shape along the different regions of the body, they do not necessarily indicate the presence of two taxa. Vertebrae are equally problematic. It is difficult to differentiate between anguine and glyptosaurine vertebrae, except on the basis of size (e.g., large vertebrae would correspond to glyptosaurines and small vertebrae to anguines, although the boundary is not always clear) and the fact that the ventral surface of the centrum is more flattened in anguines. The two recovered anguid vertebral types are small enough to be referred tentatively to Anguinae, and correspond to the two commonly recognized morphotypes (Rage and Augé, 2010): a derived one (Form A, Figure 6.9) in which the ventral margins of the centrum are parallel (seen only in *Anguis*), and a more generalised one in which the margins converge towards the condyle, giving a roughly triangular shape (Form B, Figure 6.10). The vertebrae of the Franco-Swiss *Helvetisaurus* are much larger than those from Sossís, and *Pseudopus* has never been recorded before the Eocene-Oligocene boundary.

Summary of the Sossís Lizard and Amphisbaenian Fauna

- Iguania
    - Iguanidae
        - *Geiseltaliellus pradiguensis*
        - *Geiseltaliellus* sp.
        - *Pseudolacerta* sp.
- Gekkota
    - Gekkota indet. Form A
    - Gekkota indet. Form B
    - Gekkota indet. Form C
- Lacertiformes
    - Lacertidae
        - *Dormaalisaurus girardoti*
        - *Dormaalisaurus rossmanni*
        - *Gracilicerta sindexi*
        - ?Lacertidae indet. (amblyodont form)
- Scincoidea
    - Cordyliformes
        - Cordyliformes indet.
    - Scincidae
        - ?Scincidae indet.
    - ?Scincoidea incertae sedis, unnamed new genus and species
- Anguimorpha
    - Anguidae
        - Glyptosaurinae
            - Glyptosaurini
                - Glyptosaurini indet.
            - Glyptosaurinae indet.
    - Anguinae
        - Anguinae indet. Form A
        - Anguinae indet. Form B
- Amphisbaenia
    - Blanidae
        - cf. Blanidae indet.

DISCUSSION

Faunal Diversity and Biogeography

Until now, the only lizard assemblage recorded from the Paleogene of the Iberian Peninsula was that from Silveirinha in Portugal (Rage and Augé, 2003). This early Eocene (MP7) locality has yielded a small but diverse collection of squamate remains including pleurodont and acrodont iguanians, gekkotans, 'scincomorphs', glyptosaurine and anguine anguimorphs, amphisbaenians, and snakes. The Sossís assemblage is younger than Silveirinha by more than 17 myr. It is richer in specimen number, but the two localities share a broadly similar herpetofauna that is also comparable to that of more northern European sites. Most Sossís specimens cannot be attributed to named genera, but the lacertids *Gracilicerta* and *Dormaalisaurus*, and the iguanian *Geiseltaliellus* occur both at Sossís and penecontemporaneous French localities (*Geiseltaliellus* also in Silveirinha). Other taxa (e.g., *Pseudolacerta*) are found at Sossís and specific French localities (e.g., Malpérié or Escamps). The only major lizard groups missing from Sossís are platynotans (e.g., necrosaurs), melanosaurin glyptosaurines, and acrodont iguanians, although the first of these is present in other Spanish Eocene localities (AB work in progress and see below). All specimens are small and the glyptosaurs, the largest lizards in the recovered assemblage, are represented by abundant osteoderms but only small fragments of dentition. 'Melanosaurins' have a patchy European distribution, mainly in early and middle Eocene deposits: *Paraplacosauriops* is reported from Lavergne (MP16) and unknown localities at the Phosphorites du Quercy (Rage, 2012), so the only confirmed record of 'Melanosaurini' in the late Eocene of Europe is *Paraxestops* (Switzerland, MP19). Acrodont iguanians are recorded from the European early Eocene (MP7-10; Augé, 2005), but appear to have been absent through the middle and most of the late Eocene, despite a reasonably good record of other lizards through this period. Considering the number and diversity of specimens from Sossís, the absence of acrodont taxa is probably not an artifact of sampling.

The Sossís lizard assemblage is diverse, but if it was subject to size-sorting then it probably underestimates the diversity present in the Iberian Peninsula at this time, particularly in relation to larger lizards like platynotans. However, Sossís is not the only new squamate locality on the Iberian Peninsula. Preliminary re-examination of Eocene screen-washing concentrates in the ICP collections shows that squamates were present at many other Spanish localities, although their abundance and diversity is highly variable. These additional localities include further samples from the Southern Pyrenean Basins (from both the Grauss-Tremp and the Ripollès-Berguedà Basins) and Eastern Ebro Basin, as well as others representing the central Iberian basins. Of the latter, the Miranda-Trebiño, Almazán, and Duero Basins form the Western Iberian Bioprovince. Analysis of the Sossís material is thus the first stage in a broader study of Eocene squamate assemblages from the Iberian Peninsula. This will contribute to a more comprehensive understanding of Paleogene European herpetofaunas generally and of the Iberian Peninsula in particular. It could also provide an independent test of biogeographic hypotheses, based mainly on mammals, relating to the degree of faunal interchange between different bioprovinces during the Eocene (e.g., Cuesta, 1991, Badiola, 2004, Badiola et al., 2009). Although the fragmentary nature of the material generally precludes the species-level identifications needed to recognise endemism, it is clear that the Sossís lizard assemblage, pertaining to the Southern-Pyrenean Basin, is similar to that of contemporaneous and near-contemporaneous localities in more northern parts of Europe. Similar observations have been made for artiodactyl mammals from Sossís (Cuesta et al., 2006), and are consistent with the view that middle and early late Eocene mammal faunas (e.g., artiodactyls, perissodactyls, rodents, and primates) from the Southern-Pyrenean Basins are more closely related to those of the rest of Europe than to those from the Western and Central Iberian basins (e.g., Casanovas-Cladellas and Santafé-Llopis, 1987; Cuesta, 1991; Badiola et al., 2009; Marigó et al., 2010; Minwer-Barakat et al., 2012). For most of the Eocene (until at least the earliest late Eocene), the central and western part of the Iberian Peninsula formed an island separated from the rest of Europe, including the Southern-Pyrenean Basins (Badiola et al., 2009, and references therein). Sporadic connections with the rest of the continent would have allowed limited faunal interchanges that would explain the mixture of endemic and widely distributed mammal taxa found in the western and central Iberian basins (e.g., Badiola et al., 2009). Analysis of the squamate assemblages from the different Iberian basins will provide an additional perspective.

Palaeoenvironment

Ectothermic vertebrates represent a well-established proxy indicator in terrestrial palaeoclimatology (Markwick, 1998; Böhme 2003, 2010; Böhme et al., 2006) because they are strongly habitat-dependent. Although a detailed analysis must await study of the remaining herpetofauna, the presence of crocodiles, turtles, frogs, and salamanders together at Sossís suggests mesic conditions (permanent water bodies) and, for at least some of these taxa, high enough temperatures for breeding. Today, most cordyliforms live in open rocky environments (Spawls et al., 2002) in Africa and Madagascar, and representatives of this group have been interpreted as among the most thermophilic taxa at the German Miocene locality of Sandelzhausen (Böhme, 2010). The presence of cordylids in Europe during the Miocene is coincident with that of other thermophilous taxa, notably Varanidae, Chamaeleonidae, Tomistomidae, Alligatoridae and giant turtles, probably in relation to the Miocene Climatic Optimum (Böhme, 2003). Similarly, the presence of pleurodont iguanians in the European Eocene is thought to coincide with a warm period that allowed the group to reach higher latitudes and thus disperse from the New World (e.g., Augé, 2005; Smith, 2009a).

Today, 11 extant lizard genera are recorded in Catalonia: two gekkonids, seven lacertids, one anguid, and one scincid (Montori et al., 2010). The amphisbaenian *Blanus* was present at the southernmost edge of the region, but has not been reported for years. Each of these families was already present at Sossís. However, as at most European Eocene fossil sites (see Augé, 2005; Rage, 2012), it is clear that diversity at Sossís was much higher than that of present-day. This is correlated with the subtropical conditions that existed in Europe during the Eocene (e.g., Rage, 2012) and, by extension, also in the Iberian Peninsula, and it is most striking in the presence of thermophilic iguanians and cordyliforms (plus platynotans at other localities). Amphisbaenians persisted at Catalan Miocene and Pliocene localities, and their current absence (at least north of the Ebro river) could be related to a late (post- Late Pliocene) southward retraction of the group (Blain and Bailon, 2006). Other groups, such as agamids and varanids, progressively disappear during the Pliocene and Pleistocene, not only from the Iberian Peninsula, but from the entirety of Western Europe (Blain and Bailon, 2006).

The Grande Coupure

The Grande Coupure, defined on the basis of mammals (Stehlin, 1909) and corresponding to the Eocene-Oligocene boundary (MP20-21; Schmidt-Kittler, 1987), marks the extinction of some lizard groups in Europe and the appearance of others (e.g., Augé, 2005; Rage, 2012). Lizards fall into two groups according to the distributions reported by Augé (2005) and Rage (2012): 1) those present in Europe before the Grande Coupure but which disappear at the boundary (glyptosaurs) and 2) those present in Europe before and after the Grande Coupure. Pleurodont iguanians were considered as absent from Oligocene levels (e.g., Augé, 2005; Rage, 2012), but have been recently reported in the form of *Geiseltaliellus* sp. from Pech-du-Fraysse (France, MP28, Augé and Pouit, 2012) and *Pseudolacerta* sp. from Grafenmühle 11 (Germany, MP22-23; Böhme and Ilg, 2003). The second group is heterogeneous in their pattern of survival. Lacertids, for example, have a continuous presence in Europe, but the taxa recorded before and after the Grande Coupure are different at the genus level, with the exception of *Plesiolacerta* which crosses the boundary but becomes extinct in the early Oligocene. The same is true for necrosaurs and helodermatids. The pleurodont iguanian *Geiseltaliellus* has been interpreted as a Lazarus taxon, because it is absent from the fossil record for seven standard levels (MP21-27), just to reappear at the MP28 (Augé and Pouit, 2012). Pre- and post-Grande Coupure scincids, cordyliforms and varanids are different and have a less continuous record. Furthermore, they do not fully recover their former range of distribution until the Miocene climate optimum (Böhme, 2003). Anguines seem to have been barely affected by the Grande Coupure, and, despite a poorer record, the same seems to apply to gekkonids and amphisbaenians. Agamids stand apart in that they are present in the early Eocene, disappear for the entire middle and late Eocene, and reappear in the early Oligocene. Thus post-Grande Coupure lizard assemblages were composed of a few survivors (some of which disappeared shortly after) and immigrants with Asian rather than American affinities (Rage, 2012). The lower diversity of Oligocene assemblages in Europe does not seem to be related to an undersampling of Oligocene localities (Smith, 2006). The analysis of late Eocene and Oligocene lizard faunas in the Iberian Peninsula will be particularly interesting as they are geographically intermediate between well-known Central European assemblages and those of Africa, a possible source for at least some of these immigrant taxa (e.g., varanids and cordylids)(Rage, 2012).

CONCLUSIONS

The new assemblage described here partially fills a gap in our knowledge of Eocene lizard faunas from Europe. Despite the better preservation of specimens from fissure-fillings (e.g., Phosphorites du Quercy) and konservat-lagerstätten (e.g., Messel), the Iberian lizard faunas show a comparable diversity of lizards through the Eocene. The Sossís assemblage is dominated by anguimorphs (glyptosaurs and anguines), scincoids (one cordyliform, one scincid, one indeterminate scincoid), lacertiforms (three or four lacertids), and iguanians, with less abundant gekkotans (probably three taxa) and amphisbaenians. Cordyliform osteoderms represent the first definitive proof of this group in the European Paleogene, possibly with African origins.

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A NEW MINIATURIZED LIZARD FROM THE LATE EOCENE OF FRANCE AND SPAIN

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A new miniaturized lizard from the late Eocene of France and Spain

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ABSTRACT

We report here a new lizard genus and species shared by two late Eocene localities situated at both versants of the present Pyrenees (South-Western Europe), one located in France (Escamps, MP19), and the other in Catalonia, Spain (Sossís, MP17a). The recovered specimens are remarkable because of their small size and peculiar morphology. Features of the dentary are interpreted as adaptations to a fossorial or semi-fossorial lifestyle, although such modifications obscure the exact phylogenetic relationships of the new taxon. We suggest that it might represent a further example of scincoid lizard that independently achieved adaptations for burrowing or surface-dwelling. This taxon reinforces the hypotheses that link the Southern Pyrenean assemblages to those from France rather than to those of the rest of the Iberian Peninsula, which are supposed to be somehow isolated and endemic to a certain degree during the middle and late Eocene, forming part of the so-called Western Iberian Bioprovince.

Key words: Squamata; late Eocene; Scincoidea; dental morphology; miniaturization; paleobiogeography

INTRODUCTION

The classical French localities at the Phosphorites du Quercy (Fig. 1) contain the best-known Paleogene sequence from Europe, mainly regarding the time span from the late Eocene to early Oligocene. They have yielded a diverse and rich herpetofauna, including the best-known Eocene lizard assemblages from Europe (see Augé, 2005). The lizards from Escamps (MP19, Phosphorites du Quercy, France) were described in Augé (2005) and the assemblage is quite similar to that of other French localities of the MP17-19 interval. Lizard-bearing localities in Southern Europe, however, are scarcely known, and thus still have a great potential regarding the paleobiogeographical and paleoenvironmental information that can be obtained from their study. The Iberian lizard assemblage from Sossís (MP17a, Catalonia, Spain; Fig. 1) shares many taxa with several French contemporaneous localities (Bolet and Evans, 2013; see also Table 1). This similarity, also reported for mammalian assemblages (Casanovas-Cladellas and Santafé-Llopis, 1987; Cuesta, 1991; Badiola et al., 2009), suggests that a connection existed between the two regions at the earliest late Eocene. In contrast, a certain degree of endemicity has been detected for mammalian taxa from localities situated in Central and Western Iberian Peninsula, allowing the definition of the Western Iberian Bioprovince (Cuesta, 1991). Examples of shared taxa with localities from Central Europe exist (e.g. artiodactyls; Badiola, 2004), but the presence of a high number of endemic taxa pertaining to different groups (perissodactyls, rodents, primates; e.g. Badiola and Cuesta, 2008; Marigó et al., 2010; Minwer-Barakat et al., 2012) points to a certain degree of isolation of a great part of the Iberian Peninsula (the Southern Pyrenean basins excluded). The lack of described lizard assemblages from the Western Iberian Bioprovince precludes comparison with Southern Pyrenean and French faunas, although the study of available material should address this issue in the close future (A. Bolet in preparation). In this contribution, an additional example of a shared taxon between the Southern Pyrenean and French late Eocene faunas is presented, supporting the similarity of the assemblages from these two regions.

MATERIALS AND METHODS

The available material comprises three specimens from the late Eocene of France and Spain. The French material belongs to the collection of the Université des Sciences et Techniques du Languedoc (USTL), Escamps B locality (UM-ECB), from the reference level MP19, and consists of a tiny, almost complete and well-preserved right dentary. The two additional specimens are from the collections of the Institut Català de Paleontologia (ICP), formerly Institut de Paleontologia de Sabadell (IPS), Sossís locality (MP17a, Catalonia, Spain), and consist of one left and one right small dentary fragments, which could belong to the same individual. Images were taken with the Environmental Scanning Electron Microscope (ESEM) Quanta 200 from the Universitat de Barcelona (UB), and drawings of the type specimen were made with a camera lucida attached to a stereoscopic binocular. Data on lizards from selected localities were taken from Augé (2005), Augé (2007) and Bolet and Evans (2013).

RESULTS

Systematic Paleontology

Reptilia Linnaeus, 1758

Squamata Oppel, 1811

Scincoidea Oppel, 1811

?Scincidae Gray, 1825

Genus *Pyrenasaurus* nov.

Type species: *Pyrenasaurus evansae* sp. nov.

Etymology: From *Pyrena*, the latin root of Pyrenaeum, the mountains that now separate Catalonia from France, the Pyrenees (Pyrénées in French, Pirineus in Catalan, Pirineos in Spanish); and *saurus*, meaning lizard in greek.

Diagnosis: As for the type and only species.

Pyrenasaurus evansae sp. nov.

Figs. 2, 3A, B

Etymology: Dedicated to Prof. Susan E. Evans for her efforts in the study on paleoherpetofauna in general, and on lepidosaurs specifically, and for her help and support to the senior author through the elaboration of his Ph.D. dissertation.

Holotype: UM-ECB 1703 (Fig. 2A-E), complete right dentary with seven preserved teeth (eleven tooth positions in total).

Type locality: Escamps B (Phosphorites du Quercy, France).

Type horizon: Escamps Standard level, MP19.

Geographical and stratigraphical distribution: Known from the type locality of Escamps (MP19 of the Phosphorites du Quercy, France) and from Sossís (MP17a, Central Southern Pyrenean Basin, also called Graus-Tremp basin, Catalonia, Spain).

Referred material: The additional specimens referred to the same taxon come from the locality of Sossís (MP17a, Central Southern Pyrenean Basin, Catalonia, Spain). They were referred to ?Scincoidea incertae sedis, unnamed new genus and species in Bolet and Evans (2013): IPS 56061 (Figs. 2F, G, I), partial left dentary with two teeth; IPS 56168, fragment of right dentary with one preserved tooth (Figs. 2H, J).

Diagnosis: Very small lizard (length of dentary equals 3.4 mm as preserved) characterized by the following combination of characters: a low tooth count (eleven tooth positions in total), a closed and fused Meckelian canal, a straight dentary ventral border, a moderately high coronoid process of the dentary (higher than the tallest tooth crown), and a highly distinctive tooth morphology: anterior teeth (first to fifth positions) where preserved, small and slightly posteriorly recurved, showing the typical scincoid pattern (sensu Richter, 1994); posterior teeth (ninth to eleventh positions) larger, labiolingually compressed, and with a characteristic deflection in the convexity of the posterior and anterior (less developed) shafts close to the tip; medial teeth (sixth to eighth positions) intermediate in shape, height and robustness. Regarding the posterior teeth, striations on the lingual side are restricted to the upper third of the crowns. *Pyrenasaurus* can be differentiated from most known lizards by its low tooth count, exceptions including all amphisbaenians, some scincids, some lacertids, some anguimorphs, xantusiids, pygopods and some fossil forms probably related to scincoids and teiioids (see discussion). It can be easily differenciated from all these taxa with reduced tooth counts by the characteristic shape of its posterior teeth, as well as an unusual dentary morphology, with a closed and fused Meckelian canal, a straight ventral border, a symphysis that does not form a sudden angle with it, and a high coronoid process.

Description

The holotype (UM-ECB 1703; Figs. 2A-E, 3A, B) is a right dentary with seven complete pleurodont teeth, and spaces for four additional teeth, adding a total tooth count of eleven. The bone is of small size, with a length of 3.4 mm. Its ventral margin is straight, and the Meckelian canal is closed and fused from the level of the third preserved tooth to the level of the anterior margin of the seventh. The open anterior region of the Meckelian canal is narrow, ventro-laterally exposed and it reaches the level of the first tooth position. In the posterior region of the dentary, the lingual curvature of the ventral margin of the bone leaves the Meckelian canal greatly exposed but only lingually, not ventrally. The subdental shelf has a rather rounded lingual surface. It is very narrow posteriorly, but widens anteriorly, and a deep but narrow sulcus dentalis is present at least until the eighth tooth position, counting from front to back. The dorsal post-dental region of the dentary extends far posteriorly, and the coronoid process of the dentary is moderately high. Lingually, the splenial probably occupied more than half the height of the dentary and was, at its time, restricted to the posterior region, not extending anteriorly to the level of the anterior margin of the penultimate tooth. The lingual anterior process of the coronoid was probably restricted to a position far behind the tooth row (no facet is preserved in the lingual surface of the conoroid process of the dentary). The extension of the posteroventral process of the dentary cannot be ascertained because it is broken. In labial view, there is one large foramen situated at the level of the third tooth position (the first preserved), and the presence of additional posteriorly positioned foramina cannot be discarded (not clear because the surface is not completely clean). The large triangular facet for the anterolateral process of the coronoid is restricted to a posterior position, far from the posteriormost-situated tooth.

The dentition gradually increases its robustness, from moderate (anterior region) to very robust (posterior region). The height of the preserved teeth slightly increases from the anterior to the posterior region, with the crowns projecting above the parapet of the dentary approximately one half of the tooth height. The anterior teeth are slighlty more anteriorly inclined than the posterior ones. The first three teeth (Fig. 2C; their morphology is best seen in the second one) are cylindrical, with a slightly posterolingually recurved tip. The morphology of the anterior teeth is not clear because it has not been possible to clean the matrix that covers them, but the second and probably the third tooth present the typical scincoid pattern (sensu Richter, 1994). Although it is not possible to observe the morphology in detail, it is clear that, apart from the lingual cusp, there is a second labially-positioned cusp (cuspis labialis), and also a well-developed antrum intercristatum. There is an increase in the size of the middle (Fig. 2D) and posterior (Fig. 2E) teeth, with the posteriormost tooth being the largest one. The last preserved teeth present a distinctive shape: they are labiolingually compressed, with a flattened lingual surface (Fig. 2E). The crowns are badly worn in this specimen, so the characteristic shape of the posterior dentition of the taxon is mainly based on observations made on other specimens (Fig. 2F-J, see below). Allowing for the worn and partially covered surface of such teeth, the crowns appear to present a deflection in the convexity of at least the posterior margin of the tooth. It is not discarded that the anterior margin was also originally deflected, but poorly preserved and covered by matrix. This gives the crowns the characteristic resemblance to a short obelisk, more clearly observable in the Sossís specimens (Fig. 2I, J). The presence of striations in the lingual side of the holotype teeth cannot be ascertained, but this could be related to a certain degree of wear. Large, posteriorly preserved resorption pits are preserved at the bases of some tooth positions, mainly the fifth and eighth.

Referred specimens

The referred dentary fragments (IPS 56168 and IPS 56061; Fig. 2F-J) present exactly the same bone and tooth morphology, and it is possible that they represent both sides of a single individual. The teeth are stout and labiolingually compressed, and show a very characteristic outline in lateral view. The anterior and posterior margins converge at an angle of 16º (close to parallel) in their bases, but there is an abrupt change to a more obtuse angle (80º) passed the mid shaft of the tooth. This gives a short obelisk profile, except that in this region, the anterior and posterior margins present a deflection in their convexity, rather than being straight (Fig. 2I, J). The tip is slightly lingually recurved. There are striations only in the lingual side of the tip, and only occupying the upper third of the crown. The Meckelian canal is open in the preserved region, but its margins approach each other (Fig. 2F, H) and may have been in contact or fused in a more anterior region (not preserved). A resorption pit is preserved at the base of the penultimate tooth, being large and posterolingually positioned.

The French and Spanish specimens are indistinguishable and they are referred to the same species *P. evansae*. Admittedly, the taxon is known only from fragmentary material at Sossís. Hence, it is possible that the specimens from Sossís represent a distinct species but until more fossils appear, showing possible significant differences, we decline to name a new species.

DISCUSSION

Morphology and systematics

The holotype is very distinctive with respect to any other known lizard, fossil or extant, and the two referred specimens provide detail on the unique tooth morphology of the posterior dentition. We are aware that describing a new genus based on dentary material alone often generates problems regarding the referral of potential new material. However, it is clear that the dentition of *Pyrenasaurus* is so unique that it will be easily recognisable even among very fragmentary material. In fact, attribution to the same taxon of additional material from a second locality (Sossís) appears secure even being based on very fragmentary specimens. The peculiar dentition of this taxon might be useful to recognize additional material from other tooth bearing bones (i.e. maxilla and perhaps the premaxilla). Regarding the affinities of the new taxon, while its status as a new genus of lizard is easy to prove, its exact relationships within Squamata are more difficult to elucidate.The observable combination of characters is not characteristic of any concrete lizard group, but the potential affinities of the taxon can be discussed in terms of their presence or absence in such groups. A reduced tooth count in the dentary is unknown for iguanians, and the presence of a sulcus dentalis, the high coronoid process of the dentary, the presence of a right angle between the parapet of the dentary and the sudbental shelf all argue against anguimorphan affinities. A reduced tooth count is rare among gekkotans (an exception would be *Aprasia*; Parker, 1956), and this group presents reduced symphyseal facets in comparison to those of *Pyrenasaurus*. Dibamids are interesting in presenting a jaw configuration similar to that of *Pyrenasaurus*, although their teeth are much higher and pointed (Fig. 3F), and the symphysis is clearly different (Meckelian canal open in this part of the dentary of *Pyrenasaurus*). Amphisbaenians are strictly burrowing forms probably related to lacertoids (e.g. Wiens et al., 2012), strongly differing from *Pyrenasaurus* in tooth morphology and jaw configuration. The maximum dentary tooth count is nine among extant forms, but two new taxa from the Paleocene of Europe referred to Amphisbaenia (Folie et al., 2012) possess 10-12 teeth. However, their exact affinities will have to wait a complete description of the material and the tooth shape is clearly different from that of *Pyrenasaurus*, the teeth being, as well as the dentary, much more robust in the former (A. Bolet, personal observation). The general morphology of later (Early Eocene onwards) European amphisbaenian dentaries is distinctive and different from *Pyrenasaurus*, mainly regarding the slender shape of the latter in contrast to more robust dentaries in European amphisbaenians (e.g. *Blanus*, Fig. 3G), which otherwise present a characteristic shape of the symphysis, as well as an open Meckelian canal for all their length (closed and fused in *Pyrenasaurus*). Again, the tooth shape of *Pyrenasaurus* is quite different from known amphisbaenians. *Cryptolacerta*, a further limb-reduced form from the middle Eocene of Germany (Müller et al., 2011), is clearly different from *Pyrenasaurus* in terms of size, dentary length, robustness and shape, and tooth count and morphology, among other characters. This leaves “Scincomorpha”

(Scincoids+Lacertiforms) as the group in which the taxon is most easily accommodated. Note, however, that this taxon has been regarded as a paraphyletic assemblage in most molecular analyses (e.g. Vidal and Hedges, 2005; Wiens et al., 2012; Pyron et al., 2013). Among lacertiforms, lacertids present certain homogeneity with jaws characterized by arched dentaries with an open Meckelian canal, a lateral facet for the articulation of the coronoid and with posterior bicuspid or tricuspid teeth. Some lacertids, however, present strong feeding adaptations including reduction of tooth count, such as *Dracaenosaurus* (from the Eocene/Oligocene of France; e.g. Müller, 2004; Augé, 2005), but the shape of the dentary still shows a clearly lacertid morphology, and in this case its massive teeth represent an adaptation to a durophagous diet, and no adaptations to fossoriality are supposed. Lacertiform teiids show a great variability regarding tooth shapes, but a reduced tooth count is very rare, except in some Late Cretaceous forms classified as polyglyphanodontids (e.g. *Adamisaurus*; Sulimski, 1972), and the lack of cementum at the base of the teeth of *Pyrenasaurus*, among other characters, argues against a referral to Teiioidea (Estes et al., 1988). Some tupinambid teiids would represent modern examples of durophagous taxa, and again their reduced dentary tooth count (e.g. 12 in *Dracaena*; Kosma, 2004) is not related to fossoriality (Montero et al., 2004). Xantusiids present a reduced tooth-count (12-14 in *Xantusia*, Hecht, 1956), but they differ from *Pyrenasaurus* in presenting a Meckelian canal that is fused to a greater extent (both anteriorly and posteriorly), as well as a very different tooth morphology and configuration of the posterior region of the dentary.

Gymnophthalmids sometimes present a closed and fused Meckelian canal, but their tooth counts are higher than in *Pyrenasaurus*, and their long lower jaws present a very different configuration (e.g. *Vanzosaura*, see Guerra and Montero, 2009 and Fig. 3H) regarding, for example, the extent of the lingual anterior process of the coronoid. Among "scincomorphans", scincoids (scincids+cordylids), and specially scincids, are the group that shows a greater variability in the tooth shape and the one in which tooth count reduction is more widespread. Extant representatives of Scincidae are too abundant and diverse to be discussed here in detail, but it is worth mentioning that a closed and fused Meckelian canal is widespread among acontine (e.g. *Acontias*, Fig. 3I) and lygosomine (e.g. *Tiliqua*, Fig. 3E; *Cyclodomorphus*, Fig. 3J) scincids. The only example of a tooth shape that vaguely recalls the posterior dentition of *Pyrenasaurus* is that of the lygosomine *Egernia stokesii*, as figured in Kosma (2004, Pl. V, Figure 11), but similarity is restricted to the outline of the tooth, and none of the characteristic features of the posteriormost teeth of *Pyrenasaurus* are observable in this taxon suggesting that they are not closely related forms.

The overall shape of the dentary of *Pyrenasaurus* (Figs. 2A, B, 3A, B), the great reduction of the tooth count, as well as the presence of a well-developed antrum intercristatum in the anterior teeth (Fig. 2C), together with a characteristic tooth shape in the posterior region (Fig. 2D, E, F, I, J), all suggest that *Pyrenasaurus* is more likely a scincid than a cordylid, because these features are not known among the latter. Most scincids present a generalized scincoid dentition (sensu Richter, 1994), although the presence of characteristic teeth in some forms usually highlights adaptations to eating a given food item (e.g. durophagy, see Estes and Williams, 1984). The Paleogene scincoids are generaly regarded as basal (e.g. Folie et al., 2005), but without testing the phylogenetic position of *Pyrenasaurus*, we cannot be positive about its affinities with any clade. These forms can be easily differentiated by their higher tooth count, apart from the lack of the distinctive posterior teeth of *Pyrenasaurus*, and include *Scincoideus haininensis* Folie et al., 2005 (Hainin, MP1-5, Belgium) and *Ornatocephalus metzleri* Weber, 2004 (Messel, MP11, Germany). The named Paleogene European scincids are *Orthoscincus malperiensis* Augé, 2005 (Malpérié, MP17, France; Fig. 3D) and *Axonoscincus sabatieri* Augé, 2003 (Prémontré, MP10, France); and a possible cordylid is *Eocordyla mathisi* Augé, 2005 (Le Bretou, MP16 and Malpérié and Les Pradigues, MP17, France). *Foliesaurus boutersemensis* Augé and Smith, 2009 (Boutersem, MP21, Belgium) is probably a scincid, and *Berruva louisi* Augé, 2005 (Berru, MP6, France), described as a scincid, has alternatively considered as a basal scincoid (Augé and Smith, 2009). All of them possess the typical scincoid tooth pattern (sensu Richter, 1994). Admittedly, the shape of the posterior teeth of *Pyrenasaurus* is not the paradigm for scincids or scincoids. However, a great number of forms with specialized dentitions are known among scincoids (e.g. Kosma, 2004; Augé, 2005), and the anterior teeth morphology fits well with this group. The most similar of the taxa listed above, regarding the overall shape and size of the dentary, is the contemporaneous *Orthoscincus* (Fig. 3D). Among the characters common in both forms are the short dentary, the reduced tooth count and the elevated coronoid process of the dentary. However, *Pyrenasaurus* differs from *Orthoscincus* in having a lower tooth count (11 vs. 14-15 in *Orthoscincus*), enlarged posterior teeth (homodont and generally smaller dentition in *Orthoscincus*), a distinctive tooth crown (contra typical scincoid shape in *Orthoscincus*) in the posterior region, a closed Meckelian canal (open in *Orthoscincus*), and a straight ventral border of the dentary (slightly arched in *Orthoscincus*). Other specimens referred to indeterminated "scincomorphs" are present in Paleogene French localities (see Augé, 2005), but one among them is particularly interesting for comparison with *Pyrenasaurus*. This specimen, USTL MAL 605, is from Malpérié (MP17, France, Fig. 3C), was referred to "Scincomorpha indéterminé Forme B" in Augé (2005) and, despite some differences, it shares with *Pyrenasaurus*, among other characters, a similar overall morphology of the dentary, a low tooth count, the enlargement of the posterior teeth, and an unusual posterior tooth shape where the tip is somehow isolated by two lateral ridges. The subdental shelf has a high lingual surface, which gradually diminishes after the eighth dental position. In this aspect, it shares with *Pyrenasaurus* the closure of the Meckelian canal, with a restricted and mostly ventral opening situated in the anterior part of the dentary, and a wide mostly lateral exposure in its posterior part. However, a subtle suture that suggests that the fusion was not complete, still remains. The lack of the posterior end of the dentary precludes any information regarding the extent of the coronoid process of the dentary. The main difference with the holotype of *Pyrenasaurus* is the shape of the posteriormost teeth, with the tip being more clearly isolated, giving them a tricuspid appearance. Moreover, the tooth implantation seems to be less deep. The morphological similarities noted above suggest affinities between *Pyrenasaurus* and USTL, MAL 605, but at the same time, the noted differences, mainly regarding the dentition, denote that they may represent not only different species, but also probably different (although possibly related) genera. An unnamed cordyliform and a possible scincid, both different from *Pyrenasaurus* on the basis of tooth shape and open Meckelian canal, were reported from Sossís (Bolet and Evans, 2013), suggesting that scincoids were not rare in the late Eocene of the Southern Pyrenean Basins, and the same could be applied to the Phosphorites du Quercy (see Augé, 2005).

Lifestyle

Some features of the dentary of *Pyrenasaurus* suggest it could represent a burrowing or surface-dwelling lizard. Among the characters that support this are miniaturization, the short length of the bone with a low number of teeth, and the high coronoid process of the dentary. Although the fusion of the Meckelian groove appears in some non-fossorial lizards, this character suggests burrowing habits when it appears in combination with miniaturization and decrease of tooth number (Broschinski and

Sigogneau-Russell, 1996). Adaptations to fossoriality appear early in the fossil record, with examples of burrowing forms reported from the Late Jurassic (e.g. *Saurillodon* from Guimarota, Portugal; Kosma, 2004) and the Early Cretaceous (e.g. *Tarratosaurus* from Anoual, Morocco; Broschinski and Sigogneau-Russell, 1996). *Jucaraseps*, a tiny lizard from the Early Cretaceous of Spain, has been interpreted as an early example of a surface-dweller lizard (Bolet and Evans, 2012), and *Chalcidosaurus* from Guimarota as a semi-fossorial form (Kosma, 2004). Since the fossil record only rarely preserves complete specimens, it is often not possible to discern between true burrowing forms and surface-dwellers, because relative length of the limbs and tail cannot be measured. This is the case of *Pyrenasaurus*, which, although it presents some jaw adaptations for a fossorial or semi-fossorial lifestyle, it is difficult to state to which of the two groups it belonged to in absence of postcranial material.

Although small lizards weighting less than one gram are said to lack the strength to burrow (Benesch and Withers 2002), the dentary of *Pyrenasaurus* is of similar size to that of recent *Blanus*, a fully burrowing form, and thus it cannot be discarded that *Pyrenasaurus* was a burrower only based on its size. An additional character that has been related to fossoriality is the presence of an angle at the symphysis of the dentary, as present in most amphisbaenians (e.g. Gans, 1974). However, it is important to note that Gans (1974) already stated that not all amphisbaenians present it, and examples of extant (e.g. *Amphisbaena ridleyi*; Pregill, 1984) and fossil (e.g. *Palaeoblanus*; Schleich, 1988; Böhme, 1999) taxa lacking this character exist. Moreover, some lizards described as fossorial forms (e.g. the gymnophthalmids *Calyptommatus nicterus*, *Scriptosaura catimbau*, and *Nothobachia ablephara*) also seem to lack this character (see figures in Roscito and Rodriges, 2010). *Pyrenasaurus* presents a subtle angle at the level of the symphysis, but it is not comparable to that existing in most amphisbaenians. However, because of the exceptions noted above, this is not an argument against an interpretation of *Pyrenasaurus* as a fossorial lizard. At least half of the origins of the burrowing morph occur in one group, the Scincidae (Wiens et al., 2006).

The peculiar tooth shape of *Pyrenasaurus* suggests an adaptation to a determinate kind of food. However, since this shape is unique among known taxa, it is not possible to ascertain to which items it can be related. The scincid genus *Acontias* (Fig. 3I), has a jaw configuration that presents overall similarities to that of *Pyrenasaurus* (see Kosma, 2004), including the low tooth count (ten in *A. percivali*), the closed and fused Meckelian canal (although it is closed for a longer way) and the great distance between the last tooth and the coronoid process of the dentary. However, differences in tooth morphology and the shape of the symphysis and the dentary in general suggest that both genera are not related, and superficial similarities should be regarded as convergences due to a similar lifestyle. Thus, the observations made for *Acontias percivali* as a surface-dweller in fallen leaves and feeding on insects (Rogner, 1994), might apply to *Pyrenasaurus*. Most species of the genus feed on beetle larvae and termites (Broadley and Greer, 1969), but two of the species feed, in addition to different kinds of insects, on other squamates. *Acontias plumbeus* consumes vertebrates such as other burrowing skinks and frogs (Broadley and Greer, 1969) and *A. meleagris* feeds upon worm snakes (*Typhlops* sp.) and juveniles of its own species (Hauschild and Gabner, 1995). It is clear that the overall similarities between *Pyrenasaurus* and *Acontias* are not enough to warrant the same lifestyle and, due to its small size, *Pyrenasaurus* would have been more easily a prey than a predator, at least regarding other vertebrates.

Pyrenasaurus was not the only squamate presenting adaptations to fossoriality found at Sossís and Escamps. Amphisbaenians (most probably blanids) have been reported from both localities (Augé, 2012; Bolet and Evans, 2013). The slender shape of the dentary suggests that the taxon was not so strongly adapted for fossoriality as, for example, an amphisbaenian. Curiously, the position of the last labial foramen, just at the level of the anterior edge of the last tooth, was reported as an unusual feature present in an indeterminated scincoid from Malpérié and Escamps (Scincoidea indet. Form B of Augé, 2005), and this unnamed taxon also possesses a characteristic posterior dentition, consisting in this case of enlarged spatulated teeth. It seems that the Eocene was a period during which scincoids radiated in Europe (see Augé, 2005) resulting in a variate collection of bizarre forms. These forms disappear at the Grande Coupure, and scincoids that appear after the Eocene-Oligocene limit (e.g. *Foliesaurus* from the Early Oligocene of Boutersem, Belgium; Augé and Smith, 2009) are clearly different from them, and are closer to the typical scincoid pattern regarding the shape of both the dentition and the dentary. Because *Pyrenasaurus* is not clearly related to any known fossorial squamate, it seems to represent a further example of a lizard that has independently achieved adaptations for burrowing/surface-dwelling (see Table 2 for characters seen in some selected fossorial lizards). Because many fossil forms are good candidates to represent independent adaptations to fossoriality, their identification is important in order to estimate the plasticity of this treat among squamates, and will probably show that these independent lineages are more widespread than what we have been able to realize up to now. It is clear, however, that the lack of articulated specimens (specimens from Messel being a notable exception) or at least associated postcranial elements in most Paleogene localities, clearly hamper discussion on this issue.

Comparison of the Sossís lizard assemblage (Spain) with those from Malpérié and Escamps (France)

In order to assess if the Southern Pyrenean basins (represented by Sossís as the single late Eocene lizard assemblage described from the Iberian Peninsula so far, see Bolet and Evans, 2013) present a similar faunal composition to contemporaneous French localities, two representative French lizard assemblages have been chosen: Malpérié (MP17), and Escamps (MP19). As seen in the resulting table (Table 1), both French localities share a great number of taxa, some of them even at the species level. Pleurodont iguanians are represented by three different genera at the Phosphorites du Quercy: *Cadurciguana*, *Geiseltaliellus* and *Pseudolacerta*. Of them, only *Cadurciguana* seems to be absent from Sossís, while *Geiseltaliellus* and *Pseudolacerta* are clearly present (Bolet and Evans, 2013). Gekkotans are represented in Malpérié and Escamps only by *Cadurcogekko*. Three gekkotan taxa have been identified from Sossís, one of them possibly related to (or at least not necessarily different from) *Cadurcogekko* (see Bolet and Evans, 2013). Regarding the lacertids, the persistance of *Dormaalisaurus* up to the MP17 at Sossís can be interpreted as a late occurrence of the genus in contrast to a previous disappearance of the taxon from more northern assemblages, as stated by its absence from all post-MP16 French localities (Augé, 2005). *Plesiolacerta* seems to be absent from Sossís. *Quercycerta* and *Escampcerta* are both absent from Sossís, but they are taxa with a restricted distribution even within the Phosphorites du Quercy (only reported from Malpérié and Escamps respectively). *Gracilicerta sindexi*, however, is a taxon shared by the three localities. Regarding the scincoids, the scincid *Orthoscincus* has been only reported from Malpérié, while cordyliforms are represented by the ?cordyloid *Eocordyla* at Malpérié (Augé, 2005) and a probably different cordyliform and a possible scincid from Sossís (Bolet and Evans, 2013).

Even if we take the contemporaneous localities from the Phosphorites du Quercy, we find some variations in the composition of the lizard assemblages, with some taxa (even at the genus level) only reported from the type locality or at most restricted to a few sites. The absence of such taxa at Sossís cannot be argued to represent an actual difference between the French localities and those of the Southern Pyrenean basins because they are variably present even among the Phosphorites du Quercy localities. These taxa include *Escampcerta*, *Quercycerta*, *Orthoscincus*, *Eocordyla*, an indeterminate "scincomorph" (here referred to Scincoidea indet. Form A) and an indeterminate lizard (referred to Lacertilia *incertae sedis* in Augé, 2005). Among the genera shared by Sossís and at least one of the two French selected localities are *Geiseltaliellus*, *Pseudolacerta*, a gekkotan (if it actually represents *Cadurcogekko*) and *Gracilicerta*. Among the taxa not identified at the genus level but that could still represent shared taxa between Sossís and at least one of the two selected French localities are an indeterminate amphisbaenian (probably referable to Blanidae), a glyptosaurine, and an anguine. If we examine which taxa are shared by the two French localities but not by Sossís, this is reduced to *Cadurciguana*, *Plesiolacerta*, *Eurheloderma* and *Necrosaurus*. Note that, with the exception of *Cadurciguana*, they correspond to mainly large taxa, and such large lizards were interpreted as underrepresented at Sossís (Bolet and Evans, 2013), although the reason is not clear. *Pyrenasaurus* is, then, another shared taxon between Sossís and one of the French localities belonging to the Phosphorites du Quercy. The future description of middle and late Eocene lizard assemblages from the different basins of the Iberian Peninsula, and their comparison with those from Sossís and the Phosphorites du Quercy, are intended to clarify if these similarities between the assemblages from North and South of the Pyrenees are extensive to the rest of the Iberian Peninsula or, if as suggested by mammals, they prove to be different enough to argue in favour of the existence of the so-called Western Iberian Bioprovince.

CONCLUSIONS

The new taxon here described is an example of a highly apomorphic form that, despite being represented by few isolated specimens, adds information to taxonomical, biogeographical, and ecomorphological discussions on Eocene squamates from Europe. *Pyrenasaurus* is situated at both versants of the Pyrenees, supporting the hypotheses that link the Southern Pyreneean basins faunas to those from France, although herpetological proofs in favour or against the presence of an endemic Western Iberian Bioprovince need to wait until the description of Central and Western Spanish assemblages. We suggest it could also represent a further example of a lineage that has independently adapted to a fossorial lifestyle, either as a burrowing form or as a surface-dweller, as suggested by the shape of its dentary and its low tooth count. We tentatively refer this new taxon to Scincoidea and suggest scincid affinities, although its phylogenetic relationships are far from being clear.

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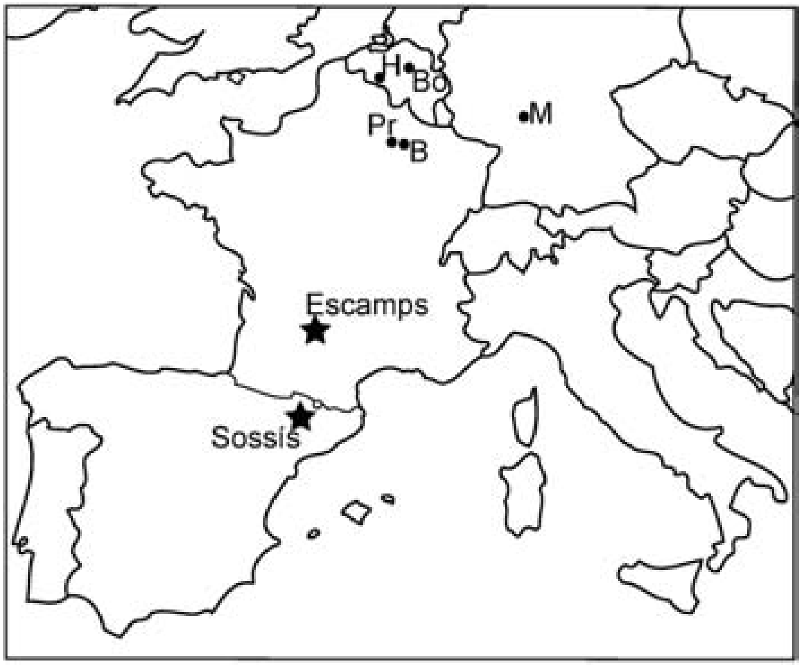
FIGURE LEGENDS

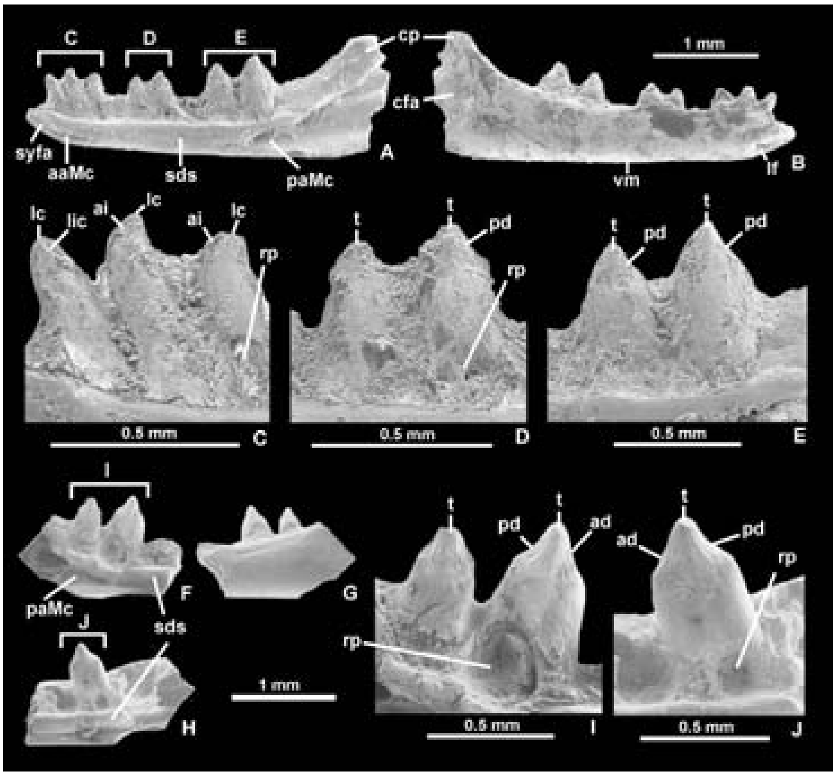
Fig. 1. Map of Western Europe with Paleogene localities mentioned in the text.; B: Berru; Bo: Boutersem; H: Hainin; M: Messel; Pr: Prémontré. Escamps is one of many Phosporites du Quercy localities. The star serves to situate Malpérié, Le Bretou and Les Pradigues.

Fig. 2. *Pyrenasaurus evansae* gen. et sp. nov. A-E: UM-ECB 1703, Holotype, almost complete right dentary in lingual (A) and labial (B) views, and close up details of anterior (C), middle (D) and posterior (E) dentition. F, G, I: IPS 56061, partial left dentary with two teeth from Sossís in lingual (F), labial (G) and detail of tooth morphology (I). H, J: IPS 56168, fragment of right dentary with one preserved tooth from Sossís in lingual view (H) and detail of the tooth (J). Abbreviations: aaMc, anterior aperture of Meckelian canal; ad, anterior deflection in the tooth shaft; ai, antrum intercristatum; cofa, coronoid facet of dentary; cop, coronoid process of dentary; lc, labial cusp; lf, labial foramen; lic, lingual cusp; paMc, posterior aperture of Meckelian canal; pd, posterior deflection in tooth shaft; rp, resorption pit; sds, subdental shelf; syfa, symphyseal facet; t, tip of crown; vm, ventral margin of dentary.

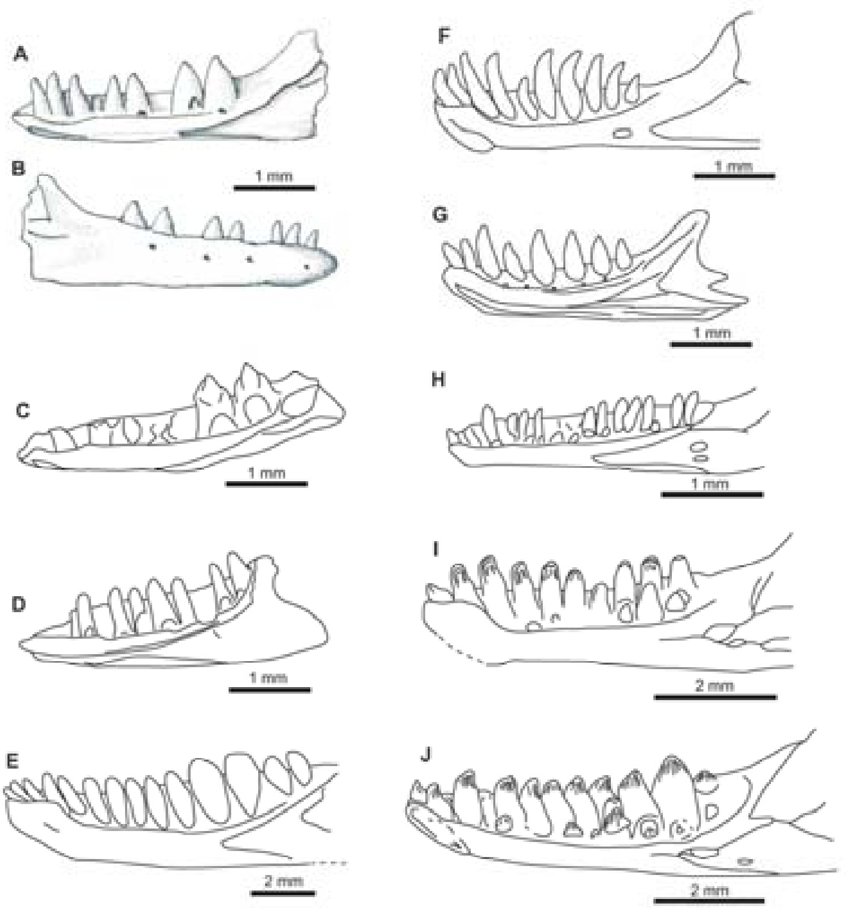
Fig. 3. Drawings of fossil (A-E) and extant (F-J) selected taxa for comparison purposes. A, B: *Pyrenasaurus evansae* gen. et sp. nov. from Escamps (late Eocene, France); C: Scincoidea indet. Form B from the late Eocene of Malpérié (late Eocene, France); D: *Orthoscincus malperiensis* (Scincidae) from Malpérié; E: *Tiliqua pusilla* (Scincidae, Lygosominae) from Riversleigh (Miocene, Australia). F: *Dibamus noveaguineae* (Dibamidae); G: *Blanus strauchi* (Blanidae); H: *Vanzosaura rubricauda* (Gymnophthalmidae); I: *Acontias percivali* (Scincidae, Acontinae); J: *Cyclodomorphus branchialis* (Scincidae, Lygosominae). A, B and G original. Others redrawn from: C, D, Augé (2005); E, Shea and Hutchinson (1992); F, Greer (1985); H, Guerra and Montero (2009); I, Kosma (2004); J, Estes and Williams (1984). E, F, H and J reversed.



70x58mm (300 x 300 DPI)



219x203mm (300 x 300 DPI)



170x180mm (300 x 300 DPI)

Table 2. List of taxa from selected late Eocene localities (data from Augé, 2005 and Bolet and Evans, 2013).

		SOSSÍS MP17A	**MALPÉRIÉ MP17**	**ESCAMPS MP19**
IGUANIA				
	IGUANIDAE			
			Geiseltaliellus lamandini	*Geiseltaliellus lamandini*
		Geiseltaliellus pradiguensis	*Geiseltaliellus pradiguensis*	
		Geiseltaliellus sp.		
			Cadurciguana hoffstetteri	*Cadurciguana hoffstetteri*
			Pseudolacerta mucronata	*Pseudolacerta mucronata*
		Pseudolacerta sp.		
GEKKOTA				
			Cadurcogekko piveteaui	*Cadurcogekko piveteaui*
		Gekkota indet. Form A		
		Gekkota indet. Form B		
		Gekkota indet. Form C		
LACERTIFORMES				
	LACERTIDAE			
			Plesiolacerta lydekkeri	*Plesiolacerta lydekkeri*
			Quercycerta maxima	*Quercycerta maxima*
		Gracilicerta sindexi	*Gracilicerta sindexi*	*Gracilicerta sindexi*
				Escampcerta amblyodonta
		Dormaalisaurus girardoti		
		Dormaalisaurus rossmanni		
		?Lacertidae indet. (amblyodont form)		
	?TEIIDAE			
			Brevisaurus smithi	
SCINCOIDEA				
			Scincoidea indet. Form A[1]	
			Scincoidea indet. Form B	Scincoidea indet. Form B
	SCINCIDAE			
			Orthoscincus malperiensis	
	?SCINCIDAE			
		Pyrenasaurus evansae[2]		*Pyrenasaurus evansae*
		?Scincidae indet.		
	CORDYLIFORMES			
		Cordyliformes indet.		

		?CORDYLIDAE			
				Eocordyla mathisi	
ANGUIMORPHA					
	ANGUIDAE				
		GLYPTOSAURINAE			
					Placosaurus sp.
			Glyptosaurinae indet		
			Glyptosaurini indet.	Glyptosaurini indet.	
		ANGUINAE			
					Helvetisaurus picteti
				Anguis sp.	*Anguis* sp.
			Anguinae indet. Form A		
			Anguinae indet. Form B		
	PLATYNOTA				
				Necrosaurus eucarinatus	*Necrosaurus eucarinatus*
				Necrosaurus cayluxi	*Necrosaurus cayluxi*
		HELODERMATIDAE			
				Eurheloderma gallicum	*Eurheloderma gallicum*
AMPHISBAENIA					
	BLANIDAE				
			cf. Blanidae indet.	Blanidae indet.	Blanidae indet.
SQUAMATA INDET.					
				Squamata indet.[3]	

[1] Scincomorpha indet. Form A in Augé (2005).

[2] ?Scincoidea incertae sedis, unnamed new genus and species in Bolet and Evans (2013)

[3] Lacertilia *incertae sedis* in Augé (2005).

Table 2. Comparisons between selected miniaturized lizards

Taxon	Dentary tooth count	Tooth shape (anterior/ posterior)	Symphysis	Meckelian canal	Size (dentary length)	Lifestyle
Dibamus novaguineae (Dibamidae)	10	Pointed, strongly recurved, unicuspid	Angled	Closed	4 mm	Fossorial
Blanus strauchi (Amphisbaenia, Blanidae)	7–9	Pointed, slightly recurved, unicuspid	Angled	Open	3-4mm	Fossorial
Vanzosaura rubricauda (Gymnophthalmidae)	19–21	Unicuspid	Angled	Closed	3 mm	Fossorial
Acontias percivali (Scincidae, Acontinae)	10	Unicuspid, scincoid morphology	Angled	Closed	ca. 6mm	Surface-dwelling
Cyclodomorphus branchialis (Scincidae, Lygosominae)	12	Unicuspid, robust, scincoid morphology	Rounded	Closed	>9mm	Surface-dwelling
Amphisbaena ridleyi (Amphisbaenia, Amphisbaenidae)	6–7	Pointed, unicuspid/ amblyodont	Barely angled	Closed	7.5mm	Semi-fossorial
Pyrenasaurus evansae (Scincoidea, ?Scincidae)	11	Unicuspid, scincoid morphology/obelisk profile	Barely angled	Closed	3.4mm	?Fossorial

SYNONYMIZATION OF THE MIOCENE VARANID LIZARD *IBEROVARANUS* HOFFSTETTER, 1969 WITH *VARANUS* MERREM, 1820

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Brief report

Synonymization of the Miocene varanid lizard *Iberovaranus* Hoffstetter, 1969 with *Varanus* Merrem, 1820

MASSIMO DELFINO, JEAN-CLAUDE RAGE, ARNAU BOLET, AND DAVID M. ALBA

***Iberovaranus* Hoffstetter, 1969 was erected as a monotypic genus of varanine varanid lizard on the basis of a single trunk vertebra from the Miocene of Spain. On the basis of the holotype, as well as a still undescribed cervical vertebra from the same locality, we show that the vertebral morphology of *Iberovaranus* is contained within the known variability of *Varanus*. Therefore, *Iberovaranus* Hoffstetter, 1969 is considered a subjective junior synonym of *Varanus* Merrem, 1820, and the species *Iberovaranus catalaunicus* Hoffstetter, 1969 should be considered a nomen dubium.**

Introduction

The phylogenetic and biogeographic relationships of fossil European Monitor lizards have recently been revised by Conrad et al. (2009, 2011), and Delfino et al. (2011) focused only on the fossils referred to *Varanus*. Conrad (2008) and Conrad et al. (2008) only minimally commented on *Iberovaranus* Hoffstetter, 1969, a monotypic genus that was erected on the basis of a single trunk vertebra from the Miocene of Can Mas, close to El Papiol, about 15 km from Barcelona (Catalonia, Spain). Hoffstetter (1969) considered *Iberovaranus* to be the most primitive member of the Varaninae, but owing to the poor quality of the material, Clos (1995) and Conrad et al. (2011) regarded *Iberovaranus* as too fragmentary to be included in phylogenetic analyses. Nonetheless, other authors identified the morphological characters of *Iberovaranus* from other localities, sometimes with doubts concerning the specific identification. For example, Antunes and Rage (1974) and Antunes and Mein (1981) referred to *Iberovaranus* a few isolated vertebrae from three early-middle Miocene localities of Portugal. Böhme and Ilg (2003) listed about 10 more localities from Spain and Germany with possible remains of *Iberovaranus*, with an age span from Burdigalian (MN3) to Langhian (MN6). Here we re-examine the holotype of *Iberovaranus*m and another specimen from the same locality, in order to consider it validity.

Institutional and locality abbreviations.—CMA, Can Mas, El Papiol, Barcelona, Spain; ICP, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Spain; IPS, collections of the ICP (formerly Institut de Paleontologia de Sabadell); ZFMK, Zoologisches Forschungsmuseum Koenig, Bonn, Germany.

Systematic palaeontology

Order Squamata Oppel, 1811
Superfamily Varanoidea Camp, 1923
Family Varanidae Gray, 1827
Genus *Varanus* Merrem, 1820
Varanus sp.
(Figs. 1,2)

Ophisaurus sp. Crusafont et al. 1955
Iberovaranus catalaunicus Hoffstetter 1969:1052, fig. 1
Iberovaranus catalaunicus Estes 1983:182
Iberovaranus catalaunicus Antunes and Rage 1974:52
Iberovaranus catalaunicus Molnar 2004:36-37, fig. 2.11

Referred material.—IPS 31701, cervical vertebra; IPS 58437, trunk vertebra, holotype of *Iberovaranus catalaunicus* Hoffstetter, 1969.

Locality and age.—CMA is a loosely-defined paleontological site, which includes Miocene levels of reddish to brownish clays from several quarries that were situated close to the house of Can Mas, about 1 km NW from the town of El Papiol (Crusafont et al. 1955). This locality—which should not be confused with the homonymous, Vallesian locality of 'Can Mas', in the area of els Hostalets de Pierola (Crusafont and Truyols 1954)—corresponds to the early Miocene Lower Continental Complex of the Vallès-Penedès Basin; it is mainly composed of reddish terrigenous deposits of varied lithology, deposited in the context of alluvial fan systems (Agustí et al. 1985; Casanovas-Vilar et al. 2011a). An MN4 age (i.e. ca. 17-16 Ma; Agustí et al. 2001) has been customarily given to CMA (Agustí et al. 1985; Fortelius 2011), which is consistent with the presence of *Gomphotherium angustidens* (cited by Crusafont et al. 1955), although this taxon does not exclude an earlier, MN3 age (Agustí et al. 2001; Casanovas-Vilar et al. 2011b). Further refinement is precluded by the lack of associated rodents. An attribution to MN4 would also be supported by the record of *Eotragus* reported by Fortelius (2011). However, an inspection of the available macromammalian fossils from CMA housed at the ICP yielded no remains of the bovid *Eotragus*. Interestingly a single mandibular fragment of the paleomerycid *Lagomeryx* (DMA, pers. obs.), was located, but does not discriminate between MN3 and MN4.

Description.—IPS 58437, the type specimen of *Iberovaranus catalaunicus*, is an eroded, partial trunk vertebra (Fig. 1). Only the base of the neural spine is preserved, and the surface of the centrum is broken at its right anterolateral sector. Conversely the synapophyses, prezygapophyses, left postzygapophysis, and the condyle are significantly eroded. The centrum is procoelous and slightly convex ventrally in transverse section. No foramina are evident. In ventral view, the centrum is approximately triangular in shape, with a clear precondylar constriction (width at the constriction 4.9 mm; maximum width of the cotyle 5.8 mm; ratio 0.84), reduced by the erosion of the condyle. The cotyle and condyle are depressed. The cotyle faces anteroventrally so that the inner surface of the cotyle is largely visible in ventral view, whereas the condyle shows a symmetric orientation with the surface only minimally exposed. Therefore, there is a significant difference between the minimum, 8.4 mm, and the maximum, 10.6 mm, centrum lengths (measures taken according to Bailon and Rage 1994, biased by the erosion of the vertebra). Prezygapophyseal facets are clearly tilted dorsally but their shape cannot be evaluated because of abrasion. The space between the prezygapophyseal facets and the neural spine is not markedly recessed. The anterior edge of the neural arch is slightly eroded (and asymmetric in dorsal view), but it seems likely that it was markedly tectiform in anterior view and approximately straight or slightly concave in dorsal view. There is no hint of a ‘pseudozygosphene’ or of a structure similar to it (see Holmes et al. 2010). The posterior edge of the neural arch is rather high, with posterodorsal edges quite steep in posterior view. A ‘pseudozygantrum’ is absent. The lateral erosion of the postzygapophyses (mostly of the left one) contributes to the narrowness of the posterior section of the neural arch. The best preserved postzygapophyseal facet is tilted at about 45° and oval-shaped. On the lateral and dorsal surfaces of the neural arch there are distinct ‘fibrous’ striae, which are particularly evident possibly following moderate surface erosion (note that the apparent striae on the ventral surface of the centrum are not ‘fibrous’ structures). Because the neural spine is broken at the base and the dorsal surface of the neural arch is eroded in the anterior sector, it cannot be confirmed that the neural spine was developed along the entire length of the neural arch as reported by Clos (1995). The thickness of the remnants of the neural spine suggests that it was likely developed only in the posterior half of the neural arch. The remnants of the synapophyses indicate that they were rather massive. The size of the neural canal, filled with matrix, cannot be evaluated.

IPS 31701 is a partially preserved posterior cervical vertebra from CMA previously catalogued as 'cf. *Testudo* sp.?' (Fig. 2). The neural spine, the left parapophysis, and the pre- and postzygapophyses are broken off, but the ventral surface of the centrum is well preserved. The centrum, 9.5 mm long, is slightly convex transversely and not as triangular in shape as that of IPS 58437. A hint of a median keel is present in its anterior sector. The centrum has a distinct, obtuse precondylar constriction (width at the constriction 4.9 mm; maximum width of the cotyle 6.2 mm; ratio 0.78), which involves a significant portion of the lateral side of the centrum. The cotyle and condyle are markedly dorsoventrally depressed; although the dorsal rim of the cotyle, as preserved, did not overhang the preceding condyle, this is likely an artefact of erosion. The ventral edge of the condyle is close to the posterior edge of the centrum (so that only a little portion of the condyle is visible in ventral view). The synapophyses are massive, nearly vertical and strikingly laterally projected, so that the vertebra is 12.3 mm wide at their level. They are ventrally linked to the edge of the cotyle by a sub-horizontal ridge ('ventral parapophyseal lamina' in Houssaye et al. 2011). The diapophysis and parapophysis are well defined and slightly separated by a posterior concavity; the former is larger than the latter. Between the parapophyses and the rim of the cotyle there is shallow concavity posteromedially marked by a step.

Discussion

After the remarkable but partial works by Mertens (1942, 1950, 1959), knowledge of the osteology of genus *Varanus* has been advanced thanks to the identification of a few hundred phylogenetically informative characters summarized and updated by Conrad et al. (2011). Although the fine morphology of the 73 species currently ascribed to *Varanus* (Uetz et al. 2011) is still imprecisely known and the intra- and interspecific variation of several characters largely underexplored, it is now clear that the degree of precondylar constriction can significantly vary among species. The constriction is always present in *Varanus*, yet can vary from weakly expressed (state 1 of character 233) to so well developed that it is less than 80% of the maximum condylar diameter and "a right or acute angle is formed between the condyle and the centrum just anterior to the posterolateral part of the condyle (state 2 of character 233)" (Conrad et al. 2011:267).

According to Hoffstetter (1969), *Iberovaranus* differs from *Varanus* in having a more elongate neural arch, a narrower condyle, and a less pronounced precondylar constriction.

These presumed differences are partly explained by the preservation of the type vertebra (condyle, pre- and postzygapophyses are somewhat eroded) and partly to interspecific variability within *Varanus*. In particular, the vertebrae of some extant species, such as *Varanus griseus* (Daudin, 1803) (Fig. 3A), match well with the trunk vertebra IPS 58437. The precondylar constriction of the latter is of 84%, corresponding to state 1 of character 233 (Conrad et al. 2011), but this result is considerably altered by the erosion of the condyle. In fact, the constriction of posterior cervical vertebra IPS 31701, which has a perfectly preserved condyle, is 78%, corresponding to state 2, indicating therefore that this could likely be the morphology and state of the vertebrae of the CMA monitor lizard. The average precondylar constriction of the trunk vertebrae of *V. griseus* ZFMK 14883 and ZFMK 53533 is about 76%, corresponding again to state 2, even if the general shape of the centrum is quite different from that of other congeneric species, such as *Varanus salvator* (Laurenti, 1768), with the same status (see Fig. 3B).

Finally, it is worth mentioning that, according to Molnar (2004), the vertebrae of *Iberovaranus catalaunicus* resemble those of helodermatids because of the slight development of the precondylar constriction. Although it is true that the condition of IPS 58437 could be considered intermediate between that shown by, for example, *V. salvator* and helodermatids, the absence of any constriction in the latter (Conrad et al. 2011; state 0 of character 233), among other characters, excludes referral of IPS 58437 to these taxa.

A further character supporting the inclusion of the holotype of *Iberovaranus*, IPS 58437, in *Varanus* is the presence of striations of the neural arch, which are considered, along with the precondylar constriction, an apomorphy of *Varanus* (Smith et al. 2008). Such striations are not present in all *Varanus* species but "have arisen on the *Varanus* stem and are retained as plesiomorphy in many crown *Varanus*, especially the African forms" (Smith et al. 2008: 911).

Conclusions

The morphology of the type vertebra of *Iberovaranus catalaunicus* Hoffstetter, 1969, IPS 58437, as well as that of the only other varanoid vertebra from the same locality, IPS 31701, is clearly contained within the variability of extant *Varanus*. The nominal taxon *Iberovaranus* Hoffstetter, 1969 must therefore be considered a subjective junior synonym of *Varanus* Merrem, 1820. The taxonomic validity of the nominal taxon *Iberovaranus catalaunicus* Hoffstetter, 1969, the type and only species of this genus, is not supported by the characters already mentioned for the genus. Given that it is available in terms of nomenclature, but from a taxonomic viewpoint it cannot be either validated or synonymized with other *Varanus* species on the basis of currently available material, it is here deemed a nomen dubium (see Mones 1989, for a review of this concept). The species binomen *Varanus catalaunicus* (Hoffstetter, 1969) comb. nov. could potentially be used in the future if a new comparative diagnosis becomes possible on the basis of new skeletal elements providing significant morphological information (e.g., skull elements, see Conrad et al. 2009; Delfino et al. 2011).

If the referral to MN3 of the CMA vertebrate assemblage is confirmed, the *Varanus* remains here described represent one of the earliest evidences of the dispersal of this genus into Europe, which is otherwise known with confidence from the MN4b of Béon 1 (Rage and Bailon 2005) and possibly from a few MN3 Spanish localities such as San Roque 4A (*Varanus* sp.) and Agramon and Ateca 1 (aff. *Iberovaranus* sp. and *Iberovaranus* cf. *I. catalaunicus*; Böhme and Ilg 2003).

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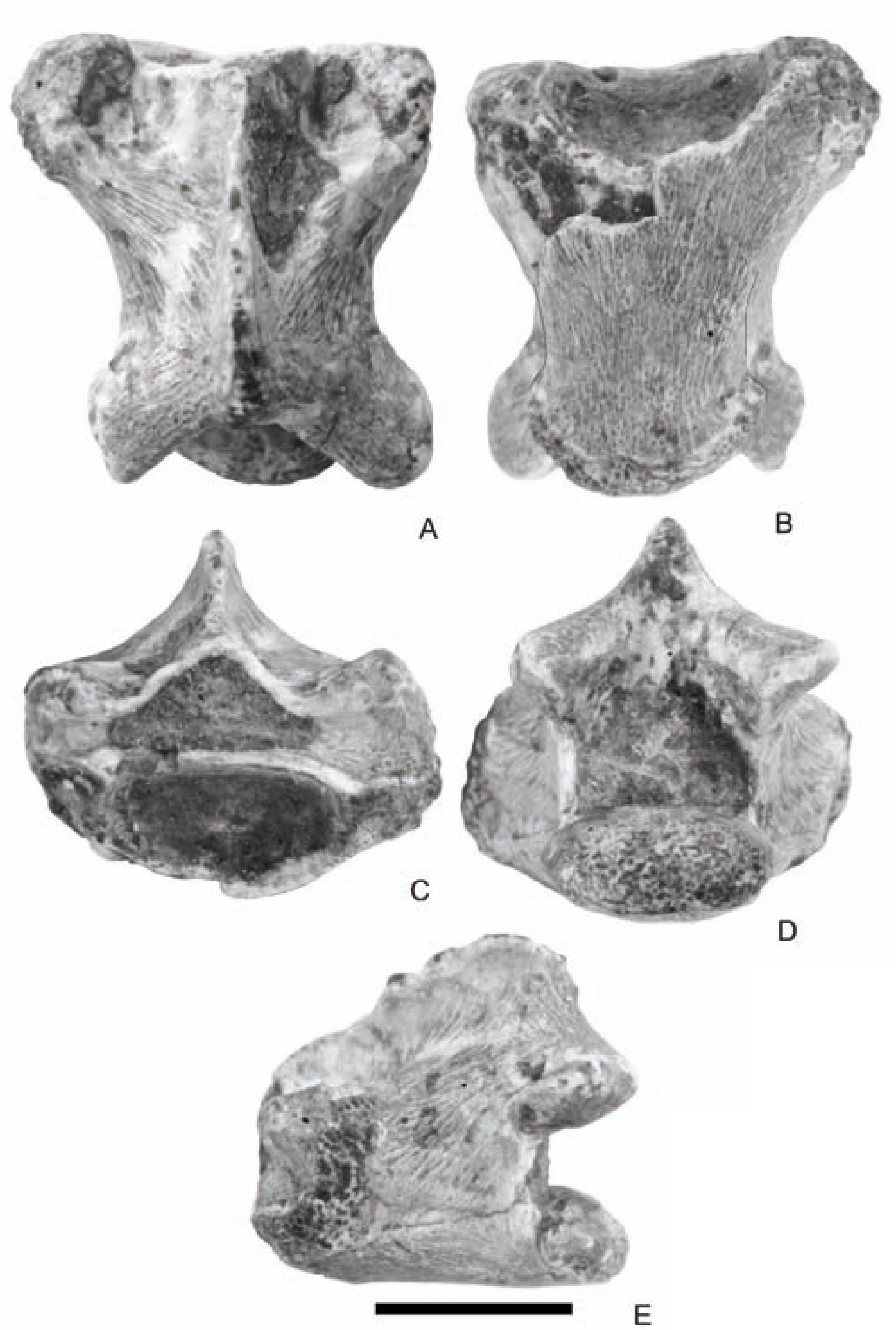
Figure Captions

Fig. 1. *Varanus* sp. from Can Mas, IPS 58437; holotype of *Iberovaranus catalaunicus* Hoffstetter 1969. **A-E**, trunk vertebra in dorsal, ventral, anterior, posterior and left lateral views, respectively. Scale bar equals 5 mm.

Fig. 2. *Varanus* sp. from Can Mas, IPS 31701. **A-E**, cervical vertebra in dorsal, ventral, anterior, posterior and left lateral views, respectively. Scale bar equals 5 mm.

Fig. 3. Trunk vertebrae of extant *Varanus* spp. in ventral view. **A**, *Varanus griseus* ZFMK 53533. **B**, *Varanus salvator* ZFMK 90471. Note the different development of the precondylar constriction (indicated by the arrows) and the proportions of the centrum and the condyle. Scale bars equal 5 mm.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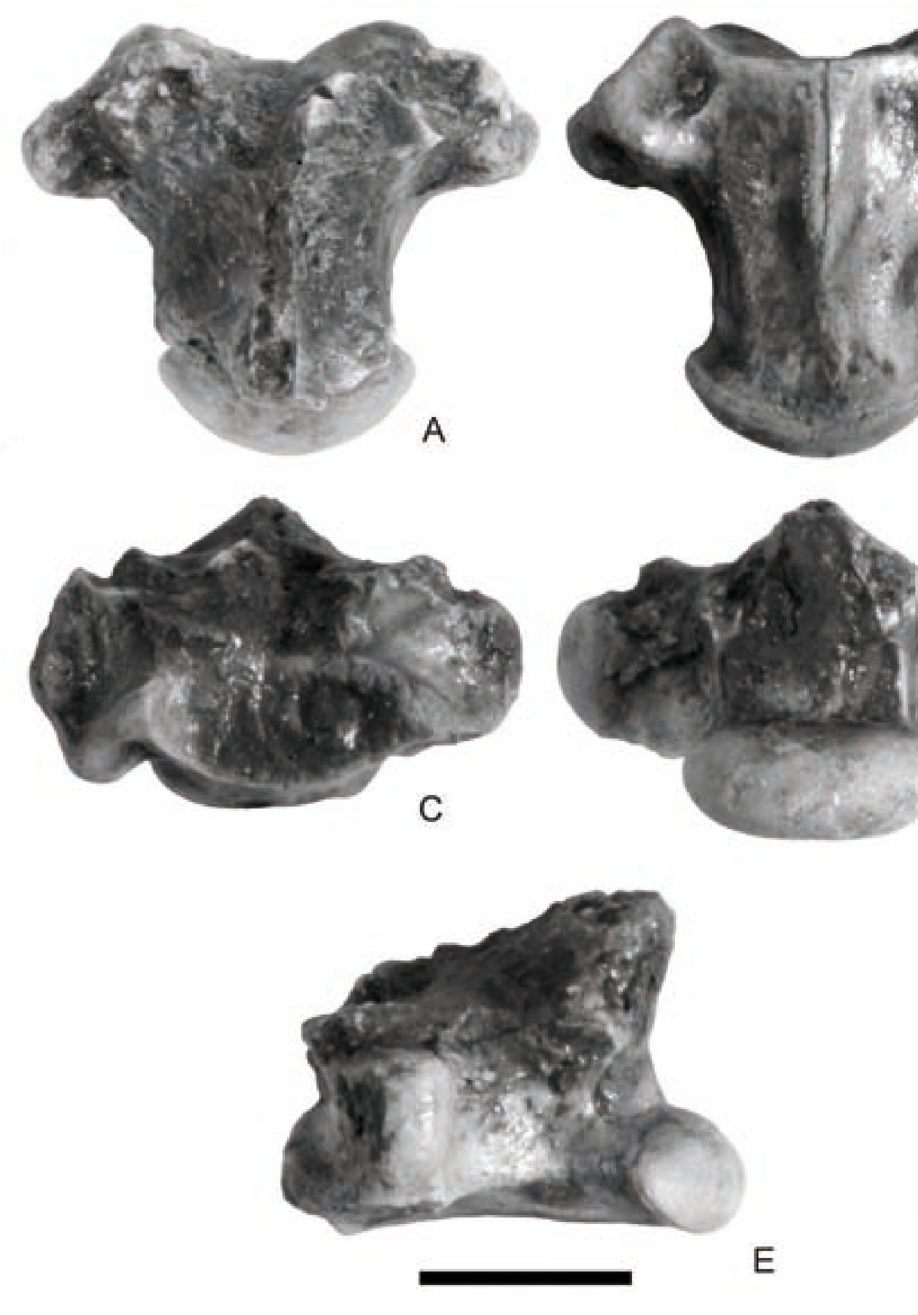
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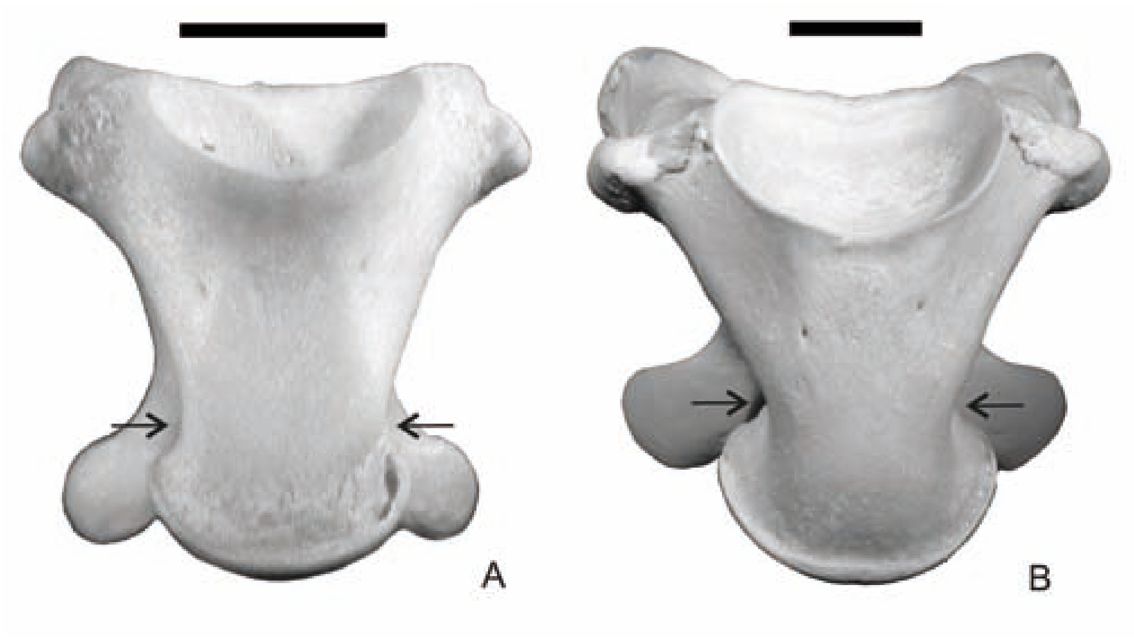
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GENERAL DISCUSSION

11

11. General discussion

The results presented in the publications included in this dissertation, and their implications for the evolutionary history of lizards in the Iberian Peninsula, are discussed below, under three headings: 1) phylogeny 2) fossil record, paleobiogeography and extinctions, and 3) paleoenvironment and ecomorphological diversity.

11.1. Phylogeny

11.1.1. Introduction to the problem and terminology

Application of phylogenetic systematics to lizards is yielding interesting but still quite variable results, mainly with respect to early forms such as those from the Late Jurassic and Early Cretaceous. In some cases these analyses have changed the placement of taxa previously based on the description of general morphology. In other cases, they have provided tentative phylogenetic positions for taxa which have otherwise been difficult to classify due to their lack of similarities with extant groups. However, the reliability on the positions of such early taxa based on morphology has faced a new problem during the last few years, namely a conflict with the general scheme proposed by molecular analyses (see Introduction). The conflict is not only restricted to the fact that the traditional 'Scleroglossa' (intended as all non-iguanian lizards) and 'Autarchoglossa' (intended as all non-gekkotan 'scleroglossans') are paraphyletic in molecular analyses, but may also affect the position of fossil taxa when they are included in combined analyses. For this reason, the problem is not solved by simply adapting the results to the molecular tree, because an important change as, for example, the position of iguanians as the sister group of anguimorphs, may have a strong effect on the position of other taxa (including those for which we are trying to find their position). This could potentially be avoided by forcing the monophyly of the groups recovered by molecular analyses (e.g. a group formed by Iguania + Anguimorpha) or, alternatively, through the analysis of combined datasets. However, because the exploration of these possibilities is beyond the scope of this work, the reported results here are based only on morphological analyses. Accordingly, the terminology used in the publications included as chapters and here, in the general discussion, includes traditional terms such as ‘Scleroglossa’ and ‘Autarchoglossa’ because performed morphological analyses consistently fail to recover the scheme proposed by molecular data. In a similar way, the use of the terms ‘Scincogekkonomorpha’ (‘Scleroglossa’ plus its stem) and ‘Evansauria’ (‘Autarchoglossa’ plus its stem) follows from the use of the matrix provided by Conrad (2008), as the same basic scheme was recovered.

11.1.2. Phylogenetic position of Jurassic and Early Cretaceous taxa

The phylogenetic position of the main Iberian Late Jurassic and Early Cretaceous taxa is discussed here. For each taxon the phylogenetic position recovered in analyses performed in this thesis (Chapters 5, 6 and 7) is reported and compared to positions recovered in previous studies. These analyses were sometimes intended to explore the relationships of one given taxon (e.g. *Pedrerasaurus*, *Scandensia*, *Jucaraseps*), but other Iberian taxa (e.g. *Meyasaurus*, *Parviraptor*, *Hoyalacerta*, *Dorsetisaurus*, *Eichstaettisaurus*) were included in the data matrix and their phylogenetic position is also relevant for the discussion of the composition of Iberian lizard assemblages.

The phylogenetic position of *Meyasaurus* has suffered multiple changes since the erection of the taxon by Vidal (1915). It was first described as a sphenodontid rhynchocephalian (Vidal, 1915; Cocude-Michel, 1963), but reinterpreted as a ‘scincomorph’ by Hoffstetter (1966). After including the genus in a phylogenetic analysis for the first time, it was placed within Lacertoidea (Evans and Barbadillo, 1997), but the large analysis of Conrad (2008) recovered it as an anguimorph, a position previously suggested by Richter (1994) for *Meyasaurus* (=*Ilerdaesaurus*) *unaensis*, although without a phylogenetic analysis. A new analysis following the addition of *Pedrerasaurus* to the matrix of Conrad (2008) placed *Meyasaurus* and *Pedrerasaurus* as sister taxa, joining numerous taxa at the base of ‘Scleroglossa’ (within Conrad’s ‘Scincogekkonomorpha’), but support was weak (see Chapter 5). In fact, the Adams consensus tree failed to recover a sister group relationship between the two genera, and *Meyasaurus* appeared closer to the crown than did *Pedrerasaurus*. An heuristic additional analysis based on a subset of the matrix including less taxa recovered both genera at the base of Anguimorpha when run in PAUP, but this result was not recovered in any subsequent search. Given the positional lability of *Meyasaurus* depending on the matrix used, it can only be placed approximately as a 'scleroglossan', with a position on the stem of Anguimorpha possible (Evans and Bolet, in press). The minor similarities between *Pedrerasaurus* and *Meyasaurus* are not reflected in the results of phylogenetic analyses, and the fragmentary nature of the former makes its placement difficult beyond 'scleroglossan', whether related to *Meyasaurus* or not.

The genus *Scandensia* was initally recovered as a stem-squamate (Evans and Barbadillo, 1988), and then moved crownward after the analysis of Conrad (2008), to a position on the stem of 'Scleroglossa' (forming part of Conrad's 'Scincogekkonomorpha'). The same position was recovered in Chapter 5 after the addition of *Pedrerasaurus* and some minor amendments to the matrix. However, the new *Scandensia* specimen described in Chapter 6 allowed a re-coding of the genus. Results were ambiguous because *Scandensia* grouped with bainguids (as defined by Conrad, 2008, comprising *Bainguis* Borsuk-Białynicka, 1984, *Myrmecodaptria* Gao and Norell, 2000, *Eoxanta* Borsuk-Białynicka, 1988, *Globaura* Borsuk-Białynicka, 1988) and *Pseudosaurillus becklesi* Hoffstetter, 1967, probably as an artifact of missing data (Chapter 6). Some additional analyses (PAUP heuristic analysis in Chapter 6, and general results in Chapter 7) placed *Scandensia* within crown-group 'Scleroglossa', as expected from the presence of osteoderms. A better knowledge of the skull (only known in the holotype, and crushed and exposed in lateral view) would be necessary to assess the position of this interesting genus.

Hoyalacerta was classified by Evans and Barbadillo (1999) as a basal squamate, but subsequent analyses using the matrix of Conrad (2008) recovered this genus at the base of Iguania (e.g. Conrad, 2008). The analysis reported in Chapter 6 also recovered *Hoyalacerta* at the stem of 'Scleroglossa' (forming part of Conrad's 'Scincogekkonomorpha'). However, the holotype is the only known specimen, and the rather poor preservation of some of its parts hamper discussion on the position of this taxon, which is otherwise quite different from a typical iguanian, in the rather elongated body and short limbs.

Phylogenetic analyses also place *Jucaraseps* within the 'group' of Mesozoic (mainly Early Cretaceous) stem 'scleroglossans' (Chapter 7), as an additional scincogekkonomorph sensu Conrad (2008). As stated in the corresponding publication (Chapter 7), the position of *Jucaraseps* is tentative because the skull is only incompletely known, apart for the same reasons explained above regarding the paraphyly of ‘Scleroglossa’.

Parviraptor was considered an early anguimorph (Evans, 1994), although recent analyses recovered it as a stem-gekkotan (Conrad, 2008). The fact that Gekkota always emerge as the sister group to other squamates in molecular analyses, sometimes with dibamids, or as the sister group to other ‘scleroglossans’ in morphological analyses has lead to a search for early fossil gekkotans. However, *Parviraptor* was nested within the subset of stem-‘scleroglossans’ reported above and including, among others, the Iberian *Eichstaettisaurus* and *Jucaraseps* in Chapter 7. Daza et al. (2012) considered the inclusion of *Parviraptor* within Gekkonomorpha to be weakly supported, and favoured a position as a basal ‘scleroglossan’.

Paramacellodidae was erected by Estes (1983) to group a number of widespread Late Jurassic-Early Cretaceous taxa initially interpreted as cordyloids. The taxonomic composition and status (monophyletic or not) of Paramacellodidae, as well as its phylogenetic position in the squamate tree have all changed since its first definition, mainly due to the description of better material and the application of morphological phylogenetic analyses. Richter (1994a) placed paramacellodids inside Scincoidea (sensu Estes et al., 1988). Evans and Chure (1998) reported a sister-group relationship of paramacellodids and scincoids (Scincidae + Cordylidae), but paramacellodids were represented in the phylogenetic analysis only by the best-known taxon *Paramacellodus*, and thus the monophyly of the group, potentially also including *Becklesius*, *Mimobecklesisaurus*, *Sharovisaurus* and, less certainly, *Pseudosaurillus*, *Saurillus* and *Saurillodon*, was not tested. The authors argued, however, that the group as suggested by Estes was not monophyletic and that *Saurillodon* should not be included. In his large phylogenetic analysis, Conrad (2008) included the genera *Pseudosaurillus* (represented by two species), *Paramacellodus*, and *Becklesius*. The results reported a paraphyletic Paramacellodidae and a paraphyletic *Pseudosaurillus* (note that Evans and Searle, 2002 had included one of these species in their *Parasaurillus*), placed on the stem of Anguimorpha, rather than related to scincoids. The 50% Majority Rule Consensus Tree of the main analysis in Chapter 5 recovered paramacellodids (to the exclusion of *Pseudosaurillus becklesi* and *Parasaurillus*) in a polytomy with lacertoids + cordyloids and a group formed by ‘Scincidae’, Gekkota, Dibamidae, Amphisbaenia and Serpentes. In the Adams consensus tree the only paramacellodid that maintained this position was *Becklesius*. Similarly, Chapter 6 recovered the two best known genera, *Paramacellodus* and *Becklesius* in separate positions, the former with anguimorphs and the latter with 'scincomorphs' + gekkotans. In contrast with Conrad's results, Gauthier et al. (2012) again recovered the paramacellodid *Paramacellodus* at the stem of Scincoidea. It is clear that the recovery of at least one well-preserved complete specimen of paramacellodid in a suitable deposit (e.g. a konservat-lagerstätten like Las Hoyas) would be of great interest, because of the problem of referral of fragmentary material to Paramacellodidae.

Dorsetisaurus, which was described from Guimarota as *Introrsisaurus* by Seiffert (1973) and then synonimized with the former by Estes (1983), is the earliest Iberian taxon that shows clear affinities to anguimorphs (Conrad et al., 2011). Its position as a basal anguimorph, as recovered in Conrad (2008), Conrad et al. (2011) as well as in analyses in Chapter 5, 6 and 7, seems to be rather stable, placing it as a good candidate for molecular clock calibrations as the earliest worldwide representative of Anguimorpha.

Forms from younger localities (Late Cretaceous, Eocene and Miocene) are not discussed in this section because they have not been included in phylogenetic analyses. They fit better in well-established groups (Gekkota, Scincoidea, Lacertoidea, Iguania, Anguimorpha, Amphisbaenia), and in most cases, they are represented by fragmentary material with a limited interest in large-scale phylogenetic analyses. Their affinities are discussed, however, in the fossil record section.

11.1.3. Implications

If the placement of iguanians as a derived group close to anguimorphs, as found by molecular analyses, is finally confirmed (e.g. Pyron et al., 2013; contra Conrad, 2008; Gauthier et al., 2012), then it will demonstrate the power of molecular analyses to avoid the influence of convergence and other factors (such as character non-independence) that lead to erroneous results in morphological analyses. However, although this will be of importance in establishing a correct general phylogenetic scheme, the study of fossils and their integration in morphological or combined studies still offer information not available to pure molecular analyses. 1) the earliest fossils of each group will always serve as calibration points in molecular analyses aiming to estimate the minimum age of divergence between groups. 2) because there is no way to obtain DNA from ancient fossils, they must be integrated into combined analyses (this affects not only isolated fossil genera, but also entire clades if they have no extant representatives). 3) the evolutionary history of important traits can be traced through fossils, while in molecular studies only the states of living taxa can be evaluated. 4) Finally, and this is not strictly related to phylogeny, fossils are the only source of information regarding the ecomorphological diversity of early assemblages, and they also add important information in order to reconstruct paleobiogeographical scenarios. This is mandatory because fossils usually contradict proposed scenarios based only on modern distribution of taxa, mainly regarding those groups with a long evolutionary history.

An additional problem regarding the phylogenetic placement of fossil lizards is the general trend for the taxa previously placed on the squamate stem to move crownwards when new data on their anatomy becomes available, providing support for the conclusion that their basal position is an artifact of missing data. This problem is not exclusive of squamates, and seems to be linked to a stemwards movement of fossil taxa due to their incompleteness related to the lack of soft parts (Sansom and Wills, 2013) in fossils. The refinement of the phylogenetic position of some taxa can be achieved either through more complete and comprehensive studies on previously described material (e.g. Conrad, 2008) and/or by the addition of new specimens of poorly known taxa (e.g. Chapter 6). In the latter study, the addition of new data resulted in a crownwards movement of the phylogenetic position of *Scandensia*.

Unfortunately, we are far from reaching definitive conclusions regarding such early taxa, given that the phylogenetic positions are only tentative. Thus the phylogenetic placement of most Late Jurassic and Early Cretaceous lizard taxa remains unstable and difficult to interpret (Chapters 5, 6 and 7). If we add the problems of incongruence with molecular analyses, there is still much work to do regarding the phylogenetic position of many of these taxa. Concerning the Iberian Mesozoic lizards, as explained above, many of the Early Cretaceous form part of a subset of stem-'scleroglossans' (e.g. Conrad, 2008, Chapters 5, 6 and 7), but the significance of these results is not clear and could be related to the large amount of missing data (Evans and Bolet, in press). Furthermore, if iguanians are actually the sister taxon of anguimorphs (as suggested by most molecular analyses), then all these stem-'scleroglossans' may represent stem-squamates. Figures 3 and 4 illustrate, respectively, the phylogeny of squamates based on morphology and molecular analyses. Note that the earliest records of iguanians and gekkotans (dot with a question mark) in the morphological tree (Fig. 3) fill what would be long ghost lineages for both groups. However, as reflected in Fig. 4, the results of molecular analyses have triggered the reinterpretation of dubious early fossils the position of which was hard to accommodate to the new scheme, and such early forms are no longer regarded as the earliest records of iguanians and gekkotans (e.g. Jones et al., 2013). The effect of removing these uncertain early records is that long ghost lineages for other taxa are greatly shortened (e.g. Hutchinson et al., 2012). After these removals, the molecular tree presents a more balanced picture, with the different groups appearing in the expected order and much shorter gaps in the fossil record. An exception to this is the relatively late appearance of gekkotans and the lack of fossil record for dibamids, although the general small size of the former and the restricted distribution of the latter may be involved. Additionally, the effect of moving iguanians to a sister-group position to Anguimorpha may have an effect on the position of the supposed basal forms, a possibility that could be explored through the use of combined molecular and morphological analyses. If the position of the Late Jurassic-Early Cretaceous taxa that appear as stem-'scleroglossans' in morphological analyses finally maintain their position in combined analyses (becoming stem-squamates), then the Iberian record would have a great potential to explain an important part of the early evolution of squamates. This is favoured by the fact that the scarce earlier worldwide localities are not expected to yield a great number of well-preserved specimens that could add better information, and that most of the first groups to diverge are well represented in the Iberian record (Fig. 4).

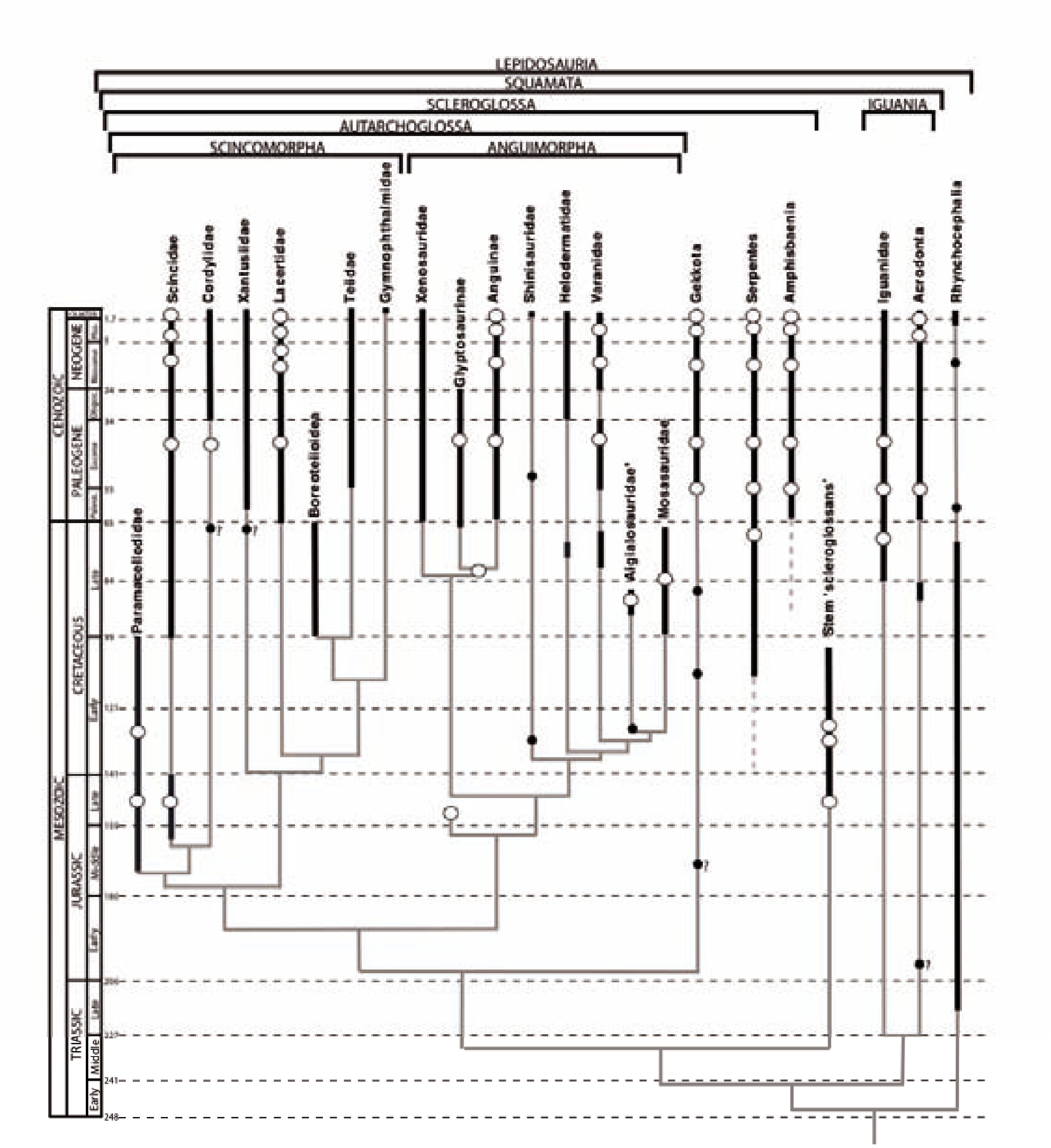

Figure 3. Fossil record of squamates plotted on a phylogeny based on morphology. The general tree is based on Estes et al., (1988), except for the position of fossil groups, which are positioned in the most widely accepted placement. Black dots indicate isolated records from outside Iberian Peninsula, white circles indicate Iberian records.

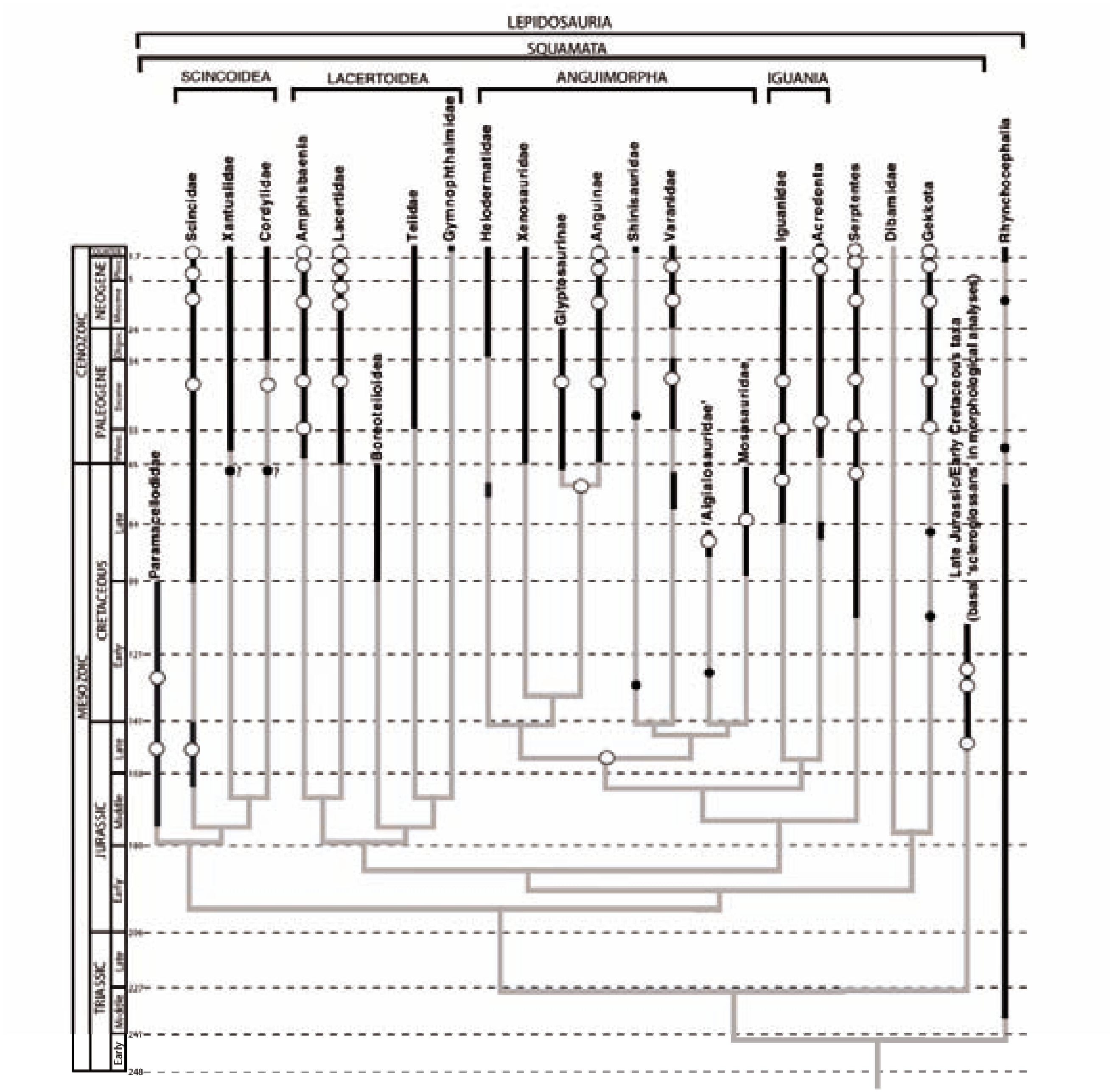

Figure 4. Fossil record of squamates plotted on a molecular phylogeny, based on Wiens et al. (2012). Because most fossil groups are not included in molecular analyses, they are positioned in their most widely accepted placement. Black lines and dots indicate records from outside Iberian Peninsula, white circles indicate Iberian records.

11.2. Fossil record, paleobiogeography and extinctions

The information resulting from the study of the Iberian fossil lizard record is interesting because it encompasses periods in which the global squamate record is poor (e.g. Early Cretaceous) and/or it complements information provided by other vertebrates (e.g. dinosaurs in the Mesozoic or mammals in the Cenozoic). In this section, an updated account on the fossil Iberian record is provided, and paleobiogeographical implications, as well as the effect of extinctions, are discussed.

11.2.1. Fossil record of the Iberian Peninsula

Iberian taxa from the Late Jurassic and Early Cretaceous belong to Paramacellodidae (possibly stem-scincoids), ?Scincidae, Anguimorpha, or to a collection of forms with a certain tendency to fall on the stem of 'Scleroglossa' (Chapter 5, and see the phylogeny section above). Paramacellodids are represented by the same two genera (*Paramacellodus* and *Becklesius*) in the Late Jurassic (where they are found with *Chalcidosaurus*) and the Early Cretaceous of the Iberian Peninsula, but in the latter they appear as a minor component of the lizard assemblages because the non-paramacellodid diversity is much higher (Chapter 5). The ?scincid *Saurillodon* (its position as a scincoid is well supported) is represented by numerous species (Kosma, 2004). Anguimorphs are represented by *Dorsetisaurus* and the non-pythonomorph varanoid *Arcanosaurus* (e.g. Broschinski, 2000; Houssaye et al., 2013a). The Iberian taxa recovered on the stem of 'Scleroglossa' include *Parviraptor*, *Eichstaettisaurus*, *Pedrerasaurus*, *Hoyalacerta*, *Scandensia* and *Meyasaurus*, but the latter two may represent more derived 'scleroglossans' (Chapters 5, 6 and 7, see above). The Iberian record of lizards from this age is exceptional both in terms of diversity and preservation of the specimens, mainly those recovered from lithographic limestones (Chapter 5).

Late Cretaceous material is, in contrast with that of the Early Cretaceous, relatively rare in the Iberian Peninsula. Screen-washing has recently yielded new material from a few localities in the Catalan Southern Pyrenees, but the fragmentary nature of these specimens has precluded any attempt at identifying them until more material is discovered. At least two forms seem to be present, one of which probably represents a new taxon on the basis of tooth morphology (pers. obs.). In any case, previously described assemblages (those from Laño) and recent additions (those from

Lo Hueco) confirm that archaic Early Cretaceous assemblages were completely replaced by taxa that are much easier to accommodate in modern groups, including possible iguanians, possible 'scincomorphs', anguids, varanoids, as well as snakes (Chapter 5).

Scincoids, possibly lacertids, 'necrosaurs' and amphisbaenians dominate the poorly sampled Paleocene squamate assemblages of Europe (Rage, 2013). It would be interesting to know whether Iberian assemblages included the same taxa or additional forms, but Paleocene lizards remain unknown from the region, possibly because there are few continental Paleocene localities yielding vertebrate remains.

The Eocene lizard assemblages of the Iberian Peninsula are, in contrast to those from the Paleocene, rich and diverse (Bolet and Evans, 2010a, 2012a; Chapters 8 and 9), although they had previously received little attention. The early Eocene squamate fauna of Silveirinha (Portugal) is composed of pleurodont iguanians, agamids, gekkotans, lacertids, amphisbaenians, glyptosaurs and platynotans (Rage and Augé, 2003) and represents the earliest record of many of these groups in Southern Europe. The diverse Late Eocene assemblage of Sossís (Catalonia, Spain) consists of pleurodont iguanians, gekkotans, lacertids, cordyliforms, ?scincids, one new taxon probably related to scincoids, glyptosaurines, anguines and amphisbaenians (Chapters 8 and 9). The iguanians include two different forms of *Geisetaliellus* (*G. pradiguensis* and *G.* sp.), and one of *Pseudolacerta* (Chapter 8). Three different forms of gekkotans have been identified, although their affinities are unknown (Chapter 8). Lacertids are represented by two species of *Dormaalisaurus* (*D. rossmanni* and *D. girardoti*), one of *Gracilicerta* (*G. sindexi*), and an amblyodont form that possibly represents an unnamed new genus of lacertid (Chapter 8). Scincoids from Sossís include one cordyliform, a possible scincid (Chapter 8), and the new genus *Pyrenasaurus*, interpreted as a possible scincoid (Chapter 9). The single amphisbaenian recorded, represented by scarce material, is possibly but not definitely related to blanids (Chapter 8). Anguimorphs include at least one form belonging to Glyptosaurini (the presence of other glyptosaurs is not discarded), and two anguines (Chapter 8). Sossís is the only late Eocene Iberian assemblage described so far, but abundant material from early, middle and late Eocene localities from the Iberian Peninsula will be object of study in the near future.

In the Oligocene, European lizard assemblages are much rarer and less diverse than those from the Eocene (Augé, 2005). Nevertheless, the absence of lizard records in the Iberian Peninsula is again due to a lack of attention rather than a real lack of material. Specimens exist in collections (pers. obs.; H.-A. Blain pers. comm., 2012), so this gap will be much easier to fill than, for example, that of the Paleocene, for which no material is known and suitable localities are very scarce.

The Neogene record of Iberian lizards is unbalanced, with Miocene assemblages poorly known, but those of the Pliocene, and particularly the Pleistocene and Holocene, being much better studied (e.g. Blain, 2009 and references therein). The composition of Miocene Iberian lizard assemblages, partially based on unpublished data from the Vallès-Penedès Basin, includes gekkotans, lacertids, scincids, blanid amphisbaenians, anguines and the varanid *Varanus* (see Chapter 10, Annex I, Bolet et al., 2013a, b, and Delfino et al., 2012, 2013). Gekkotans, lacertids and scincids have yet to be identified, but anguines include at least the genera *Pseudopus* and *Ophisaurus* (Bolet et al., 2013b). The exceptional specimen described in Annex I confirms the presence of the amphisbaenian genus *Blanus* in the European Miocene, a record that previously relied only on fragmentary remains, mainly dentaries, maxillae and premaxillae. Chapter 10 reports one of the earliest records of *Varanus* in Europe through the synonymization of *Iberovaranus* (MN3 if the dating is correct), and an extensive review of this genus in the Iberian Peninsula is in progress (see Delfino, 2011, 2012a, b for preliminary results). The Iberian post-Miocene record is reviewed in the Introduction, and, because the papers in this thesis do not include assemblages from this age, here it is only stated that they represent the natural continuation of Miocene assemblages. Many of the extant genera were already present in the Miocene (e.g. *Blanus*, probably some lacertids and scincids, *Pseudopus*) or may have been present but are awaiting definitive identification. Some taxa finally disappeared from Iberian assemblages during the Quaternary, giving place to the composition that we observe today, dominated by lacertids together with poorly diverse gekkotans, scincids, anguines and amphisbaenians.

11.2.2. Paleobiogeography

One of the important contributions of the study of Iberian fossil lizards is the paleobiogeographic information yielded by taxa with European, African and North American affinities. The presence of squamates with Gondwanan (mainly African and from the Late Cretaceous onwards) affinities in the Iberian Peninsula are the result of the position of this territory in the southern edge of Europe, which allowed intermittent connections and faunal interchanges (e.g. Gheerbrant and Rage, 2006). The presence of taxa with North American affinities is more difficult to justify, and different explanations may apply to the different situations represented in the Jurassic and the Eocene (see below).

Jurassic Iberian lizards provide support for the interpretation of the presence of faunal interchange between Portuguese and North American contemporaneous assemblages (e.g. that of the Morrison Formation at Como Bluff), the shared taxa including *Dorsetisaurus*, *Parviraptor* and paramacellodids (e.g. Prothero and Estes, 1980; Evans and Chure, 1998). This interpretation is supported by the recovery of rhynchocephalians referred to Opisthodontia, a group reported from the Jurassic of North America and the United Kingdom, in contemporaneous beds of Portugal (e.g. Ortega et al., 2006). However, although these similarities between faunas across Laurasia have also been reported for other groups, the modern tendency is towards the description of endemic taxa in Portugal (mainly regarding crocodiles and dinosaurs), and this could be related to the opening of the northern proto-Atlantic (Ortega et al., 2009) or to the fact that Europe was a series of small island landmasses through much of the Mesozoic. Ortega et al. (2009) contemplated vicariance and dispersal scenarios to explain this admixture of shared and endemic taxa, but the paleogeographic interpretation of Western Europe as a group of islands suggests that the assemblages could have been formed by relictuals of a more widely distributed fauna that was present before continental break-up or the rise in sea level (Chapter 5).

The specimens described in Chapters 5, 6 and 7 contribute to the interpretation of the Iberian Peninsula as forming part of a Western European archipelago in the Early Cretaceous. The two new genera erected (namely *Pedrerasaurus* and *Jucaraseps*) increase the number of apparently endemic forms known from the region at that time. With the exception of *Meyasaurus*, which has also been reported from England (Sweetman, 2009), many of the recovered taxa from las Hoyas, Uña and Montsec are currently only known from the Iberian Peninsula. These include *Hoyalacerta*, *Scandensia*, *Cuencasaurus*, *Pedrerasaurus* and *Jucaraseps* (Chapters 5 and 7; Evans and Bolet, in press), as well as the slightly younger *Arcanosaurus* (Houssaye et al., 2013a). With the exception of *Arcanosaurus*, which is probably an early varanoid, most of these taxa are difficult to accommodate in modern groups. As explained above, previous assemblages (those from the Jurassic) were composed of taxa with a wide Laurasian distribution, most of them shared with North American assemblages. This suggests that the apparently high degree of endemicity of later (Early Cretaceous) assemblages could be linked to a greater isolation of the Iberian Peninsula from both North America and also the rest of Europe. This isolation was also suggested for the Italian assemblage of Pietraroia (Evans et al., 2004), where it is further supported by the relictual presence of rhynchocephalians. Moreover, the presence of paramacellodids at Morocco suggests that the Iberian (and other landmasses) may have provided a dispersal route between Europe and Africa at that time (Gheerbrant and Rage, 2006). However, it remains possible that some of the supposed Iberian endemic taxa were represented in other European regions, but are difficult to identify from disarticulated fragmentary remains. It is noticeable that *Meyasaurus*, with a characteristic frontal and bicuspid dentition has been recorded from southern Britain (Sweetman, 2009), whereas other genera, with a less diagnostic dentition are only known from Iberian localities providing specimens with a poorly characteristic (in most cases also poorly known) dentition (e.g. *Hoyalacerta*, *Scandensia* and *Jucaraseps*; Chapters 5, 6 and 7; Evans and Barbadillo, 1998a, 1999; Evans and Bolet, in press).

The Late Cretaceous squamates from the Iberian Peninsula are still poorly known, and the paleobiogeographic information yielded is limited. Lizards with a tricuspid dentition in Campanian and Maastrichtian localities have been tentatively referred to pleurodont iguanians (Rage, 1999; Blain, 2010; pers. obs.). If confirmed, they would favour the interpretation that pleurodont iguanians were widespread across Laurasia (North America, Asia and Europe) in the Late Cretaceous. Eocene iguanians could be related to these forms or to a later incursion of North American taxa, as suggested by Smith (2009). The other represented taxa had a wide Laurasian distribution at that time, and offer little additional information. However, the first Iberian snakes, which appear in the Late Campanian-Early Maastrichtian of Laño in the form of two madstoiids, have African affinities (Rage, 2013).

Regarding the Paleogene, the Iberian assemblage of Silveirinha is similar to those from the Early Eocene of rest of Europe, being composed of a mixture of Paleocene survivors and newcomers that reached the continent in a wave of dispersal (Rage, 2012). Late Eocene European assemblages were also diverse, being composed of Paleocene survivors and a great number of endemic forms resulting from in-situ evolution during the isolation of Europe (Rage, 2013). Except for the absence of large taxa like platynotans, which is probably due to a sampling bias, the Sossís fauna compares well with contemporaneous French localities (Chapters 8 and 9) at both the group and species level (e.g. *Geiseltaliellus pradiguensis*, *Dormaalisaurus girardoti*, *D. rossmanni*, *Gracilicerta sindexi*, *Pyrenasaurus evansae*) or at least the genus level (e.g. *Pseudolacerta*) (Chapters 8 and 9). The case of *Pyrenasaurus* is particularly clear, as its highly characteristic dentition is only known in material from two localities situated at both sides of the Pyrenees, Escamps in the north and Sossís in the south. The analysis of Western Iberian assemblages should clarify whether this similarity of southern Pyrenean localities to those of southern France applies to the rest of the Iberian Peninsula, or, on the contrary, whether the presence of endemic forms will be found to support the existence of a Western Iberian bioprovince (Chapters 8 and 9), as suggested by mammals (e.g., Casanovas-Cladellas and Santafé-Llopis, 1987; Cuesta Ruiz-Colmenares, 1991; Badiola et al., 2009; Marigó et al., 2010; Minwer-Barakat et al., 2012).

The study of Oligocene faunas should shed light on the influence of the Grande Coupure over lizard assemblages in a more southern location than those reported so far. It will be also interesting to check whether taxa that disappeared from more northern European localities in the Early Oligocene persisted in the Iberian Peninsula and could be a source for subsequent re-appearances in northern regions. However, discussion on this issue will need to wait until ongoing studies in Oligocene Iberian localities are finished.

The Miocene Climatic Optimum allowed the incursion of some thermophilic taxa from Africa, including chameleons, cordyliforms and the genus *Varanus* (Böhme, 2003, 2010). Ongoing research on Miocene assemblages from Catalonia reveals a similar composition to those of France, but at least one new form of uncertain affinities has been identified (work in progress). A better knowledge of Iberian Miocene assemblages should clarify whether this absence is real or an artifact of sampling, but if these taxa were actually absent from the Iberian Peninsula, this might be indicative of a dispersal route via Eastern Europe, taking advantage of the early Miocene contact between Africa and Europe. In Annex I it is demonstrated that by MN7+8, the Western and Eastern Mediterranean clades of *Blanus* were already distinct, and the fossil appears to represent a good calibration point for molecular clocks (Bolet et al., 2013a; Delfino et al., 2013; Annex I). *Varanus*, the presence of which in the Iberian Miocene has long been obscured by the referral of varanine material to '*Iberovaranus*', has a wide distribution probably related to the greater dispersal capabilities of a rather large form. A better knowledge of its fossil record at the species level would allow further discussions on paleobiogeography.

The levels of endemicity among Iberian lizards seem to range from moderate in moments of connection with the rest of Europe (and sporadically with Africa) to high in moments of isolation, when the Iberian Peninsula is supposed to be an island of an European archipelago. It is interesting that the level of endemicity of extant Iberian lizards, at least at the species level, remains high because despite the presence of a connection with the rest of the continent, the high altitude of the Pyrenees represents a barrier for the dispersal of some taxa.

11.2.3. Extinctions

Two recent papers have considered different periods of squamate replacement during the Mesozoic from a global perspective. Benson et al. (2012) analyzed faunal turnover between the Late Jurassic-Early Cretaceous and the Late Cretaceous. Allowing for a generally poor Gondwanan record, and the poor sampling of terrestrial faunas during the critical Turonian-Santonian interval in North America and Europe, the authors concluded that archaic squamate clades were progressively replaced by derived modern forms including snakes, iguanians and gekkotans. In the Iberian Peninsula (see Chapters 5, 6 and 7) it is clear that Early Cretaceous taxa are not recorded in the Late Cretaceous, because stem-representatives of modern groups were replaced by crown representatives of the same or other groups. The few known Late Cretaceous assemblages from the Iberian Peninsula do not contradict the proposed trend of replacement (see Chapter 5 and fossil record section above), because the known taxa, despite being represented by fragmentary and scarce material, are clearly different from those of the Early Cretaceous. Tricuspid and multicuspid pleurodont iguanians (Rage, 1999; Narváez and Ortega, 2010), and characteristic anguid and snake vertebrae all are absent from previous Iberian assemblages (Chapter 5). The anguid from Laño is among the earliest anguids reported so far, and varanoids are present at both time periods, but represented by two unrelated forms, a non-pythonomorph varanoid in the Early Cretaceous (Houssaye et al., 2013a) and a possible pythonomorph in the Late

Cretaceous (Houssaye et al., 2013b).

The second paper (Longrich et al., 2012) explored how the mass extinction at the Cretaceous-Paleogene (K-Pg) boundary affected squamate diversity in western North America. The fauna is said to show extremely high turnover across the K-Pg boundary, with an extinction rate of 83% at the species level. An important conclusion was that in a traditional, Linnean framework, virtually all families appear to cross the K-Pg boundary because lineages that became extinct were included within modern families or excluded from the analysis because they could not be classified. Other interesting conclusions were that the recovery of squamates after the K-Pg boundary was slower than that of mammals, and, unlike them, squamates appear to have simply reoccupied the niches they occupied before the extinction. Finally, Longrich et al. (2012) stated that the end-Cretaceous extinction of squamates was likely a global phenomenon, as confirmed by the dramatic turnover that took place in Asia. Regarding the Iberian Peninsula, the latest Cretaceous record has a good potential although studies have been mainly focused on dinosaurs, and micro-vertebrates remain understudied. The knowledge on the lizard assemblages from this age will improve in the next years with the increase of screen-washing efforts, so the problem for the study of the K-Pg boundary in the Iberian Peninsula will be the lack of Paleocene localities yielding terrestrial vertebrates. Meanwhile, the analysis of the influence of the K-Pg extinction necessarily relies on comparison of Late Cretaceous assemblages to those of the Eocene. Although pleurodont iguanians and anguids form part of assemblages from both epochs, it is not known if they are directly related or, on the contrary, they correspond to a new wave of incomers after an impoverished Paleocene like the rest of Eocene taxa (Chapter 8).

From the Late Cretaceous onwards, lizards from the Iberian Peninsula mainly belong to groups that have had a continuous presence in the region (allowing for gaps in the fossil record relating to poorly sampled periods), with sporadic incursions of ‘exotic’ taxa (mainly related to periods of increased temperatures, see below). The Grande Coupure, a severe extinction event initially identified on the basis of mammals (Stehlin, 1909), and corresponding to an abrupt change of faunas across the Eocene-Oligocene boundary (Schmidt-Kittler, 1987), had different effects on the groups represented in the late Eocene. Although some forms (e.g. glyptosaurs) completely disappeared, most squamate groups that were present before the Grande Coupure (e.g.

pleurodont iguanians, gekkotans, lacertids, scincids, amphisbaenians, anguines, platynotans) are also represented after this event (Chapter 8). However, most of them were represented by different taxa after the Grande Coupure, and the presence of others became increasingly rare until they disappeared along the Oligocene (e.g. pleurodont iguanians; Chapter 8). It would be interesting to see if some of these taxa survived longer in the Iberian Peninsula and if in some cases the Iberian faunas could be the source of subsequent repopulations of other European regions after the extinction. Unfortunately, the evaluation of the role of Iberian faunas across the Grande Coupure will have to await the description of latest Eocene and Oligocene assemblages (work on localities from both periods is in progress).

Gekkotans, scincids, amphisbaenians and anguines make a discrete contribution to the lizard diversity of most European Cenozoic assemblages, including those from the Iberian Peninsula, but their presence is continuous and widespread (Chapter 8, Annex I and see above). Lacertids underwent a radiation reflected today in the great diversity found in Europe and, particularly, in the Iberian Peninsula. Other groups, however, were more affected by the several extinctions that occurred during the Cenozoic, and became sporadically or definitively extinct from the region. Pleurodont iguanians disappeared (temporarily) in the K-Pg boundary, and definitively disappeared after the Grande Coupure. Agamids were present in the Eocene and the Miocene-Quaternary (Chapter 8) but are not represented today. It is not possible to ascertain if they disappeared from Iberian Oligocene localities because this period has not been sampled, so their continuous presence in the Iberian Peninsula cannot be discounted. Their final extinction from the region occurred during the Early Pleistocene, representing the youngest record of the group in Western Europe (Blain et al., in press). Chameleons may represent a recent introduction or a natural incursion during the Holocene (Bolet and Evans, 2014). Cordyliforms, only recorded from the late Eocene of Sossís, represent an sporadic incursion of a group typical of Africa and Madagascar (Chapter 8). Their characteristic osteoderms are absent from Iberian localities from MP18-MP20 (pers. obs.), so cordyliforms might have disappeared from the Iberian Peninsula before the Grande Coupure. Glyptosaurs, are recorded in the early and late Eocene of the Iberian Peninsula (Chapter 8), and are also recorded at the latest available Eocene localities (pers. obs.), suggesting that they disappeared at the Grande Coupure. Finally varanoids are currently absent from the region, but they were recorded at different times (Early Cretaceous, Late Cretaceous, early Eocene, Miocene-Quaternary; Chapter 9 and above) so, regardless of the effect of extinctions, the group has been able to disperse into Europe multiple times.

It is clear that discussion of the effects of major extinctions on Iberian lizard faunas is hampered by the fact that post-event localities are very scarce or absent. Although the impoverishment of faunas is the predicted situation in a post-extinction scenario, the situation is probably aggravated by the fact that marine transgressions during key periods reduced the area of emerged lands in the Iberian Peninsula and, accordingly, the number of localities suitable for the recovery of terrestrial vertebrates diminished. In other cases (e.g. Oligocene), under-sampling is probably also involved. A better sampling of suitable periods (preferably reaching identifications at the species level) is expected to allow a more detailed discussion on these and other minor extinctions.

11.3. Paleoenvironment and ecomorphological diversity

As ectotherms, squamate distribution, richness and diversity are correlated with climatic conditions, especially temperature, and climate changes have strongly influenced their distribution through time (Rage, 2013). As lizards vary in their thermoregulatory capabilities, an analysis of the composition of a given lizard assemblage can shed light on the paleoenvironment of the locality in which they are found. At the same time, incursions of thermophilic taxa into areas where they are usually absent not only suggests a rise in ambient temperature in that region, but may also reveal dispersal routes and thus have paleobiogeographical implications (see above). Actualistic conclusions can be drawn by comparing members of fossil assemblages with extant forms, but these comparisons work better the closer the phylogenetic affinities of analysed taxa are, and, accordingly, they are more reliable for younger assemblages than for older ones.

11.3.1. Paleoenvironment

The paleoenvironmental significance of the presence of a given lizard taxon in the Mesozoic is difficult to interpret because in most cases close relatives that could indicate preferences for determinate habitats do not exist. For well-known localities as

Guimarota, Las Hoyas or La Pedrera de Meià, the paleoenvironment is deduced from sedimentological features and the global composition of the assemblage. The resulting inferences can be applied to lizards, in an inverse process as the one pursued in posterior assemblages (e.g. Eocene or Miocene), where the presence of a taxon with known preferences for a given habitat provides insights on the paleoenvironment of the locality. To give an example, we know that Las Hoyas was a wetland, and that recorded lizards lived around it, but the taxonomical composition of the lizard assemblage itself gives little paleoenvironmental information. The same problem applies to interpretations of the paleoclimate of the region, because the preferences of such lizards for a warmer/cooler or dryer/wetter climates are unknown.

In the Cenozoic the fact that the recorded lizards are much easier to link to modern taxa facilitates paleoenvironmental inferences. The appearance of ‘exotic’ taxa in Europe is always linked to periods of global warming, namely the PETM (Paleocene-Eocene Thermal Maximum) and/or IETEM (Initial Eocene Thermal Maximum)(Rage, 2013), and the Miocene Climatic Optimum (Böhme, 2003). These taxa reached northern latitudes during periods of maximum temperatures, but disappeared earlier from the north than from southern regions, the latter including the Iberian Peninsula. At different times, as today, the Iberian Peninsula acted as a refugium for European taxa that had wider distributions in the past. In the Eocene, some recorded Iberian lizards (pleurodont iguanians, cordyliforms and platynotans) are suggestive of subtropical conditions, supporting previous interpretations based on the presence of, for example, primates (e.g. Marigó et al., 2010, 2012). Regarding the Neogene, the Miocene Climatic Optimum allowed incursions of thermophilic taxa with an African origin into Europe and, a completely different set of primates reached the Iberian Peninsula (e.g. Alba, 2012). However, some of the thermophilic Miocene taxa reported from other parts of Europe (e.g. chameleons, agamids, cordylids) have not yet been reported from the Iberian Peninsula. Because the climatic conditions in the Miocene of the region are supposed to be at least as appropriate for thermophilic taxa as those in the rest of Europe, their absence is best explained by a sampling bias or by potential geographical barriers (see Paleobiogeography section). As explained in Annex I, *Blanus* was widely distributed throughout Europe during the Miocene, but subsequent periods of lower temperatures showed a progressive reduction of its range, until it became restricted to Mediterranean shores in the Pliocene. Note however, that the presence of two different clades at that time (Annex I), could be indicating some kind of barrier between them. The presence of *Varanus* is again indicative of high temperatures, and the genus only disappeared from Europe (and from the Iberian Peninsula) during the cooler periods of the Quaternary.

11.3.2. Ecomorphological diversity

Squamates are currently not only taxonomically diverse, but also widely distributed and adapted to a wide range of habitats and diets. Admittedly, the typical lizard is rather unspecialised, being a small, insectivorous, quadrupedal runner (e.g. lacertids). However, there are many examples of specialisation, mainly regarding the mode of locomotion and adaptations of dentition to different diets.

The earliest squamates were probably tetrapodal, terrestrial and insectivorous, like most living lizards (Evans, 2003). However, some taxa modified this body plan in order to invade different niches. We know from fossils that Mesozoic lizards were already ecomorphologically diverse (Evans, 2003). Adaptations to different diets and modes of locomotion are the most easily observable in the fossil record, because they affect the skull (including dentition) and skeleton, respectively. This information is more complete in the few lithographic limestone localities that provide a significant number of rather complete specimens (e.g. Las Hoyas and La Pedrera de Meià; Chapters 5, 6 and 7).

Limb reduction and limb loss are locomotive adaptations that have appeared multiple times among lizards. Fossorial adaptations have been proposed for some Mesozoic forms, including the Jurassic genus *Saurillodon* (Kosma, 2004) found in the Iberian Peninsula, although articulated specimens showing the relative length of the limbs are not known. The recently described Early Cretaceous Iberian taxon *Jucaraseps* has been interpreted as a sand-swimmer on the basis of its small size, long body, long tail and reduced limbs (Chapter 7). Later, in the Eocene, the Iberian (and French) fossorial or semifossorial *Pyrenasaurus*, adds to the truly fossorial amphisbaenians (Chapter 8) of the same locality. The basis for interpreting *Pyrenasaurus* as fossorial or semifossorial is the shape of the dentary, as well as the low tooth count (Chapter 9). Limb reduction is present in extant Iberian scincids (e.g. *Chalcides*), but it has not been possible to confirm in fossil forms, which are mainly represented by tooth-bearing bones (Chapter 8). Limb loss is the main trend among amphisbaenians and anguines, and, although complete specimens showing the lack of limbs are not known among Iberian fossils, it can be inferred that blanid, *Ophisaurus* and *Pseudopus* representatives were limbless or at least lacked functional limbs.

The earliest Iberian gekkotans appear relatively late, in the form of indeterminate gekkotans found at Sossís (Chapter, 8) and are the classical example of climbers. There is at least one additional taxon of non-gekkotan lizard, the Early Cretaceous Iberian genus *Scandensia*, which was clearly adapted for a scansorial lifestyle (Chapter 6). This lizard had long recurved penultimate phalanges for climbing and broad ribs that may have been an adaptation for flattening down on to a surface, as in some recent lizards (Evans and Barbadillo, 1998a; Chapter 6). The observed combination of characters is suggestive of a climber on tree trunks or rocks (Chapter 6).

Some of the most extreme specializations are seen in lizards adapted, or partially adapted to life in marine environment, like aigialosaurs and related forms (e.g. Caldwell, 2001). In the Iberian Peninsula, varanoids are represented by an Early Cretaceous terrestrial non-pythonomorph, *Arcanosaurus*, and a Late Cretaceous amphibious or terrestrial pythonomorph (Houssaye et al., 2013a, b), which probably represent intermediate stages in an adaptation for fully aquatic life. Mosasaurs, as marine forms, were not included in this thesis, but are also present in the Iberian fossil record (e.g. Bardet and Pereda-Suberbiola, 1996) and were adapted to live their entire lives in open waters, extending the range of locomotor adaptations in Iberian lizards.

The teeth of basal lepidosaurs were conical with a small degree of apical faceting or striation, but alterations to this pattern occur within many living and fossil groups (Evans, 2003). An Iberian form from Lo Hueco (Late Cretaceous, Spain) has derived multicuspid crowns ("leaf-shaped") suggestive of an herbivorous diet (Narváez and Ortega, 2010). Simple, bicuspid or tricuspid teeth are characteristic of insectivores, and some omnivores. Teeth of this kind were common among Mesozoic Iberian lizards (straight unicuspid: paramacellodids, *Scandensia*, *Hoyalacerta*, *Jucaraseps*; bicuspid: *Meyasaurus*, *Pedrerasaurus*; tricuspid: pleurodont iguanids; Chapters 5 and 7). Again, the Eocene and Miocene assemblages are dominated by forms suggestive of insectivory or omnivory, with straight unicuspid (e.g. gekkotans, scincids), bicuspid (lacertids) and tricuspid (pleurodont iguanians) teeth (Chapter 8). The dentition of the new taxon *Pyrenasaurus* is highly characteristic, with anterior teeth presenting a scincoid appearance, and posterior teeth labiolingually compressed, with a characteristic deflection in the convexity of the posterior and anterior (less developed) shafts close to the tip (Chapter 9). The peculiar posterior dentition of *Pyrenasaurus* probably reflects adaptation to a given kind of food, maybe some kind of insect (Chapter 9). The dentition of Iberian Eocene amphisbaenians (Chapter 8) is unknown, but if they are related to blanids, also represented from the Miocene onwards (Annex I), they were most probably insectivorous. Clearly carnivorous lizards also appeared early among Iberian lizards (Chapter 5) as shown by the large and slightly recurved or fang-like teeth of *Parviraptor* (Middle Jurassic-Early Cretaceous: Evans, 1994) and *Dorsetisaurus* (Late Jurassic-Early Cretaceous: Hoffstetter, 1967). The dentition of the Cretaceous Iberian varanoids *Arcanosaurus* and the Late Cretaceous pythonomorph from Lo Hueco is unknown (they are only represented by vertebrae), but their large size and the fact that platynotans are ususally carnivorous, point to this kind of diet. The adaptations for carnivory of the Miocene-Pliocene *Varanus* and *Ophisaurus* are clearer because the characteristic trenchant dentition is well known. Durophagy, a dietary adaptation that allows the inclusion of hard-shelled items in the diet, is characterized by the presence of blunt teeth at least at the back of the dentary. This trait appears relatively late among Iberian terrestrial lizards, with the amblyodont form from the late Eocene of Sossís described in Chapter 8, which shows a level of amblyodonty that approaches that of the roughly contemporaneous French *Dracaenosaurus*. The Miocene representatives of the amblyodont *Pseudopus* (e.g. Crusafont and Villata, 1952; Bolet et al., 2013b) probably preyed on invertebrates and small vertebrates, as does the extant *Pseudopus apodus*.

Iberian fossil squamates are known to have occupied a wide range of trophic levels since as early as the Late Jurassic, ranging from primary consumers to top-predators. The presence of fish remains in the gut contents of a *Meyasaurus* specimen from La Pedrera de Meià (Hoffstetter, 1965) is an early example of vertebrate predation by lizards, and, as explained above, the recurved and trenchant teeth of the earlier *Parviraptor* and *Dorsetisaurus* suggest they were carnivorous. The size range of fossil squamates was greater than it is today. Mosasaurs, were the largest squamates ever (*Mosasaurus, Hainosaurus* and *Tylosaurus*, with lengths of more than 15 meters) although Iberian forms were probably slightly smaller. The smallest living lizards have a SVL of only 16mm (*Sphaeradactylus*, Hedges and Thomas, 2001). No fossil lizard of this size is known, but the Early Cretaceous sand-swimmer *Jucaraseps* comes close, and could have been prey of other vertebrates and even of large invertebrates (Chapter

7). Even if there existed smaller Mesozoic lizards, the probability of finding them in the fossil record is low because of a preservational bias. The Eocene *Pyrenasaurus* is also a miniaturized lizard that probably occupied a low level in the trophic chain of the Sossís assemblage (Chapter 9). In the Miocene, lizard assemblages were composed of a majority of small insectivorous taxa (e.g. gekkotans, lacertids, scincids) accompanied by a few predators like *Varanus* and, to a lesser degree *Ophisaurus* and *Pseudopus* (Chapter 10; Bolet et al., 2013b).

The study of Iberian lizard assemblages confirm that lizards essentially occupied the same niches after the K/Pg boundary, in strong contrast to mammals, which occupied the niches that other vertebrates left empty (e.g. Longrich et al., 2013).

GENERAL CONCLUSIONS

12

12. General conclusions

12.1. Conclusions

Iberian fossil lizard assemblages have undergone many changes in their composition through time, mostly linked to paleogeographical and mass extinction events, as well as incursions from neighbour areas. Late Jurassic assemblages were composed of the stem-'scleroglossan' *Parviraptor* and crown lizards (stem-scincoid paramacellodids, possible scincoids, and anguimorphs) with a widespread distribution in Laurasia. Some of these forms (e.g. paramacellodids) persisted into the Early Cretaceous, but the apparent increase in endemic forms (including the newly described *Pedrerasaurus* and *Jucaraseps*) in the Iberian Peninsula suggest a certain degree of isolation, coinciding with a time when Europe is interpreted as having been an archipelago. Most of these Early Cretaceous Iberian lizards are difficult to allocate to modern groups and they tend to fall into basal positions in phylogenetic morphological analyses. However, whether this is the correct position for these taxa or an artefact of missing data is not known. They may have belonged to an earlier radiation of lizards that persisted in this and other islands (e.g. Pietraroia, Italy) as part of a relictual fauna, but this will need to be tested with further material. These early forms include a high ecomorphological diversity with examples of scansorial (*Scandensia*), cryptic surface or subsurface dwelling (*Jucaraseps*) and occasionally swimmer (*Meyasaurus*) lizards. The remaining taxa probably had a more generalized terrestrial lifestyle as suggested by the lack of locomotive specializations. Late Cretaceous Iberian lizard assemblages are different, and share no taxa with Early Cretaceous assemblages. The fragmentary nature of the recovered specimens hampers discussion, but most of them have been referred to modern groups such as Iguania, possible 'Scincomorpha', Anguidae, Varanoidea or Serpentes. The absence of Paleocene localities complicates evaluation of the role of the K/Pg event in molding Iberian Paleogene assemblages. In any case, none of the abundant Eocene forms is closely related to those of the Late Cretaceous. The high taxonomic diversity of Eocene lizard assemblages (gekkotans, pleurodont iguanians, agamids, scincids, cordyliforms, lacertids, anguines, glyptosaurines, platynotans and amphisbaenians) corresponds to a period of global warming. It has previously been suggested that the endemism of some mammal faunas in Central and Western Iberian Peninsula is linked to an isolation from Europe during the middle and late Eocene.

Lizard faunas from this region have not been yet studied, but the similarity between the Sossís lizard assemblage (the new miniaturized taxon *Pyrenasaurus* included) in northeastern Iberian Peninsula and those from France supports previous suggestions of direct faunal interchanges between basins situated at both sides of the Pyrenees. An eventual recognition of endemic lizards in the Western Iberian Bioprovince would agree with paleogeographic reconstructions where the Mediterraneum and Cantabric seas were connected, isolating the greatest part of the Iberian Peninsula, whereas the region where Sossís is situated would have remained in connection to the rest of Europe. From a paleonvironmental point of view, the late Eocene paleoherpetofauna from Sossís is indicative of mesic conditions (permanent water bodies) and high temperatures. Lizards from this assemblage are adapted to a variety of lifestyles, from burrowing (amphisbaenians) or at least semi-fossorial (e.g. *Pyrenasaurus*) habits, to strongly thermophilic taxa that needed direct exposure to the sun, and thus lived on the surface of rocks or on vegetation (e.g. iguanians, scincids, cordyliforms). The warm period known as PETM and/or IETEM allowed thermophilic taxa to reach Europe, most of them persisting until the Grande Coupure at the Eocene-Oligocene boundary. Iberian pleurodont iguanians and glyptosaurs are probably of North American origin, whereas cordyliforms (represented for the first time in the Eocene of Europe by highly diagnostic osteoderms at Sossís) probably have an African origin. Again, the lack of Oligocene assemblages makes it difficult to assess the effect of the Grande Coupure on the composition of Iberian lizard assemblages. However, Miocene assemblages already have a modern aspect, with gekkotans, lacertids, scincids, anguines, varanids and blanid amphisbaenians. The synonymization of the Miocene *Iberovaranus* with *Varanus* highlights that the Catalan material represents one of the earliest records of the latter in Europe, and confirms its widespread distribution across the continent. The material of *Blanus* described in this thesis provides the best proof of the presence of the genus in the European Miocene, and also provides evidence that an Eastern and a Western Mediterranean clades were already different by the Middle-Late Miocene. The main differences between the Miocene assemblages and the present fauna of the Iberian Peninsula are the absence of the most thermophilic taxa (e.g. agamids, varanines, cordyliforms), clearly resulting from the relatively lower present temperatures and drier conditions. Some of the remaining taxa have a wide distribution across Europe (e.g. anguines, lacertids), whereas others (e.g. *Blanus*, scincids, gekkotans) represent relicts resulting from a southwards retraction related to Quaternary glaciations.

12.2. Summary statements

1. Knowledge of the fossil record of lizards from the Iberian Península (Mesozoic and Tertiary) is revised and expanded through the description of new material from the Early Cretaceous-Miocene interval. Paleobiogeographical and paleoecological implications of these additions are discussed.

2. A new genus and species, *Pedrerasaurus latifrontalis*, from the Early Cretaceous of Catalonia is erected and described. This species is possibly but not definitively related to *Meyasaurus*, a lizard that is widespread in the Early Cretaceous of the Iberian Peninsula, and adds to the known diversity of the classical locality of La Pedrera de Meià.

3. New material of the Early Cretaceous genus *Scandensia* from Las Hoyas is described. This new articulated specimen has allowed a refinement of its phylogenetic position, and confirms and expands previous interpretations on its lifestyle through additional morphological data.

4. A new genus and species, *Jucaraseps grandipes*, from the Early Cretaceous of Las Hoyas is erected and described. This form stands out as being one of the smallest fossil lizards ever described. This, in combination with the possible fossorial or semi-fossorial habits of this short-legged form, add to the diversity of paleoecological niches recorded at Las Hoyas. *Jucaraseps* also adds to the apparent endemicity of Iberian Early Cretaceous lizard assemblages.

5. A diverse late Eocene assemblage from Catalonia is described. For many taxa, it contains the first record in the Spanish Eocene (pleurodont iguanians, gekkotans, lacertids, cordyliforms, ?scincids, glyptosaurines, anguines and amphisbaenians), as well as representing the only late Eocene lizard assemblage known from Southern Europe. Comparisons with contemporaneous French localities demonstrate a strong resemblance, supporting previous paleobiogeographical hypotheses based on mammals.

6. A new genus and species, *Pyrenasaurus evansae*, from the French locality of Escamps and the Catalan locality of Sossís is erected and described. This small lizard is highly diagnostic and its presence on both sides of the Pyrenees demonstrates the similarity between French and Catalan late Eocene assemblages. The supposed endemicity of the Western Iberian Bioprovince, however, remains to be tested on

lizards because material has yet to be described from Western assemblages.

7. The varanine genus *Iberovaranus* Hoffstetter, 1969 is synonymized with *Varanus* Merrem, 1820. The species *Iberovaranus catalaunicus* is considered a nomen dubium. The material from Catalan localities in the Vallès-Penedès Basin provides one of the earliest records (?MN3) of *Varanus* in Europe.
8. A new species of *Blanus* (Amphisbaenia, Blanidae) is described. It is based on the most informative fossil specimen of a blanid ever found, and it represents the first opportunity to evaluate the relationships of a fossil blanid in relation to extant taxa.

12.3. Future directions

The particularities of the Iberian fossil record in terms of the exceptional preservation, its wide geographical and temporal distribution, and a priviliged geographical situation, all multiply the possibilities of investigation beyond the simple identification of affinities of the recorded taxa. Paleobiogeographical and paleonvironmental conclusions are expected to move forward as our knowledge of the fossil record increases. This will be continued in future years through the description of new material from new and classical localities, and through the application of updated techniques that are expected to improve results. Among these techniques, combined phylogenetic analyses are expected to provide better supported trees, recovering the basic scheme of molecular trees and an accurate position for early fossil taxa. The application of CT-scans to new and previously described specimens will yield important information that would have been unreachable before. Moreover, the refinement in the identification of material, mainly at the species level, should have a great impact on the related paleobiogeographical and paleoecological information by providing better supported hypotheses. The results provided by the analysis of lizard assemblages should also be integrated into broader studies of paleoherpetofauna and, if possible, including the complete composition of assemblages.

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ANNEX I

Taxonomic disclaimer

The name of the new taxon described in Annex I is not valid under the rules of the International Code of Zoological Nomenclature. The publication where it will be formally erected is in process of review, and the name proposed here will be retained if possible.

An amphisbaenian skull from the European Miocene and the evolution of Mediterranean worm lizards

Short title: The first amphisbaenian fossil skull from Europe

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Keywords: Squamata, Amphisbaenia, Blanidae, *Blanus*, Iberian Peninsula, taxonomy

Abstract

The evolution of blanid amphisbaenians (Mediterranean worm lizards) is mainly inferred based on molecular studies, despite their fossils are common in Cenozoic European localities. This is because the fossil record exclusively consists in isolated elements of limited taxonomic value. We describe the only known fossil amphisbaenian skull from Europe—attributed to *Blanus mendezi* sp. nov. (Amphisbaenia, Blanidae)—which represents the most informative fossil blanid material ever described. This specimen, from the Middle Miocene of Abocador de Can Mata (11.6 Ma, MN7+8) in the Vallès-Penedès Basin (Catalonia, NE Iberian Peninsula), unambiguously asserts the presence of *Blanus* in the Miocene of Europe. This reinforces the referral to this genus of the previously-known, much more incomplete and poorly-diagnostic material from other localities of the European Neogene. Our analysis—integrating the available molecular, paleontological and biogeographic data—suggests that the new species postdates the divergence between the two main (Eastern and Western Mediterranean) extant clades of blanids, and probably precedes the split between the Iberian and North-Western African subclades. This supports previous paleobiogeographic scenarios for blanid evolution and provides a significant minimum divergence time for calibrating molecular analyses of blanid phylogeny.

Significance Statement

We describe a new species of *Blanus* based on the first known fossil skull of a Mediterranean worm lizard, recovered from the Iberian Miocene. The cranium and lower jaw of this blanid amphisbaenian are both exceptionally well preserved, but covered with a calcitic crust that obscures their morphology. We performed a CT-scan that granted access to the external and internal morphology of the specimen, allowing a detailed description of the skull bones. Based on this exceptional fossil, we critically review the evolutionary history of blanids from a phylogenetic, chronologic and paleobiogeographic viewpoints. The specimen represents a milestone for understanding the evolution of the group and further provides a significant calibration point for molecular phylogenetic studies.

Introduction

Amphisbaenians (worm lizards) constitute a poorly understood clade of burrowing and usually completely limbless squamates (1, 2). Both molecular (3–8) and paleontological (9) data currently indicate that amphisbaenians are the sister-taxon of lacertids, so that the former's limbless condition evolved independently from snakes. Amphisbaenians and lacertids probably diverged during the Late Cretaceous (9), although worm lizards are only undoubtedly recorded from the Paleogene onwards (10). Among the 150-190 species of extant amphisbaenians (2, 11), most of them inhabit the southern continents (Afro-Arabia and South America), and only a few species are distributed in the Mediterranean region. Apart from *Trogonophis wiegmanni* (Trogonophidae), all extant Mediterranean amphisbaenians are included in the genus *Blanus* —previously allocated to the Amphisbaenidae, but currently included into a more basal family of their own, the Blanidae, both on the basis of molecular and morphologic evidence (2, 8, 12, 13).

The divergence of the various amphibaenians extant clades has been mainly related to vicariance events (5). Intercontinental oceanic dispersal events might have also occurred, as indicated by the purported sister-taxon relationship between the Mediterranean Blanidae and the Caribbean Cadeidae (5), although more recent results indicate that such relationship is uncertain (8). With regard to Mediterranean worm lizards, molecular data consistently distinguish three extant clades of current disjunct distribution (14): an Eastern Mediterranean clade (*Blanus strauchi*) (15); an Iberian one (*Blanus cinereus*, and possibly the recently described cryptic species *Blanus mariae*—but see ref. (16); and a North-Western African one (*Blanus mettetali* and *Blanus tingitanus*). Molecular evidence indicates that Iberian and North-Western African clades are more closely related to each other, with the Eastern Mediterranean clade having diverged first (12). Molecular estimates of the divergence time among clades is mainly based on paleobiogeographic assumptions (12), due to the restricted information provided by the European fossil record of amphisbaenians, in spite of its relative abundance throughout the European Cenozoic (17).

The fossorial adaptations of amphisbaenians (2) are reflected in their cranial and postcranial osteology, thus facilitating their recognition in the fossil record, even if only disarticulated material is available. In Europe, the presence of a single family (Blanidae), at least regarding the Neogene, enables an easy identification at least at this level. Most findings consist in vertebrae or, more rarely, isolated tooth-bearing skull bones. The former, given the uniformity in postcranial anatomy of amphisbaenians (18), do not enable an attribution below the family level; the latter, in turn, display a rather uniform morphology across the European fossil record and only provide restricted taxonomic information. Such a morphologic homogeneity, coupled with the high intraspecific variability inferred from some extant species, hinders the identification at the species level of most isolated fossil remains. The much more informative, but tiny and fragile, skulls of amphisbaenians are only rarely preserved. Thus, although some crania are known from the Cenozoic of North America (19–23) and Africa (24), in Europe a single cranial specimen from a putative stem amphisbaenian is known from the Eocene (9). This preservational bias explains why, for extinct blanids, only three species of two different genera are currently recognized (on the basis of lower jaws): *Palaeoblanus tobieni*, from MP27-MN13 of France, Germany, Italy and Spain (25–27); *Blanus antiquus*, from the MN3-MN6 of Austria and Germany (28); and *Blanus gracilis*, from the MN2-MN4 of the Czech Republic and Italy (and, with doubts, from the MN7+8 of Romania) (29–31).

Here we describe a new species of *Blanus*, based on an exceptionally preserved, complete skull and numerous vertebrae from a single Middle Miocene locality of the Vallès-Penedès Basin (NE Iberian Peninsula). The described cranial specimen, which represents the first fossil blanid skull thus far described, sheds new light on the evolution of Mediterranean worm lizards.

Results

Age and geological background. The described fossil remains come from locality ACM/C8-A4 in the Abocador de Can Mata (ACM) local stratigraphic series (32–34), which is situated in els Hostalets de Pierola (Vallès-Penedès Basin, NE Iberian Peninsula). Based on litho- and magnetostratigraphic data, ACM/C8-A4 is correlated to chron C5r.2n, with an interpolated estimated age of 11.6 Ma (MN7+8, late Aragonian, around the Middle/Late Miocene boundary). See supporting information (*SI Text*) for further details.

Systematic Paleontology. Order Squamata Oppel, 1811; Suborder Amphisbaenia Gray, 1844; Family Blanidae Kearney, 2003; Genus *Blanus* Wagler, 1830; *Blanus mendezi* sp. nov. Holotype: IPS60464, complete skull (cranium with articulated lower jaw; Figs. 1–3, Fig. S1 and Video S1), housed at the ICP. Paratypes: IPS63989, four cervical vertebrae in anatomical connection (Fig. S2*A–D*); IPS63990, trunk vertebra (Fig. S2*E–I*); IPS63991, trunk vertebra (Fig. S2*J–N*); IPS63992, trunk vertebra (Fig. S2*O–S*); IPS63993, trunk vertebra (Fig. S2*T–X*); IPS63995, 40 trunk vertebrae. Type locality: ACM/C8-A4, 11.6 Ma (Middle Miocene), Catalonia, Spain. Etymology: dedicated to ICP technician Josep M. Méndez, who found the holotype while carefully picking up microvertebrate remains.

Diagnosis. Large-sized species of *Blanus* with a slightly protruding snout. Dentition heterodont, with robust pleurodont teeth (seven premaxillary, five maxillary, eight dentary), the first dentary tooth being smaller than the third one. Tooth-bearing bones robust. Nasal process of the premaxilla long. Frontals long relative to the skull, with an almost straight suture between them, and a well-developed facet for articulation with the maxilla and the prefrontal; frontoparietal suture strongly interdigitated. Long, acuminated and medially-directed orbital process present in the maxilla. Premaxilla anteriorly (not ventrally) projected. Cervical and anterior trunk vertebrae with paracotylar tubercles.

Differential diagnosis. Regarding extinct taxa, the new species differs from *B. antiquus* in the larger size and more heterodont dentition (greater variability in the height and robustness of the teeth); and from *B. gracilis*, in the much larger size, the more robust tooth-bearing bones and teeth, and the more closely packed teeth. The new species also differs from all extant *Blanus* spp. in the larger size and—as far as it can be ascertained for those species for which cranial osteology is known (*B. cinereus* and *B. strauchi*)—in the longer nasal process of the premaxilla, the relatively longer frontals compared to the rest of the skull, the more straighter suture between the frontals, the more developed frontal articular facet for the maxilla and prefrontal, and the presence of a longer and posterodorsally directed maxillary orbital process. Additionally, the new species further differs from *B. strauchi* in the less protruding snout lacking a ventrally-projected proximal tip of the premaxilla, as well as in the stouter teeth; and from both *B. cinereus* and *B. strauchi*, in the stronger interdigitation of the frontoparietal suture. The paracotylar tubercles of the cervical and trunk vertebrae are unknown in the rest of *Blanus* spp., but a similar structure might be present in *B. gracilis*.

Description and comparisons. IPS60464 is an almost complete skull (11.3 mm in length) that includes the right lower jaw in articulation (Fig. 1 and Fig. S1). The specimen is exceptionally well preserved, including all unpaired elements, whereas all paired bones are represented at least in one side (Figs. 1 and 2). The skull is however covered by a carbonate concretion that obscures most of its external morphology. It also displays a matrix infilling that precludes the observation of the palate, the inner surfaces of the skull roof and the lingual surfaces of the lower jaw. The small size and fragility of the specimen precluded mechanical preparation, so its description is based on computed tomography (CT) scans. The latter not only revealed the external morphology, but further granted access to the internal cranial morphology (otherwise unobservable), thereby enabling the description of isolated bones and their joint surfaces. A succinct description of the skull and vertebrae (Fig. 1 and Fig. S2) is provided below, followed by comparisons with fossil and extinct blanids (see *SI Text* for a more detailed description and details on the comparative sample). Both skull and vertebral measurements are reported in Table S1.

IPS60464 bears seven premaxillary (Fig. 2*C*), five maxillary (Fig. 2*D*) and eight dentary (Figs. 1 and 3*A*) pleurodont teeth; the first dentary tooth is smaller than the third one, as in other species of *Blanus*. The teeth are robust (comparable to *B. cinereus*, *B. antiquus* and *P. tobieni*), contrasting with the much more slender dentition of *B. gracilis* and *B. strauchi* (Fig. 4). The premaxilla bears a very long, apically truncated nasal process (Fig. 2*A–C*), and the snout is only weakly protruding—similar to that of *B. cinereus* (Fig. S3*T*) and fossil forms, but contrasting with the more clearly protruding snout with a ventrally-directed premaxilla of *B. strauchi* (Fig. S3*U*). The frontals are relatively long (3.1 mm) and roughly rectangular (Fig. 2*R–U*), with an almost straight suture between them and a strong interdigitation with the parietal (Fig. 1*A*). The nasals are short relative to the frontals (Fig. 1*A*). The maxilla has a medially directed rostral process (Figs. 1*B* and 2*F*) and an unusually long and pointed orbital process (Fig. 2*D–G*). The prefrontal is present and well developed (Figs. 1*A* and *B*, and 2*V* and *W*), precluding the contact between the maxilla and frontal except in the anterior lateral margin of the latter (Fig. 1*A*). Elements of the palate (Fig. 2*J–Q*) are observable, but at present provide little taxonomic information because their morphology in other taxa is barely known. The parietal (Figs. 1*A–C* and 2*X–Z*) is by far the largest bone of the skull; although its limits with the otic-occipital complex (Figs. 1*B* and 2*Y* and *Z*) are clear in some regions, we were unable to completely separate them, probably due to partial fusion. The cranial proportions of IPS60464 roughly fit those reported for extant species—only described for *B. cinereus* and *B. strauchi* (35, 36)—except for the relatively shorter preorbital region displayed by the fossil specimen (ca. 25%, in front of 30% in the two morphotypes of *B. cinereus*, see Fig. S4). The quadrate (Figs. 1, and 2*AA* and *AB*) is rather robust. The cranium of the new species (length, 11.3 mm; width, 5.8 mm) is larger (ca. 25% longer) than that of all extant blanids (37). The comparison of the dimensions of isolated tooth-bearing bones also indicate for *B. mendezi* a slightly larger size than for *B. antiquus* and *P. tobieni*, and a much larger size than for *B. gracilis* (Fig. 4).

The lower jaw (Fig. 1*B* and 3*A–D*) displays the typical blanid configuration (2); the dentary (Fig. 3*E*), due to its heterodonty (Fig. 4), is clearly distinct from those of both *Palaeoblanus tobieni* and *Blanus antiquus*, which display a homodont dentition (see figures in refs. 28, 38) mainly regarding tooth height and robustnes. The dentary of IPS60464 is much larger than those of *B. gracilis*, *B. strauchi* and *B. cinereus*, but only slightly larger than those of *B. antiquus* and *P. tobieni* (Fig. 4).

Both the neck and anterior trunk vertebrae (Fig. S2) show the typical amphisbaenian morphology (i.e., dorsoventrally flattened and without neural spine) (e.g. 39). They are however further characterized by the presence of paracotylar turbercles, which are unknown from other *Blanus* spp. The largest vertebrae of the new species, in agreement with skull size, are slightly larger than the largest Neogene *Blanus* vertebrae reported so far (38), also much larger than those of extant species—at least regarding *B. cinereus* and *B. strauchi* (AB pers. obs.), since these are unknown for *B. mettetali* or *B. tingitanus*, although these two species are reported to be smaller than *B. cinereus* (40).

Discussion

***Blanus mendezi* sp. nov.** The described skull, IPS60464, represents the most informative blanid fossil material ever described. Both the general configuration of the skull and the dental morphology of IPS60464 are in accordance with those of extant blanids, represented by the single extant genus *Blanus*. Similarities include: the tooth count (premaxilla: seven; maxilla: five; dentary: eight); the morphology, proportions and arrangement of skull bones (see *SI Text*); and the shape and arrangement of the sutures—for a description of the cranial osteology of *B. cinereus* and *B. strauchi*, see ref. (36) and *SI Text*. Truncated nasals such as those displayed by IPS60464 (Fig. 2*H*,*I*) are the only diagnostic cranial features of blanids reported in the literature (2). This character is unknown for fossil purported blanids, so that the ascription of isolated fossil material to this family has been mostly based on its overall similarity with the extant species of *Blanus.* Despite a recognized similarity to the genus *Blanus*, *Palaeoblanus* has not been formally referred to Blanidae—it was not mentioned in the erection of the family (2), and it was referred to the Amphisbaenidae by other authors (25, 26, 41). In contrast, we refer *Palaeoblanus* to the Blanidae on the basis of dentary morphologic similarities. IPS60464 differs from the extinct *Palaeoblanus* in lacking an enlarged first dentary tooth, and in displaying a heterodont and pointed dentition as well as a marked angle at the symphyseal level. These features allow an unambiguous attribution to the extant genus *Blanus*. IPS60464 therefore unambiguously confirms the presence of this genus in the European Miocene.

Moreover, as stated in the differential diagnosis above, the described cranial material differs from the two previously-described extinct species of this genus (*B. antiquus* and *B. gracilis*)—known from somewhat older localities (28, 29)—and also from extant *Blanus* spp. Besides the larger size of the former, differences include several dentognathic and/or cranial features (skull proportions, the shape of some sutures, and various morphologic details of the premaxilla, maxilla, frontals, nasals and dentary), thereby requiring the erection of the new species, *Blanus mendezi* sp. nov. (see diagnosis above and *SI Text*). A more detailed evaluation of the taxonomic status of previously-known fossil blanid species is precluded by their incomplete preservation. Thus, whereas tooth-bearing bones easily allow the discrimination between the monotypic genus *Paleoblanus* and *Blanus* spp., differences in this regard among *Blanus* species are subtler. Accordingly, the taxonomic status of both *B. antiquus* and *B. gracilis* should be subject to further scrutiny when more complete (cranial) remains become available, although they can be distinguished from *B. mendezi* on the basis of available evidence. With regard to extant species of this genus, a more detailed diagnosis of *B. mendezi* is also precluded—not by the morphology preserved in the holotype of the new species, but rather by the partial current knowledge on the osteology of living taxa. Thus, although the cranial morphology of extant amphisbaenians has been reported in several studies (42, 43), only that of *B. cinereus* and *B. strauchi* among extant blanids have been described in some detail (36). In spite of this fact, the material described here sheds new light in the evolution of

Mediterranean worm lizards from both a phylogenetic and a paleobiogeographic viewpoints.

Paleobiogeography and phylogeny. The extensive similarities in cranial morphology between *B. mendezi* and extant Mediterranean worm lizards indicate that the genus *Blanus* is not only conservative regarding the tooth-bearing bones and vertebrae—as shown by the identification of *Blanus*-like forms already in the Eocene (10)—but also regarding the rest of skull bones and lower jaw. Contrasting with its present disjunct and restricted, almost relictual distribution (15, 44), the genus *Blanus* was much more widely distributed across Europe in the past. The oldest report of this genus dates back to the Late Eocene of England (17, 45), although it is based on very fragmentary remains that do not allow an unambiguous attribution to *Blanus* (10, 38). The amphisbaenian Paleogene European record has recently improved (10), so that when better known it might shed further light on the initial steps of blanid evolution. Meanwhile, IPS60464 provides key information for discussing the more recent evolution of this family.

Blanus was widely distributed in Europe during the Miocene, subsequently showing a progressive reduction of its range, until it became restricted to the Mediterranean shores in the Pliocene (17). In the tree depicted in Fig. 4 we synthesize currently available evidence for blanid evolution based on molecular, paleontological and biogeographic data. Blanids would have diverged from other amphisbaenians before 25 Ma (12, 37), and possibly much earlier if at least some of the Eocene forms belong to the family (10). *Palaeoblanus* displays homodont dentaries, with blunt, large and robust cusps, and also bears a characteristic enlarged first tooth and a rounded symphysis. Among these features, the first enlarged tooth, the blunt cusps and the rounded symphysis characterize *Palaeoblanus* alone, whereas homodonty, large size and robustness are characters shared with *Blanus antiquus*. According to our phylogenetic hypothesis, the non-enlarged first tooth, the pointed crowns, and the well-marked symphyseal angle would be synapomorphies of the *Blanus* clade. All the species of this genus, to the exception of *B. antiquus*, further share a marked heterodonty in their dentaries, best expressed by the evident size reduction of the fourth tooth. Among these species, the Western clade is characterized by the robustness of its dentitions and dentaries, whereas the Eastern clade possesses much slenderer dentaries with well-spaced, gracile teeth.

The Eastern clade is formed by the extinct *B. gracilis* and the extant *B. strauchi*.

Dentaries in both forms can be barely differentiated, but the premaxilla of *B. strauchi* is easily distinguished from that of *B. gracilis* (and from all other species for which this bone is known) because of its ventrally projected proximal tip. The Western clade, in turn, is constituted by the large and robust fossil form *B. mendezi*, together with four extant species that, according to molecular analyses, can be further divided into an Iberian clade (*B. cinereus* + *B. mariae*) and a North-Western African clade (*B. mettetali* + *B. tingitanus*). Many morphologic skull characters distinguish *B. mendezi* from *B. cinereus* (see Differential Diagnosis above, and *SI Text*). However, given that the morphology of the remaining members of the Western clade is barely known, it is difficult to discern whether the features of *B. mendezi* characterize it in front of the rest of the Western clade, or merely in front of part of its members (e.g., the Iberian clade). However, all of the Western members share a much smaller size (see *SI Text*), and reported external morphologic differences from *B. cinereus* are minimal (*B. tingitanus*, *B. mettetali* and *B. mariae* were formerly included in *B. cinereus*). Therefore, we consider it more likely that the species of this clade diverged late, most probably well after the split of *B. mendezi*. This interpretation also fits well with the scenario proposed in ref. (12), in which the divergence between the Eastern and Western Mediterranean clades would have occurred 8-9 Ma due to the opening of the Betic corridor. Alternatively, if a strict Iberian clade (with *B. cinereus* + *B. mariae* + *B. mendezi*) was recognized in the future based on morphologic evidence, then the minimum divergence date between the Iberian and African clades should be moved backwards from 8-9 Ma (12) to at least 11.6 Ma.

The geographic and temporal distribution of fossil worm lizards is congruent with the phylogenetic relationships proposed in Fig. 4 for the Blanidae. *Palaeoblanus* and *B. antiquus* have the oldest records, and are widespread in Central and Western Europe. Given that the late Paleogene and early Neogene record in Eastern Europe is quite poor, it cannot be discounted that their distribution actually reached Eastern Europe (where the records would be lacking due to a sampling artifact). The record of *B. gracilis* at Dolnice (MN4b, 14-16 Ma) would mark the minimum divergence time between the Eastern and Western clades. The long ghost lineage of *B. strauchi* could be easily explained by the poor fossil record from the Neogene of Eastern-most Europe. The Middle Miocene age of *B. mendezi* and the slightly older age of *B. gracilis* are both congruent with molecular estimates of the divergence time between *B. strauchi* and Western *Blanus* to the Early Miocene (16.5 Ma). However, this is not a maximum divergence time—contra ref. (12)—but a minimum one. It has been proposed that the divergence between the Western and Eastern Mediterranean clades would have been caused by an extinction of the Central European populations (15), so that the split between these two clades could not be older than the youngest Central European record, i.e., Middle Miocene (12). However, this is contradicted by the fact that *B. antiquus*, from Central Europe, is contemporaneous with *B. gracilis*, which is a member of the Eastern Mediterranean clade (Fig. 4). This fact indicates that the divergence between the Western and Eastern clades predates the youngest Central European record, so that their split would not be related to the extinction of Central European populations (which would have persisted afterwards).

After the divergence of the Iberian and North Western African subclades, the genus *Blanus* was much more widely distributed than nowadays throughout the circum-Mediterranean region (17)—being recorded from areas currently not inhabited by worm lizards. These areas include the Balkans, the Italian Peninsula and concomitant islands, where they survived until the Late Pleistocene (46, 47), as well as the Balearic Islands, which blanids probably reached during the Messinian Salinity Crisis by the latest Miocene (48). More complete (cranial) fossil remains of Late Miocene and Pliocene *Blanus*, in particular from those areas where they are currently absent, would be required to further test the molecular divergence times between the various species of the Western clade. *Blanus mendezi*, in any case, represents the oldest record of the Western Mediterranean clade, slightly postdating the oldest record of the Eastern Mediterranean clade. Unlike previously calibration points employed by molecular studies (12, 37), the evidence provided by *B. mendezi* is not based on paleobiogeographic assumptions, but on fossil evidence, thus being of greatest significance for further refining molecular phylogenetic studies in the future. Furthermore, *B. mendezi* will serve as a solid comparative reference for deciphering the internal phylogeny of the genus *Blanus* as well as their position among amphisbaenians and its most likely sister taxon—especially once the cranial osteology of the extant species of this genus is known in greater detail.

Materials and Methods

Computed tomography. IPS60464 was scanned on a GE phoenix v|tome|x s180 (GE Measurement & Control Solutions, Hanover, Germany) at the American Museum of

Natural History (AMNH) using a nanofocus X-ray tube with the following parameters: voltage 105 kV and current 70 mA and a magnification of 15.86723491. We obtained 1100 slices with slice thickness of 0.2 mm and a pixel size of 0.01260459 mm. The raw data were imported to VG Studio Max 2.1 and exported to Avizo 7.0 for analysis, segmentation, and visualization. We segmented each bone slide by slide and deleted the covering crust and the infilling matrix present in the original fossil by considering the different densities of bone, crust and sediment in Avizo 7.0.

Institutional abbreviations. AMNH, American Museum of Natural History (New York, USA); ICP, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona (Spain); IPS, acronym of the ICP collections.

Anatomical abbreviations. ap: articular process of dentary; apc: anterior process of coronoid; app: apical process of parietal; apc: anterior process of coronoid; appr: alar process of prootic; bps: basipterygoid process; cec: cephalic condyle of quadrate; chp: choanal process of vomer; chv: choanal vault; cp: cultriform process of parabasisphenoid; cop: coronoid process of coronoid; copd: coronoid process of dentary; dcr: dorsal crest of quadrate; dp: descending process of frontal; dlf: dentary labial foramina; dentary teeth; epm: ectopterygoid process of maxilla; epp: ectopterygoid process of palatine; fnpp: frontal facet for the nasal process of premaxilla; fpm: frontal process of maxilla; fpn: frontal process of nasal; fpp: frontal process of prefrontal; fps: frontoparietal suture; fvo: fenestra vomeronasalis; fvp: facet for palatine vomerine process; Gf: Gasserian foramen; gf: glenoid fossa; hf: hypoglossal foramen; is: intramandibular septum; lptp: lateral pterygoid process of ectopterygoid; mac: mandibular condyle of quadrate; mafa: ectopterygoid facet for the articulation of the ectopterygoid process of maxilla; map: median articular plane; Mc: Meckelian canal; mfo: maxilla labial foramina; mfp: maxillary facial process of nasal; mp: maxillary process of palatine; mpf: maxillary process of frontal; mpp: maxillary process of prefrontal; mrp: maxillary rostral process of nasal; mt: maxillary teeth; mptp: medial pterygoid process of ectopterygoid; mf: frontal facet for maxilla and prefrontal; nc: nasal chamber; np: nassal process of premaxilla; npk: nasal process of premaxilla keel; occ: occipital condyle; oocl: otic-occipital lapet; op: orbital process of maxilla, osp: orbitosphenoid process of frontal; pa: parietal; paf: frontal facet for parietal; pfa: facet of frontal for the nasal process of premaxilla; pbs: parabasisphenoid; pff: frontal facet for prefrontal; pfp: prefrontal process of maxilla; pmf: premaxilla foramina; pmp: premaxillary process of nasal; pmt: premaxillary teeth; pp: palatal process of premaxilla; ppc: posterior process of coronoid; ptfa: ectopterygoid facet for pterygoid; ptp: pterygoid process of palatine; pvp: posteroventral process of quadrate; qp: quadrate process of pterygoid; rp: retroarticular process; rpm: rostral process of maxilla; rpv: rostral process of vomer; saf: superior alveolar foramen; sap: surangular process; sbs: subdental shelf of dentary; ss: supradental shelf of maxilla; sy: symphysis; tp: transverse process of pterygoid; vf: vagus foramen; vlp/X: ventrolateral process/“element X”; vp: vomerine process of palatine.

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Figure legends

Fig. 1. *Blanus mendezi* sp. nov. Virtual model of the holotype (IPS60464) after removing the covering crust and the infilling matrix in (A) dorsal, (B) right lateral, (C) left lateral, (D) ventral and (E) anterior and (F) posterior views.

Fig. 2. Virtual model of selected skull bones of the holotype (IPS60464) of *Blanus mendezi* sp. nov. A-C, premaxilla in left lateral (A), dorsal (B), and ventral (C) views. D-G, right maxilla in labial (D), lingual (E), dorsal (F) and ventral (G) views. H, I, right nasal in dorsal (H) and ventral (I) views. J, K, right vomer in dorsal (J) and ventral (K) views. L, M, right palatine in dorsal (L) and ventral (M) views. N, O, right ectopterygoid in labial (N) and anterior (O) views. P, Q, right pterygoid in dorsal (P) and ventral (Q) views. R-U, right frontal in dorsal (R), ventral (S), lateral (T) and medial (U) views. V, W, right prefrontal in lateral (V) and medial (W) views. X-Z, Parietal/otic-occipital complex/parabasisphenoid in dorsal (X), right lateral (Y) and ventral (Z) views. AA, AB, left quadrate in lateral (AA) and medial (AB) views. Colors correspond to those in Fig. 1.

Fig. 3. Virtual model of the lower jaw of *Blanus mendezi* sp. nov., based on the holotype (IPS60464), after digitally removing the covering concretion and matrix. A-D, lower jaw, in lingual (A), labial (B), ventral (C) and dorsal (D) views. E, dentary in lingual view.

Fig. 4. Evolutionary tree of the Blanidae based on molecular phylogeny, paleobiogeographic evidence and the paleontological data discussed in this paper. Black branches depict the phylogeny and estimated divergence times for extant taxa based on molecular data (12, 37); grey branches, in turn, depict inferred stratigraphic ranges (dashed when uncertain) based on fossil finds and divergence times, as well as the hypothesized branching order for extinct species, based on morphology and biogeography. *Blanus cinereus* and *B. antiquus* redrawn from ref. (28); *B. gracilis* redrawn from ref. (29); *B. strauchi* redrawn from ref. (49); *Palaeoblanus tobieni* redrawn from ref. (38).

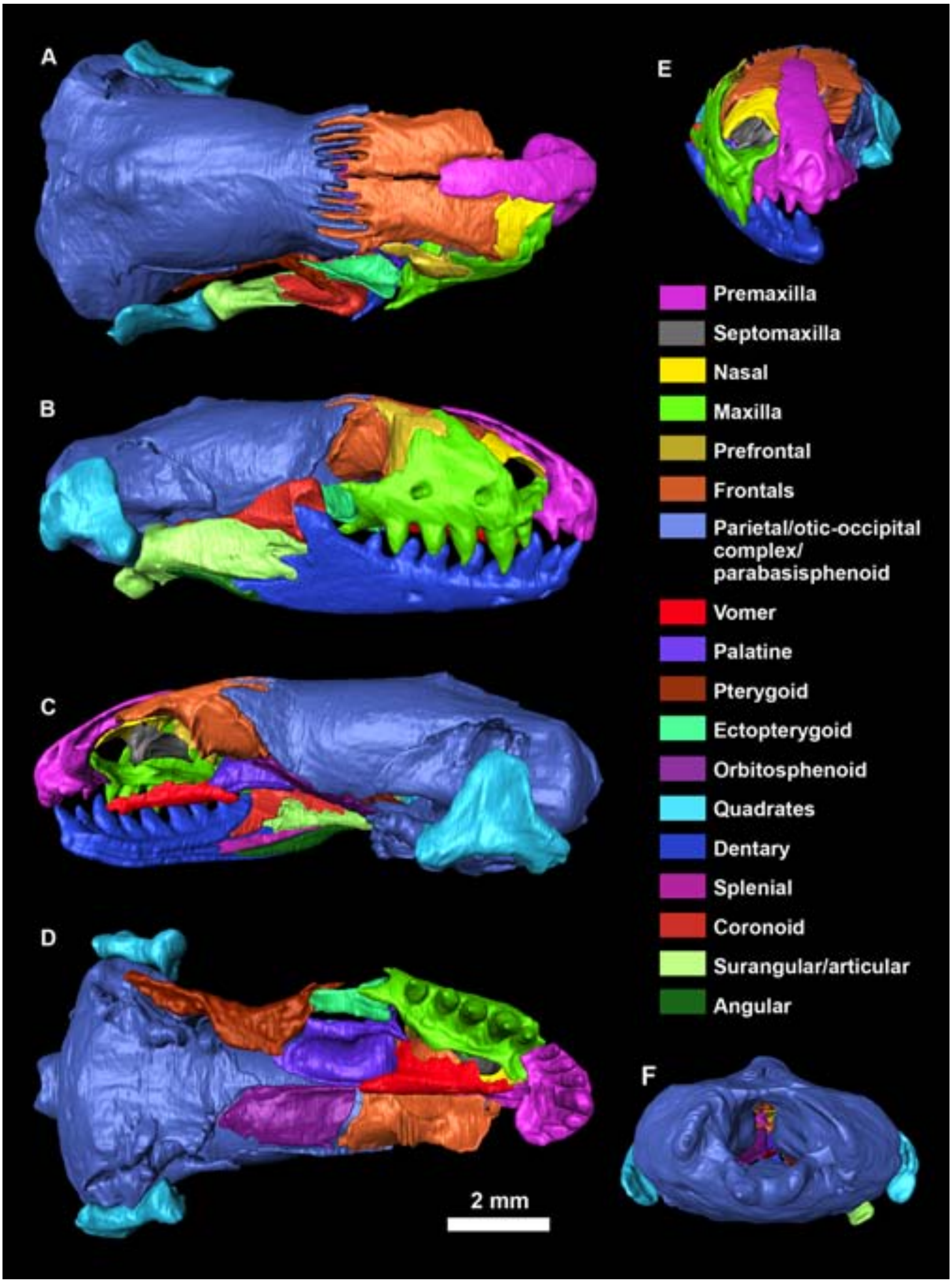
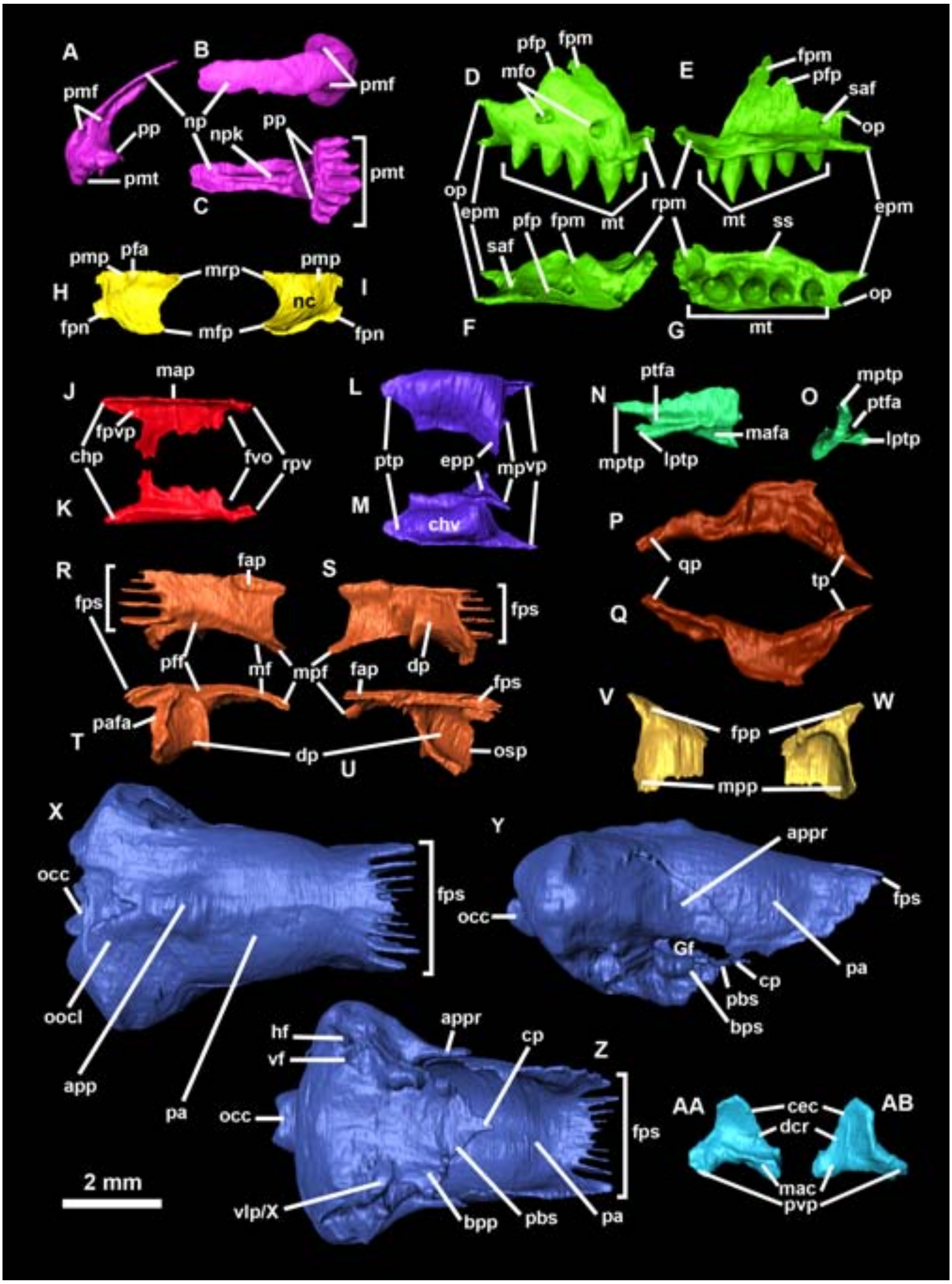

A
B
C
D
E
F
Premaxilla
Septomaxilla
Nasal
Maxilla
Prefrontal
Frontals
Parietal/otic-occipital complex/ parabasisphenoid
Vomer
Palatine
Pterygoid
Ectopterygoid
Orbitosphenoid
Quadrates
Dentary
Splenial
Coronoid
Surangular/articular
Angular
2 mm

Figure 1


A
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pmf
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C
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D
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fpp
W
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X
occ
fps
oocl
app
pa
Y
appr
occ
fps
Gf
cp
pbs
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pa
hf
vf
appr
cp
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vlp/X
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AA
cec
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mac
pvp
2 mm

Figure 2

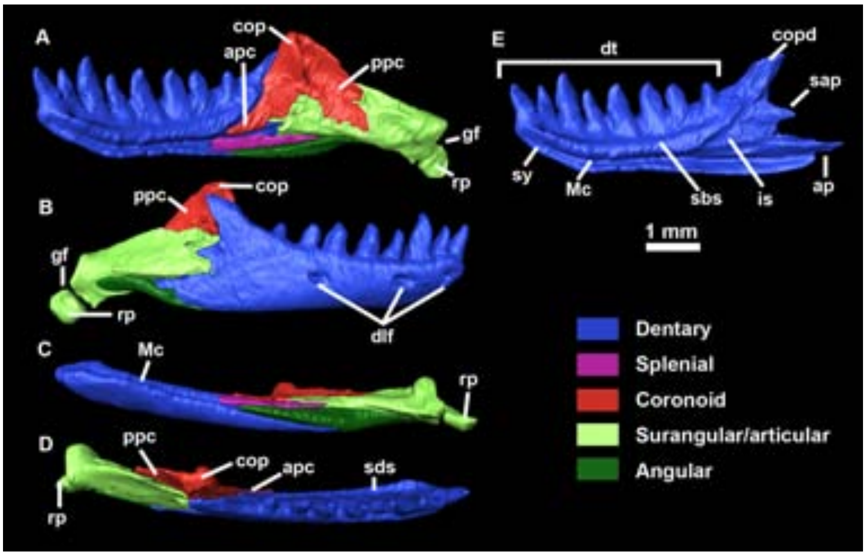

Figure 3

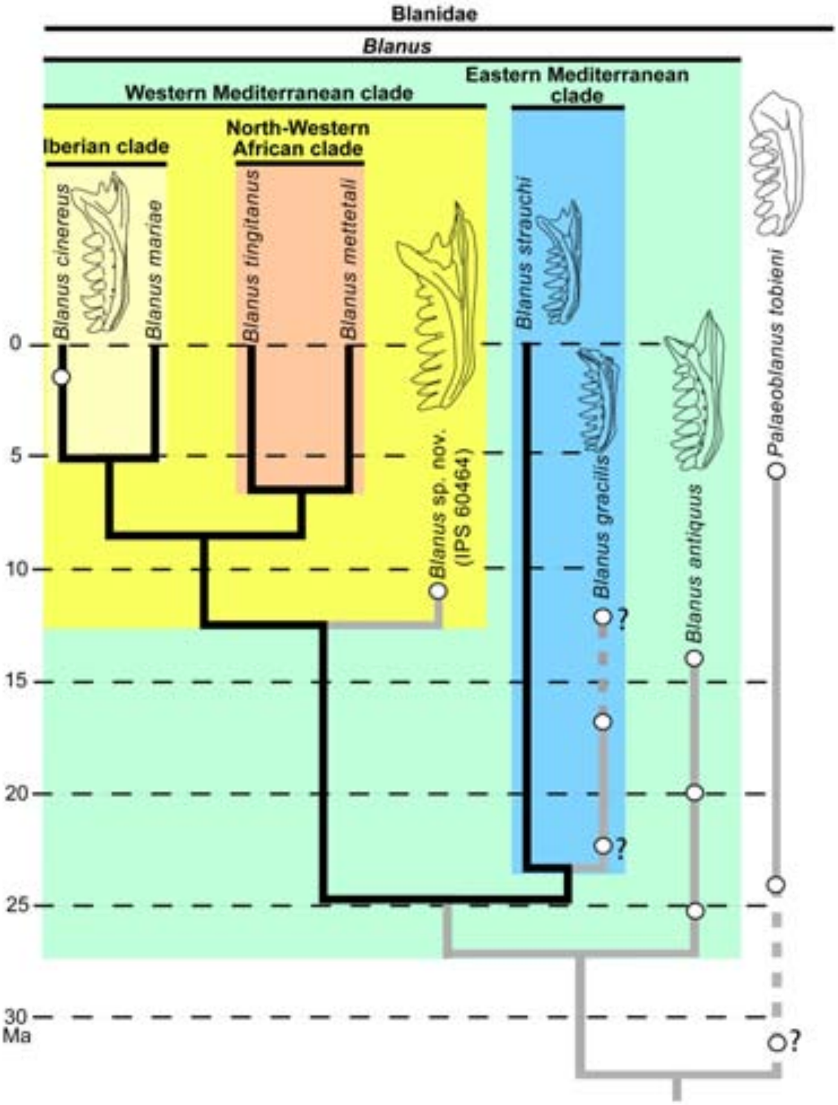

Figure 4

Supporting Information

An amphisbaenian skull from the European Miocene and the evolution of Mediterranean worm lizards

Arnau Bolet*, Massimo Delfino, Josep Fortuny, Sergio Almécija, Josep M. Robles, and David M. Alba

SI Text

Introduction

The fossil record of Mediterranean worm lizards. Although amphisbaenians are abundant in Paleogene and Neogene localities from Europe, the usually fragmentary nature of the material hinders their identification. The basal phylogenetic position of the Blanidae among the Amphisbaenia points to a long fossil history for the former (1–7). It is therefore possible that blanids were already present in Europe at least by the late Eocene, as suggested by some fossils (8, 9). Paleogene material previously referred to indeterminate amphisbaenids (8, 10, 11) is better attributed to indeterminate blanids (9), because the genus *Blanus* (to which similarities have been pointed) is no longer included in the former family (12). The only exception regarding the incompleteness of the material is the articulated skeleton of *Cryptolacerta* from Messel (Germany), interpreted as a stem worm lizard (13).

Also on the basis of fragmentary remains, amphisbaenians other than blanids may be similarly present in early Paleogene localities from Belgium and France (14), probably corresponding to basal forms that only represent a small portion of the Paleogene European record of the group. Moreover, uncertainties remain with regard to the attribution of several taxa. Thus, *Campinosaurus woutersi*—initially described as an anguimorph (15) and later argued to be an amphisbaenian (8)—may not belong to this group, because the tooth count and morphology of the dentary both indicate scincoid affinities (16).

Even more problematic is the purported record in the early Eocene of France (9) of the North American genus *Anniealexandria*, with important paleobiogeographic implications. Such a referral is doubtful (16), because it is based on the presence of nine dentary teeth—a diagnostic character of this genus (9), which is seldom present in other genera. There is however some variability in the number of tooth positions among extant amphisbaenians. Thus, a count of nine dentary teeth has been also reported for several species of *Amphisbaena*, such as *Amphisbaena fuliginosa* (17), and it is also observable in the *Amphisbaena alba* figured in the literature (18, 19). We further report a posteriorly located ninth small tooth in an extant *Blanus strauchi* dentary from Vic Siirt (Turkey) in the S. Bailon personal collection. In *Amphisbaena alba*, the replacement and the replaced tooth sometimes coexist (20), so that apparently increased counts (from typically eight to nine dentary teeth) might be related to the temporary retention of an old replaced tooth with the new, replacement one. It is also possible that ontogenetically older specimens, possessing longer dentaries, might accommodate a larger number of teeth. Although this should be confirmed through the study of ontogenetic series, dental counts are likely to be related to ontogenetic stage, so that adult, large squamate individuals would give more reliable tooth counts (21). Unfortunately, the ontogenetic stage is usually difficult to ascertain from fossil specimens. Given these considerations, the referral of European material to the North American genus *Annialexandria* might be incorrect (16), being alternatively attributable to an indeterminate amphisbaenian (?blanid) with nine dentary teeth.

The taxonomic status of other amphisbaenian genera from the Paleogene of Europe is also unclear. *Omoiotyphlops priscus*, from the Phosphorites du Quercy (Eocene or Oligocene from France) (22), is currently considered a nomen dubium, because it is based on a few, undiagnostic vertebrae (9, 23). *Louisamphisbaena ferox* from Grisolles (latest middle Eocene, France), in turn, is arguably a blanid (9), but the taxonomic validity of this genus is unclear, since the reported presence of a second curved tooth in the maxilla and the widely spaced teeth in the dentary do not enable a clear-cut distinction from *Blanus*. Moreover, no comparison to *Palaeoblanus tobieni* was made in the original description, despite sharing with the latter an enlarged first tooth—although *Louisamphisbaena* certainly lacks other characters of *Palaeoblanus*. Among Paleogene amphisbaenians, only the monotypic blanid genus *Palaeoblanus* (24) is more clearly diagnosable than the other above-mentioned genera. This genus, originally described from the Miocene of Germany (24), has been also identified from the late Oligocene and Miocene of France, Germany, Italy and Spain (24–27).

Palaeoblanus was not included in the Blanidae when the family was erected (12). This is probably due to the poorly informative material referred to *Palaeoblanus* and the uncertainty of this distinctiveness of this genus from *Blanus*, rather than to any evidence against *Palaeoblanus* belonging to this family. Dentaries of *Palaeoblanus* possess a distinctly larger first tooth (24, 25), a more homogeneous and blunt dentition, and a more rounded symphysis (Fig. 4) than species of *Blanus*. On the basis of these features, we therefore support the distinct generic status of *Palaeoblanus*. At the same time, we support the ascription of *Palaeoblanus* to the Blanidae, thus representing the only extinct blanid genus recorded from the Neogene. A potential, currently unnamed, second species of *Palaeoblanus* has been reported from the middle Miocene of Sandelzhausen (Germany) (28), based on the divergence of the lateral teeth. Such feature is however doubtful, because we found several specimens of *B. cinereus* (e.g., MDHC 156) with the same morphology—which is variable intraspecifically, and hence of no taxonomic value for diagnosing species. Moreover, the features purportedly justifying the referral of this material to *Palaeoblanus*—the proportion of the lateral teeth and the relatively larger size of the premaxillary foramina (28)—are insufficient to discount an alternative attribution to *Blanus* of the Saldenzhausen blanid material, which is best referred to as Blanidae indet. The French records at Mas de Got and Pech Desse (29) correspond to a large form with homodont, blunt teeth, most probably representing MP22 and MP28 records of *Palaeoblanus*.

Besides *Palaeoblanus tobieni*, only two extinct species of *Blanus—B. gracilis* and *B. antiquus*, from several German and Austrian localities (29, 30)—are recognized in the Miocene. Even though similarities with the extant genus *Blanus* were noted, *Blanus gracilis* was originally attributed to a different genus, *Omoiotyphlops* (29), which is currently well established as a junior synonym of *Blanus* (23). In fact, *B. gracilis* and *B. antiquus* have been considered synonymous by some authors (25), in which case the nomen *B. gracilis* would have priority (31). However, the smaller size, slenderer dentary and teeth, greater interdental space, and more heterodont dentition of *B. gracilis* compared to *B. antiquus* support their different species status. As it is evident in the corresponding drawings of Fig. 4, *B. strauchi* and *B. gracilis* are much more similar to each other than to either *B. gracilis* or *B. antiquus*. Material from Sansan (32) clearly shows that two different forms are present in the same locality. Although similarities to *B. gracilis* and *B. antiquus* were noted for the smaller form, referred to *Blanus* sp. (32), in fact it shows greater similarities (mainly regarding the robust, heterodont and closely-packed dentition as well as the robustness of the dentary) with *B. mendezi* sp. nov. The slightly larger form (dentary length of 7 mm), left unassigned at the genus level, resembles instead *Palaeoblanus* (blunt crowns, rather homodont dentition, and rather rounded symphysis) (32).

There is no morphologic evidence that the above-mentioned extinct species of *Blanus* already belong to any of the several clades identified by molecular studies among the extant taxa (33, 34). In contrast, fossil remains from Pliocene, Pleistocene and Holocene deposits of Western Europe (mainly Iberian Peninsula and Southern France) have been attributed to the extant *B. cinereus* (35–37). Material from the latest Pliocene of Casablanca (Morocco), in turn, was referred to *Blanus* sp. (38). Given that this locality is comprised within the present distribution range of *B. mettetali*, and very close to that of *B. tingitanus*, it is likely that these remains belong to one of the two extant species of the North-Western African clade. The same situation applies to the Pliocene record of an indeterminate amphisbaenian from Turkey (39), which might potentially belong to *B. strauchi*—or to an extinct species closely related to the latter from the Eastern clade.

The amphisbaenian fossil record in the Iberian Peninsula. According to the available literature, amphisbaenian fossil remains from the Iberian Peninsula are not particularly abundant. However, if it is taken into account that Paleogene and Neogene herpetofaunas from this area remain understudied, this fact seems to be largely a sampling artifact that does not reflect a real absence.

With regard to the Paleogene, amphisbaenians have been described from the Early Eocene of Silveirinha (10), the late Eocene of Sossís (16) and the Oligocene of Montalbán (40). Despite the rather fragmentary nature of the described remains, there is no clear evidence that these Paleogene specimens belong to an amphisbaenian group other than the Blanidae (16). The Iberian Neogene record is substantially better than that from the Paleogene, although the material described so far is quite scarce. Miocene amphisbaenian remains have been reported from the early Miocene of Córcoles, the middle Miocene of Tarazona de Aragón, and the late Miocene of Can Missert, Los Valles de Fuentidueña, Viladecavalls, Can Llobateres and Bacochas, among other localities (27, 41, 42). The possible presence of an amphisbaenian skull was reported decades ago from Viladecavalls (41), but the specimen was never described and it is currently lost (we were unable to locate it among the collections of the ICP). Amphisbaenian records from Iberian Plio-Pleistocene localities are more numerous (35, 36, 43), including currently undescribed material (27).

In Iberia, *Palaeoblanus* has been reported from several early to middle Miocene localities (MN3-MN6) (27), but material has never been described or figured. The numerous blanid records from Spain (and France) reported in ref. (27), mainly based on undescribed material, show that Miocene remains are generally attributed to either *Blanus* sp. or *Palaeoblanus* sp., whereas the Plio-Pleistocene material is customarily attributed to *B. cinereus*. This higher taxonomic resolution for the more recent material is not attributable to a better knowledge (more complete preservation and/or higher number of recovered specimens), but related to the fact that researchers are more cautious when referring Miocene material to an extant species. The referral of Plio-Pleistocene Iberian remains to *B. cinereus* is further complicated by the recent description, mostly on molecular grounds, of the cryptic sibling species *B. mariae*, which would be morphologically very similar to *B. cinereus* (34). Besides molecular differences, *B. mariae* has been reported to display a slightly larger size and some external morphologic differences compared to *B. cinereus*, but further research is required to confirm the distinct taxonomic status of the former as a distinct species instead of a subspecies of the latter—especially because it is unknown whether such differences are maintained or not in their contact zone (44). The currently lack of osteological data for *B. mariae* seriously hinders the identification of Plio-Pleistocene Iberian blanids at the species level.

Age and geological background of the type locality of *Blanus mendezi* sp. nov. The fossil remains described in this paper come from ACM (45–47). This stratigraphic series is situated in the Vallès-Penedès Basin (NE Iberian Peninsula)—a NNE-SSW-oriented half-graben limited by the Littoral and Pre-littoral Catalan Coastal Ranges, which was generated by the rifting of the NW Mediterranean region during the Neogene (48–51). Except for some early and middle Miocene shallow marine and transitional sequences, most of the basin infill consists of marginal alluvial fan sediments with a rich fossil record of early, late middle and late Miocene terrestrial vertebrates (52, 53).

ACM localities are situated in the area of els Hostalets de Pierola, which displays thick middle to late Miocene alluvial sequences. They were deposited in distal-to-marginal, inter-fan zones of the coalescing alluvial fan systems of els Hostalets de Pierola and Olesa (54). More than 250 localities have been defined along the ACM composite series (ca. 250 m in thickness), which can be accurately dated based on lithostratigraphic, magnetostratigraphic and biostratigraphic correlation (46, 47, 53, 55). The whole series spans from ca. 12.5 to 11.4 Ma (55), whereas locality ACM/C8-A4 (from which all the remains reported in this paper come from) is correlated to subchron C5r.2n, with an interpolated age of 11.6 Ma (late Aragonian, close to the middle to late Miocene boundary).

Materials and methods

Locality and institutional abbreviations. ACM, local stratigraphic series of Abocador de Can Mata; C8, Cell 4 of ACM; DP FNSP, Department of Palaeontology, Charles University, Prague (Czech Republic); ICP, Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona (Spain); IPS, collections from the ICP; MDHC, Massimo Delfino's Herpetological Collection, housed at the Dipartimento di Scienze della Terra, Università di Torino (Italy).

Comparative material. The accessed recent specimens include mostly disarticulated skulls and vertebrae of one *Blanus cinereus* (MDHC 156) and three *B. strauchi* (MDHC 286-8) (Fig. S3), as well as articulated and disarticulated material of both species from the personal collection of S. Bailon (MNHN, Paris). Fossil amphisbaenians have been accessed at the MNHN, and the ICP.

Extended description of the skull

Cranium. The cranium measures 11.3 mm from the tip of the snout to its most posterior projection (Figs. 1, S1), 5.8 mm of maximum width at the posterior region of the parietal, and 3.9 mm of maximum height. The preorbital region measures 3 mm, representing 26% of the total length.

The azygous premaxilla (Fig. 2*A*–*C*) bears seven tooth positions; the central one is greatly enlarged, and all of them are robust and cylindrical. This is evident even considering the poor preservation of the central tooth and the right lateral teeth being broken at different levels. It is not possible to discern whether the lateral teeth were much shorter than the others, but a moderate decrease in size is suggested by the CT sections. The nasal process of the premaxilla is broad and very long, slightly tapering dorsally and with a subtle waisting at its base. The inner surface of the nasal process is provided with a prominent and long medial keel (Fig. 2*C*). The anterior external surface is pierced by two large foramina having their exit on the inner side. The nasal process of the premaxilla precludes the dorsal contact between the nasals and that of the frontals in their anterior third (Fig. 1*A*). The poorly developed palatal process laterally contacts the rostral process of the maxilla. The palatal process probably contacted the vomer in its original position, but displacement or incomplete preservation of the latter results in the lack of contact in the fossil (Fig. 1*D*). The supradental platform is horizontal and thin, and displays a central notch.

The right septomaxilla (Fig. 1*C*) is present and appears rather simple in structure, although it should be taken into account that some processes formed by thin bone may have been either not preserved or artificially deleted during the CT-scan processing. This is supported by the fact that the septomaxilla does not contact the surrounding bones, whereas it should be in contact with the premaxilla, maxilla and/or nasal. The general ventrally convex shape of the septomaxilla, however, agrees with that of *Blanus cinereus* according to the material figured in the literature (56) and examined in the comparative sample.

The maxilla (Figs. 1, 2*D–G*), only preserved on the right side, bears five robust and only weakly curved teeth, the second one being the largest, and the first one the smallest. The reduction of the first maxillary and the most lateral premaxillary teeth allows for the necessary space to accommodate the enlarged third dentary tooth when the mouth is closed (Fig. 1*B*). Distalwards from the second tooth, there is a reduction in maxillary tooth height. The supradental shelf is wide, and the sulcus dentalis is apparently lacking or only slightly developed (Fig. 2*G*). The superior alveolar foramen is situated at the level of the distal margin of the last tooth (Fig. 2*E*). The maxilla contacts the premaxilla and the maxillary rostral process of the nasal through a rather wide and medially directed rostral process, sensu ref. (57) (Fig. 2*D–G*), as well as the frontal and prefrontal bones in its dorsal and posterior margins, respectively (Fig. 1*A*,*B*). The orbital process, situated dorsolabially, is relatively long (Fig. 2*D–G*) compared to other *Blanus* species. The dorsal process approaches the bifurcated condition seen in trogonophids (58) as well as *B. cinereus* and *B. strauchi* (Fig. S3*K–N*), although in the former the prefrontal is absent (57). The maxilla has a long posteroventrally positioned process (ectopterygoid process; Fig. 2*D–G*), which lies ventrolaterally to the anterior extension of the ectopterygoid. Two large foramina pierce the maxilla at the level of the posterior edge of the second and fourth tooth (Fig. 2*D*).

The nasal (Figs 1*A*,*B* and 2*H*,*I*), only preserved on the right side, is large and trough-shaped. A medial deep facet receives the nasal process of the premaxilla (Fig. 2*H*,*I*). Anteriorly, a ventrally-directed process approaches the maxillary rostral process, whereas a less developed and laterally-positioned process contacts the dorsal margin of the maxilla (Fig. 2*H*,*I*). Its anterior margin is truncated, sensu ref. (12). Posteriorly, the frontal process lies ventrally to the frontal (Fig. 2*H*,*I*). The snout is rounded, and the naris (formed by the premaxilla, the nasal and the maxilla) opens anterodorsally (Fig. 1*A*,*B*,*E*). The protrusion of the snout is only weakly developed.

The palate is preserved on the right side, formed by the palatal processes of the premaxilla, the supradental shelf of the maxilla, the vomer, the palatine, the ectopterygoid and the pterygoid (Fig. 1*D*). Teeth are absent from the palate (pterygoid, vomer and palatine are edentulous; Fig. 1*D*). The paired vomer is elongate, with a straight median articular plane and a poorly developed rostral process that surrounds the anterior margin of a small fenestra vomeronasalis (Figs. 1*D* and 2*J*,*K*). Posteriorly, this bone displays a facet for the articulation of the vomerine process of the palatine and the posteriorly directed choanal process (Fig. 2*J*,*K*). The paired palatine (Figs. 1*D* and 2*L*,*M*) is wide and its inferior surface is highly arched, forming the roof of the choanal vault. It bears a vomerine process anteromedially, a maxillary process anterolaterally, and a pterygoid process laterally; its lateral margin runs parallel to the ectopterygoid. Posteriorly, it displays a roughly triangular pterygoid process (Fig. 2*L,M*), which contacts the transverse process of the pterygoid (Fig. 1*D*). The paired ectopterygoid (Fig. 2*N,O*) bears a forked anterior maxillary process; laterally, the latter process bears a facet for the maxillary facial ectopterygoid process (Fig. 2*O*), as well as a posterolaterally-situated, deep and narrow facial facet for the articulation with the transverse process of the pterygoid, which is clasped by two (dorsomedial and ventrolateral) processes (Fig. 2*N*). The paired pterygoid (Figs. 1*D* and 2*P*,*Q*) articulates with the ectopterygoid and the palatine anteriorly, with the parabasisphenoid medially, and with the quadrate posteriorly (Fig. 1*D*). The pterygoid has a very long and slender posterior region, with a poorly defined quadrate process, whereas it suddenly widens anteriorly, where it forms a platform that contributes to the palate (Figs. 1*D* and 2*P*,*Q*). The transverse process is laterally directed and receives the pterygoid process of the ectopterygoid (Figs. 1*D* and 2*P*,*Q*).

The frontals are paired, with a rather straight suture between them, and a strongly interdigitated suture with the parietal (Figs. 1*A*, 2*R*–*U*). These bones are almost three times longer than wide, and the long nasal process of the premaxilla precludes the dorsal contact between the two frontals for at least one third of their length (Figs. 1*A*, 2*R,U*). However, the frontals are in contact below the nasal process of the premaxilla, and have a well-marked facet to receive it (Fig. 2*R*,*U*). Posteroventrally, they show strong and ventrally-directed (descending) processes (Fig. 2*S–U*), which meet each other in the midline and contact the orbitosphenoid posteriorly (Fig. 1*D*). The suture between the frontal and the nasal, which has been slightly displaced below the frontal, is arched (Fig. 1*A*). The frontal contacts the maxilla, separating the large prefrontal from the nasals (Fig. 1*A*,*B*). The dorsolateral surface of the frontals bears a marked facet for articulation with the maxilla and prefrontal (Figs. 1*A* and 2*R*).

The paired prefrontal (Figs. 1*A*,*B* and 2*V*,*W*), only preserved on the right side, precludes the contact between the maxilla and the frontals only in the posterior-most portion of the former. The prefrontal has a posterodorsally-directed, pointed frontal process as well as a wider, ventrally-directed maxillary process (Fig. 2*V*,*W*).

The unpaired parietal (Figs. 1*A–C* and 2*X–Z*) is long, more than twice the length of the frontals. It displays a dorsal protuberance (Fig. 2*X*) that marks the beginning of what might represent an incipient sagittal crest—in fact, the latter is observable in the CT sections, in spite of not being clearly expressed on the surface. The lateral walls of the parietal are vertically developed, being closed by the frontals anteriorly, the orbitosphenoid anteroventrally, the parabasisphenoid ventrally, and the otic-occipital complex posteroventrally (Figs. 1*C*,*D* and 2*Y*). The occipital condyle is bicipital.

The orbit is formed by a small anterior portion of the parietal and the orbitosphenoid, the lateral margin of the frontal, the prefrontal, a small posterior portion of the maxilla and the dorsal margin of the ectopterygoid (Fig. 1*A*,*B*). The orbitosphenoid—tabulosphenoid of ref. (59)—only preserved on the left side, is a paired element situated dorsally from both the palatine and pterygoid; it contacts anteriorly with the posteroventral margin of the descending process of the frontal (Fig. 1*C*,*D*). It is possible that the parabasisphenoid is co-ossified (Figs. 1*D* and 2*Z*), although this bone sometimes appears disarticulated in *Blanus* specimens (this could also be related to a younger ontogenetic age of the accessed specimens). The orbital rim is incomplete posteriorly, due to the lack of a jugal (Fig. 1*B*).

Both quadrates are preserved (Figs. 1*A–F* and 2*AA*,*AB*), the right one in articulation with the lower jaw (Fig. 1*A*,*B*). They are robust, and their dorsal articulation contacts the otic capsule, whereas a reduced mandibular condyle articulates with the lower jaw

(Figs. 1*A*,*B* and 2*AA*,*AB*). The presence or absence of the squamosal is difficult to ascertain, but this is not unexpected, as this bone is barely identifiable even in extant specimens.

Lower jaw. The right lower jaw (Figs. 1*B* and 3*A–D*) is complete and in articulation with the quadrate. The dentition is pleurodont and closely packed. The dentary (Fig. 3*A–E*), short and robust, bears eight teeth: the third tooth is the largest, whereas the fourth and the last ones are the smallest. The first tooth is not particularly enlarged, especially when compared to the third, which is clearly the largest. The symphysis shapes a marked angle with the ventral border of the dentary, which is roughly straight, only with a slightly convex central region. The subdental shelf has a high and rather rounded lingual surface (Fig. 3*E*). The Meckelian canal is open throughout all of its length (Fig. 3*E*), although it is posteriorly covered by a rather large splenial preserved in anatomical connection (Fig. 3*A*). A fused intramandibular septum (Fig. 3*E*), covered by the anterior process of the coronoid and the anterior portion of the surangular/articular, closes the region between the posteroventral margin of the subdental shelf and the dorsal margin of the Meckelian canal. There are three large labial foramina situated at the levels between the first and second tooth, between the third and fourth, and under the sixth (Fig. 3*B*) Posteriorly, the dentary bears three different structures (Fig. 3*B*,*E*): a dorsally-positioned coronoid process, which is higher than wide and rather long; a surangular process that reaches a slightly more posterior position; and an angular process that marks the posterior-most point of the dentary. The postdentary region (Fig. 3*A–D*) is shorter than the dentary, but not as reduced as in other amphisbaenians, such as for example *Diplometopon* (57). In contrast to most amphisbaenians (59), the postdentary bones do not constitute a compound bone (Fig. 3*A–D*). The splenial and the angular can be distinguished, and although the articular and surangular are more difficult to separate in the CT scan, they probably further represent separate bones (they are clearly distinct in accessed comparative material of *Blanus*). The retroarticular process (Fig. 3*A–D*) is present, posteriorly directed, and not enlarged. The lower jaw has a dorsally-arched postdentary ventral region (Fig. 3*A*,*B*).

Vertebrae. Both cervical and trunk vertebrae are preserved (Fig. S2). They are all procoelous. The cervical segment is represented by four fragmentary vertebrae encrusted by a concretion that keeps them together (Fig. 2*A–D*). Their morphology is barely visible, but the referral to an amphisbaenian is supported by the following features: neural arch without neural spine; presence of a hint of prezygapophyseal processes; large and protruding synapophyses; and centra proportionally very short and narrow, slightly convex ventrally, and provided of a small hypapophysis. Moreover, the cervical vertebrae have neural arches with a truncated posterior tip and small paracotylar tubercles well separated from the large synapophyses. The remaining 45 isolated trunk vertebrae represent all trunk sectors and display a variety of morphologies and length (Fig. S2*E*–*X*). These vertebrae are rather large, with a centrum length (from the ventral edge of the cotyle to the posterior tip of the condyle) varying from 2.0 to 3.1 mm (Fig. S2*E*–*X*). Anterior trunk vertebrae are characterized by being wider and shorter than the posterior ones, with a taller neural arch and at least a hint of paracotylar foramina. Trunk vertebrae are otherwise characterized by the following morphology. In dorsal view, the prezygapophyses are prominent and developed in anterolateral direction; the prezygapophyseal facets are roundish or vaguely drop-shaped; the prezygapophyseal processes are small and stout (preserved only in few cases); the interzygapophyseal constriction is distinctly developed; the anterior edge of the neural arch is convex, whereas the posterior edge is notched (the median notch is delimited on both sides by a small convexity); the dorsal surface of the arch is thickened in the area surrounding such median notch, forming in some cases a ridge with the shape of an inverse V; the neural spine is absent, but a sort of sagittal ridge is developed in all the cases. In ventral view, the lower rim of the cotyle is regularly concave and posteriorly placed as compared to the dorsal rim; the most anterior trunk vertebrae show small paracotylar tubercles, which are regularly absent in the other vertebrae; the prezygapophyses are anterolaterally directed and show at least a hint of their process also in the cases in which they are not visible in dorsal view; the synapophyses are roundish and laterally protruding; the centrum is variably eleongated (especially in the most posterior vertebrae); the ventral surface of the centrum is rather flat and well delimited by straight or slightly concave lateral edges; two foramina pierce the ventral surface of the centrum in its anterior quarter; the cotyle surface is only minimally visible; the postzygapophyseal facets are elongated and drop-shaped. In lateral view, the neural spine is regularly absent; the dorsal edge of the neural arch can be variably concave—more concave in the anterior vertebrae, nearly straight in the most posterior ones—but is often flat close to the posterior edge (where the above-described V-shaped ridge is developed); the synapophyses are massive and globular; there are no lateral foramina; the boundary between the lateral and ventral surface is neat and corresponds to the ventral edge (there is no gradually sloping lateral surface); the dorsal edge of the dorsoventrally depressed condyle is placed much more anteriorly than the ventral edge. In anterior view, the cotyle is distinctly dorsoventrally depressed, oval with a nearly straight ventral rim; the neural canal is generally small and triangular; the dorsal edge of the neural arch is distinctly convex and in some cases tectiform and apically pointed; the zygosphene is regularly absent; the prezygapophyseal facets are distinctly tilted in dorsolateral direction; the synapophyses are massive and laterally protruding. In posterior view, the shape of the condyle matches that of the cotyle; the neural canal is wider than in anterior view; the posterior edge of the neural arch is markedly depressed and medially flat or nearly so; there is no evidence of zyganthra, but in some cases the dorsal surface of the medial edge of the postzygapophyseal facet delimits a small concavity along with the ventral surface of the neural arch; the ventral edge of the postzygapophyseal facets is tilted in dorsolateral direction.

Comparisons with extant and extinct blanids

Comparison of *Blanus mendezi* sp. nov. with extant and extinct blanids. Many of the characters described in this paper for *Blanus mendezi* sp. nov. are unknown for other extinct blanids, thus being only directly comparable to extant members of the genus *Blanus* (Fig. S3). Among the four (or five) extant species of *Blanus*, only the osteology of *B. cinereus* and *B. strauchi* is partly known (56), and only the former has been previously reported from the fossil record. As a result, neither the inter- nor the intraspecific variability of osteological features within the genus *Blanus* is well known. Our survey of extant specimens suggests indeed that many cranial features display a considerable degree of intraspecific variability, supporting previous observations in this regard based on tooth-bearing bones (35). For example, the maxillary tooth count in both *B. cinereus* and *B. strauchi* displays a range of variation between 3 and 5, so that the differences in this regard between the figured specimen of *B. cinereus* and *B. strauchi* (Fig. S3K,N) are not diagnostic at the species level. We also observed bilateral variability regarding the maxillary tooth count in one specimen of *B. strauchi* (MDHC 286), with the right maxilla having four teeth, and the left one just three. The specimens of *B. strauchi* MDHC 288, in turn, displays three teeth on the right maxilla and a protuberance on the posterior portion of the left maxilla, which indicates that a fourth tooth was about to erupt. Similarly, the number of premaxillary foramina seems to be variable, at least in *B. cinereus*, since we observed the presence of two foramina only in the left side of *B. strauchi* MDHC 287 (Fig. S3*T*); this fact contrasts with the usual condition of having a single foramen on each side (Figs. 2*A*,*B*, S3*U*). A similar bilateral variation has been noted for *B*. cf. *gracilis* (60), although in this case the double foramen was on the internal side. Intraspecific variability notwithstanding, cranial features are in general more taxonomically informative than postcranial ones for amphisbaenians; and, from a taxonomic viewpoint, the most informative cranial bones are the premaxilla and the frontals. We provide below detailed comparisons of *B. mendezi* with both extant and extinct blanids, by focusing on the most informative features.

Skull size. There are no published measurements of skull length for all extant blanid species, although the reported maximum head lengths can be used as a good proxy: 8.5 mm in *B. cinereus,* 7.9 mm in *B. mettetali*, and 7.3 mm in *B. tingitanus*, according to ref. (61); a maximum of 8.5 mm in *B. cinereus*, a maximum of 9.6 mm in *B. mariae*, an average of 6 mm in *B. tingitanus*, and an average of ca. 5.6 mm in *B. mettetali*, according to ref. (34). Direct measurements of maximum skull length of 8.0-8.1 mm for *B. cinereus* (56, 62) are only slightly smaller than external measurements, thus indicating only a slightly larger size for *B. strauchi*, on the basis of a maximum skull length of 8.5 mm for the former (56). The skull length of 11.3 mm in *B. mendezi* therefore clearly shows that the new taxon was larger than all extant species of Mediterranean worm lizards—at least 15% longer than the largest skull reported (34). Given the lack of complete skulls of extinct blanids other than *B. mendezi*, size comparisons between them must necessarily rely on the size of the dentaries. On this basis, the extinct *B. gracilis* would be roughly comparable in size to (only slightly smaller than) extant *B. cinereus* and *B. strauchi* (dentary length around 3.5 mm, maximum 4 mm in MDH 288 and 286), whereas the North-African *B. mettetali* and *B. tingitanus* would be even slightly smaller, based on reported skull size (see above). *B. antiquus* (dentary length up to 5 mm) and *B. mendezi* (6 mm) would be therefore larger than both *B. gracilis* and extant blanids. Some Plio-Pleistocene remains from the Iberian Peninsula have been sometimes reported to be larger than those of *B. cinereus*, the dentaries measuring 5-6.25 mm in the Early Pleistocene material from Illes Medes referred to *B. cinereus* (35). Interestingly, some of the dentaries from Illes Medes display a small separation between the fifth and sixth teeth and, more rarely, between the seventh and the eighth ones (35). These small gaps are present in *B. mendezi*, although it is unknown whether this character is shared with other members of the Western Mediterranean clade (it seems to be lacking in members of the Eastern Mediterranean clade). This might indicate that the material from Illes Medes does not belong to *B. cinereus*, and a possible referral to *B. mendezi* should be taken into account. Alternatively, if the material from Illes Medes belongs to *B. cinereus*, the species might have attained larger sizes in the past. In relation to this observation, a form similar in morphology to *B. cinereus*, but much larger, has been reported from the Late Miocene locality of Bacochas-1 (MN13) (63). This large form might correspond to an additional record of *B. mendezi*, although further research would be required to confirm this possibility.

Nasal process of the premaxilla. An attribution of Miocene blanid remains to any of the extant clades is usually precluded by the incomplete preservation of the former. Among other features, the length of the nasal process of the premaxilla cannot be evaluated in most instances, because this bone is usually broken. Nonetheless, a complete premaxilla (DP FNSP 317) from the MN4 of Dolnice (Czech Republic) (fig. 5 in ref. 29) deserves in this regard a detailed comparison with the holotype of *Blanus mendezi*. The former specimen was referred to the Squamata indet., but on the basis of its morphology and size, it most likely belongs to *B. gracilis*, which has been reported on the basis of other remains from this very same locality *(60)*. Like *B. mendezi*, the premaxilla from Dolnice displays a long nasal process. In *B. mendezi*, such morphology is related to the fact that this process precludes the dorsal contact between the frontals for almost one-third of their length. The nasal process is generally shorter in *B. cinereus* than in *B. strauchi*, in spite of some variability among the specimens of the former examined while preparing this work (Fig. S3) and figured in the literature (56, 64; see also Fig. S4). In some specimens, the nasal process of the premaxilla barely prevents the dorsal contact of the frontals, whereas in others their contact is precluded for a somewhat greater length. However, in none of the examined specimens the dorsal contact of the frontals is precluded to the same extent as in *B. mendezi*, thereby supporting the diagnostic validity of this feature.

Snout shape. Besides the length of the nasal process of the premaxilla per se, one of the few osteological features further enabling the distinction between extant species of *Blanus* is the projection of the snout relative to the lower jaws. In *B. strauchi*, the muzzle protrudes beyond the anterior-most level of the lower jaws and slightly curves downwards, whereas in *B. cinereus* the snout is not projecting (56, 65). Such a projection of the snout in *B. strauchi* is also reflected in the shape of the premaxilla (Fig. S3*U*)—with an expansion at the anteroventral tip of the bone and an inward position of the teeth, which are situated relatively far from the anterior tip of the bone—thereby enabling the identification of *B. strauchi* from isolated premaxillae. In these regards, *B. mendezi* differs from *B. strauchi* and more closely resembles *B. cinereus* (and other previously-reported fossil blanid premaxillae), since in the former the anteroventral projection of the premaxilla is rather short, and the central tooth is almost aligned with the distalmost tip of this bone (Figs. 1*A*, 2*A–C* and S3*T,U*). The anteroventral projection of the premaxilla (reflecting the ventral projection of the snout over the retracted lower jaws) may the therefore interpreted as an autapomorphy of *B. strauchi*, given the fact that this feature is lacking in the rest of extant and fossil blanids.

Frontal and nasal length and shape. Some authors have noted the existence of two different extant morphs of *B. cinereus* in Spain (28): one with strongly reduced lateral teeth and the typically robust nasal process of the premaxilla; and another one with lateral teeth not strongly-reduced and with a long and slender nasal process. The second morphotype is however based on a purported specimen of *B. cinereus* figured in ref. (30), which does not look amphisbaenian at all but resembles instead a lacertid premaxilla—i.e., with seven teeth equal in size and morphology, long and slender nasal process, and triangular posteroventral processes. An examination of previously figured blanids from the Iberian Peninsula (56, 64), however, shows that there are evident differences in frontal and nasal length and shape among several individuals (Fig. S4). In the specimen figured in ref. (56), the frontal is much longer and has a roughly rectangular shape, contrasting to the short and roughly square frontal in the specimen figured in ref. (64); moreover, in the former the nasal is comparatively reduced, and the contribution of the dorsal margin of the maxilla to the dorsal region of the snout is restricted. It is uncertain whether these morphotypes might correspond, as speculated by some authors (28), to the two presumably cryptic species mainly distinguished on molecular grounds (34, 44)—i.e., *B. cinereus* (for the Central Iberian clade) and *B.*

mariae (for the Southwestern Iberian clade). Their taxonomic status as a distinct (sub)species aside, the nominal taxa to be employed for each of these taxa is uncertain: first, because the lectotype designation for *B. cinereus* (34), based on a presumed syntype from the type series (66), is nomenclaturally incorrect (44); second, because the exact localization of the type locality of this taxon (other than Portugal) is unknown (66–68); and third, because old names until recently considered junior synonyms of this species (68) should be examined, since depending on their type locality they might be senior synonyms of *B. mariae* (44).

A single frontal bone has been described from the European fossil record of amphisbaenians. This specimen, from the early Pleistocene of Illes Medes (Spain) and attributed to *Blanus cinereus*, was incorrectly described as a nasal (35); it actually corresponds to a frontal, which does not display significant differences compared to the extant *B. cinereus* (Fig. S3*R*,*S*) morphotype figured in ref. (56). *Blanus mendezi* is more similar regarding frontal and nasal length and shape to these two specimens than to that figured in ref. (64). The phylogenetic implications of this fact cannot be further evaluated at present, given the uncertain taxonomic status of *B. mariae* and the lack of osteological data for this taxon. In any case, the possibility cannot be discounted at present that the apparent variability in the length of the frontals in published specimens of *B. cinereus* is related to the presence of two different species. In this regard, the frontal of *B. mendezi* is clearly more elongated than that of both *B. strauchi* and *B. cinereus*, thus supporting the diagnostic value of this feature. This view is further strengthened by other distinctive features of the frontal of *B. mendezi*, namely: the marked and constantly-wide lateral facet for the articulation of the nasal, the maxilla and the prefrontal; the long anteromedial facet for the articulation of the premaxilla; the straight interfrontal suture; and the stronger interdigitation of the frontoparietal suture. Similarly, the nasal of the specimen figured in ref. (64) stands out by being much larger than those of *B. cinereus* and *B. mendezi*.

Maxilla. This element has not been described for either *P. tobieni* or *B. gracilis*. Compared to that of *B. antiquus* (24), the maxilla of *B. mendezi* displays a much longer and more pointed medial process (orbital process). In addition, the medially directed rostral process of the maxilla (which makes this process to appear shorter) in *B. mendezi* clearly differs from that of *B. strauchi* (Fig. S3*M*,*N*), which is long and anteriorly directed (35). In this regard, *B. cinereus* (Fig. S3*K*,*L*) displays an intermediate morphology, which is however more similar to that of *B*. *mendezi* than to that of *B*. *strauchi*.

Sagittal crest. Although a sagittal crest on the parietal has been reported to be absent from *Blanus* (12), a faint crest can be observed on the anterior region of the parietal in both *B*. *cinereus* and *B*. *strauchi*, according to the specimens examined by us (Fig. S3*U*). A similar structure is apparently displayed by *B. mendezi* (Fig. 1*A*), which is most clearly seen in the CT sections than on the virtually reconstructed bone surface. Like in *B*. *strauchi* (Fig. S3Q), the faint crest of *B*. *mendezi* ends in a posteriorly situated protuberance (Fig. 1*A*). It therefore seems that, as in extant species of *Blanus*, in *B*. *mendezi* the sagittal crest is less developed than in other amphisbaenians, but not entirely lacking. The implications of this feature are not clear, because the presence of a sagittal crest is found in trogonophids, some amphisbaenids and some rhineurids (12). Regarding amphisbaenids, the presence of a protuberance is variable among the different taxa (12). We suggest that the sagittal crest and the presence of a protuberance on the parietal should be both regarded as present in *Blanus*.

Dentary and tooth counts. The extinct species of *Blanus* show some peculiarities in the dentary, although the taxonomic validity of such features (curvature and robustness of the teeth, as well as tooth count) is uncertain, due to the intraspecific variability shown in this regard by extant species. Compared to *B*. *mendezi*, the dentary of *B*. *gracilis* is smaller and slenderer, and displays straighter teeth and a greater interdental distance, thus more closely resembling *B*. *strauchi* (Figs. 4 and S3*O,P*). In contrast, *B*. *antiquus* displays a more robust and homodont dentition, with the teeth almost contacting each other at their bases (Fig. 4). *Blanus cinereus* and *B*. *mendezi* would be intermediate regarding the robustness of their dentition (Fig. 4). The dentition of *B*. *strauchi* has been reported (35) as being more slender and well spaced (approaching the condition of *B*. *gracilis*) than those of *B*. *cinereus* and *B*. *antiquus* (Fig. 4), which further holds when compared to *B*. *mendezi*.

A splenial in the dentary of *Blanus* has been variously reported as lacking (12) or present (37). We can confirm the presence of this bone in extant *Blanus strauchi*, *B*. *cinereus* and also the fossil *Blanus mendezi* (Fig. 3*A*).

Tooth counts are similarly of little help for distinguishing *B*. *mendezi*, not only regarding the premaxilla and maxilla, but also with regard to the dentary (Figs. 1D and

4). Thus, *B. mendezi* displays seven teeth in the premaxilla, as extant species of *Blanus* (56), and five teeth in the maxilla; extant *Blanus* display 3-5 maxillary teeth (30), the second one being the largest when five teeth are present, as in *B. mendezi*. With regard to the dentary, the 8 teeth present in *B. mendezi* fit well with the range of 7-8 teeth usually reported for extant *Blanus* (30). This feature is in fact quite variable, since we have observed the presence of nine teeth in at least one specimen of *B. strauchi* in which the posterior-most tooth is extremely small, but present in both dentaries.

Vertebrae. The vertebrae of *B. cinereus* and *B. strauchi* are indistinguishable (Fig. S3*A–J*). In fact, amphisbaenian vertebrae are generally not diagnostic at the genus or even the family levels—blanid and amphisbaenid vertebrae being difficult to differentiate. The abundant amphisbaenian vertebrae recovered from the type locality of *B. mendezi* are attributed to this taxon, given the lack of non-blanid worm lizards in the European fossil record—both Paleogene (9) and Neogene (27)—and the fact that they are consistent in size with the holotype of the new species—being, like the skull, larger than those of either extinct and extant blanids. In *Blanus*, the length of the centrum usually ranges from 1.5 to 2.0 mm (MDHC 187 for *B. cinereus* and MDHC 286, 287, 288 for *B. strauchi*), whereas those of *B. mendezi* reach a maximum length of 3.1 mm. This length is exceeded by the vertebrae from the collection of Sansan (32), in which vertebrae reach a maximum length of 4 mm. However, as reported above, two forms are present at Sansan on the basis of size of the dentaries. A more abundant form, smaller in size, is referred to *Blanus* sp., whereas the other, much more scarce and much larger, probably belongs to *Palaeoblanus*.

With regard to morphology, the cervical vertebrae of *B. mendezi* are very similar to those of extant *B. cinereus* and *B. strauchi* (Fig. S2). The vertebrae of *B. mendezi*, however, can be distinguished from those of both *B. cinereus* and *B. strauchi* not only by the larger size of the former, but also by the presence of paracotylar tubercles in the cervical and anterior trunk vertebrae. This fact further supports the distinct species status of *B. mendezi*, although additional extant blanid specimens should be examined to completely discount that this feature is intraspecifically variable and/or size-related. The same structure might be present in *B. gracilis*, where a conspicuous protuberance has been reported close to the margin of the cotyle and ventrally from the synapophysis (29). This structure has not been described in any other blanid, and is certainly absent from accessed extant material (*B. cinereus* and *B. strauchi*) and fossil *Palaeoblanus* from the MN13 of Gargano (Italy) (26).

7. References

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Figure legends

Fig. S1. *Blanus mendezi* sp, nov. IPS60464 as preserved, in (A) dorsal, (B) right lateral, (C) left lateral and (D) ventral views.

Fig. S2. Selected vertebrae (paratypes) of *Blanus mendezi* sp. nov. A–D, four cervical vertebrae in anatomical connection (IPS63989), in left lateral (A), right lateral (B), dorsal (C) and ventral (D) views. E–X, dorsal vertebrae (IPS63990-IPS63993), in dorsal (E, J, O, T), ventral (F, K, P, U), left lateral (L), right lateral (B, G, Q, V), cranial (H, M, R, W) and caudal (I, N, S, X) views.

Fig. S3. Selected material of extant *Blanus cinereus* (MDHC 156) and *Blanus strauchi* (MDHC 286) for comparison purposes. A–H, Cervical vertebrae of *B. cinereus* (A–D) and *B. strauchi* (E–H), in left lateral view. I–J, Dorsal vertebrae of *B. cinereus* (I) and *B. strauchi* (J), in dorsal view. K–N, Left maxillae of *B. cinereus* (K) and *B. strauchi* (M), in lingual view; right maxillae of *B. cinereus* (L) and *B. strauchi* (N), in labial view. O–P, Left dentary of *B. strauchi*, in lingual (O) and labial (P) views. Q, Articulated parietal and frontals of *B. strauchi*, in dorsal view. R–S, Frontals of *B. strauchi*; right frontal in dorsal view (R), and left frontal in ventral view (S). T–U, Premaxillae of *B. cinereus* (T) and *B. strauchi* (U), in left lateral view. V, Left quadrate, in lateral view.

Fig. S4. Schematic drawings of the cranium of *Blanus mendezi* sp. nov., in dorsal view, compared to that of *Blanus cinereus*. A, *B. mendezi*, based on the virtual model of the holotype (IPS60464). B–C, *B. cinereus*, redrawn from ref. (56) (B) and ref. (64) (C).

Video S1. IPS60464, digital removal of the covering crust and infilling matrix, and rotation of the resulting virtual model in different axes.

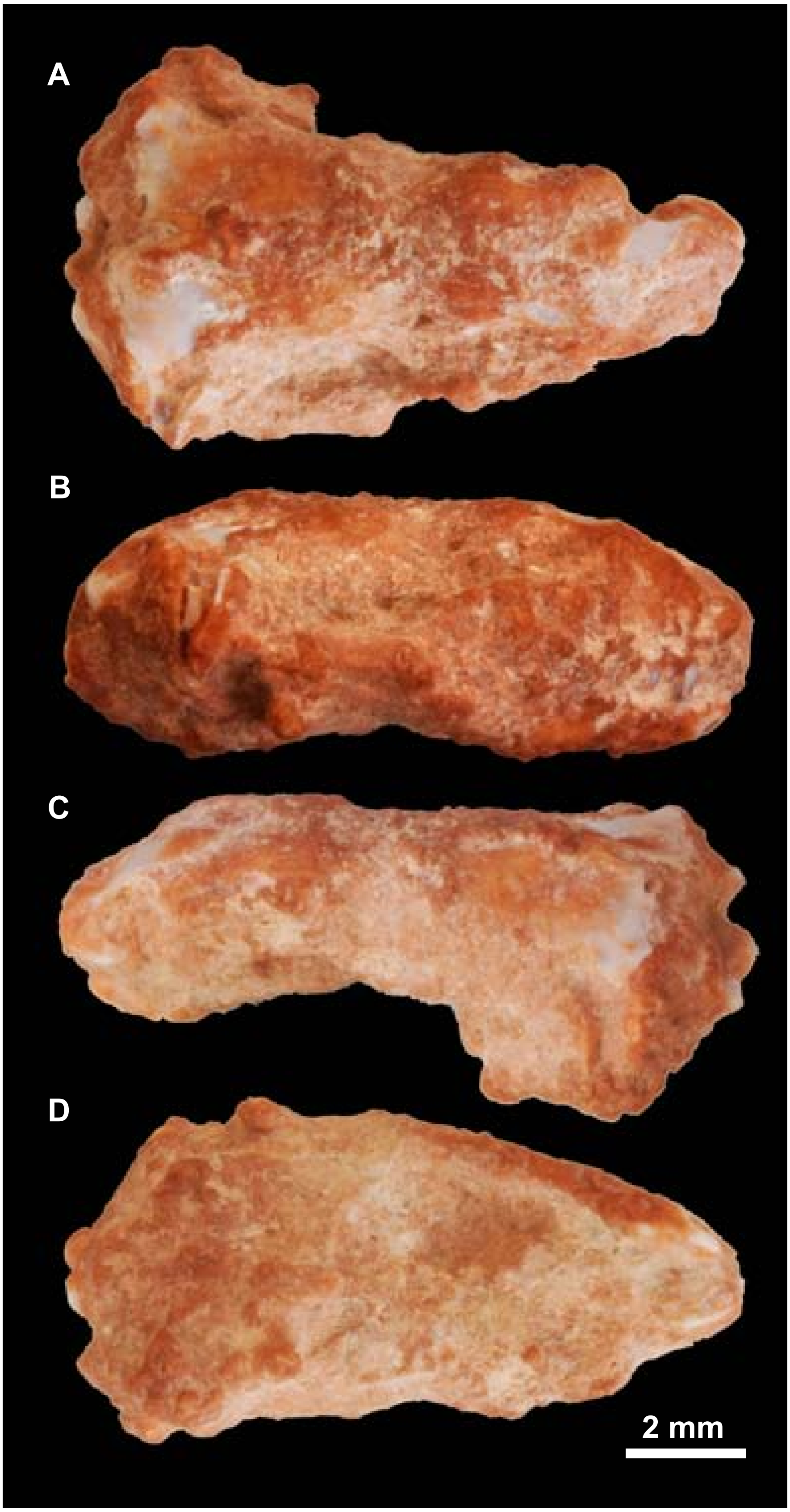

Figure S1

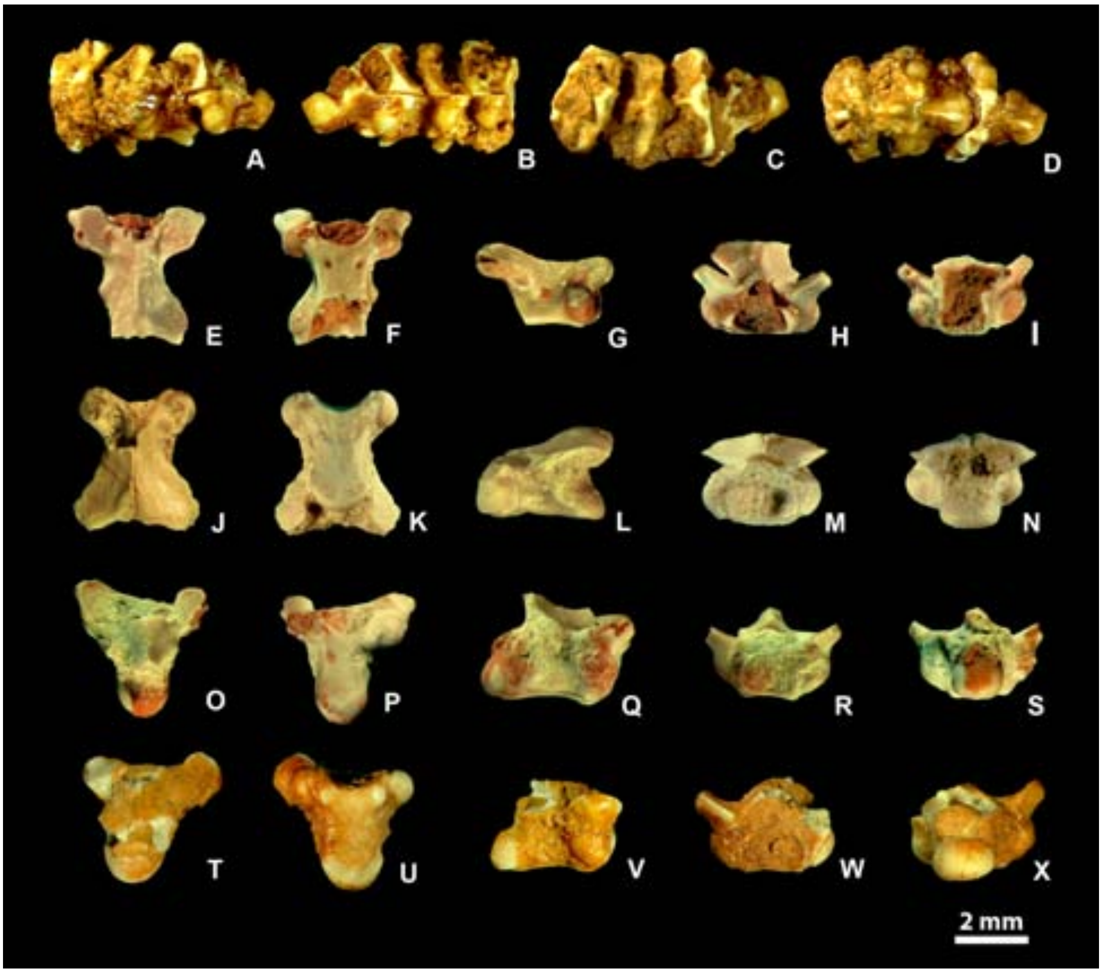

Figure S2

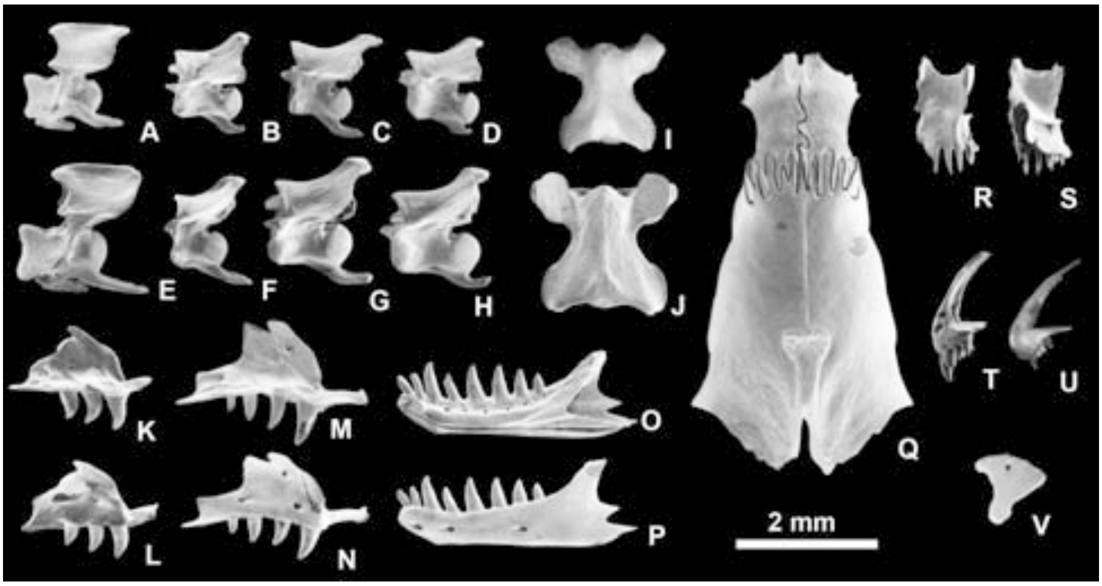

Figure S3

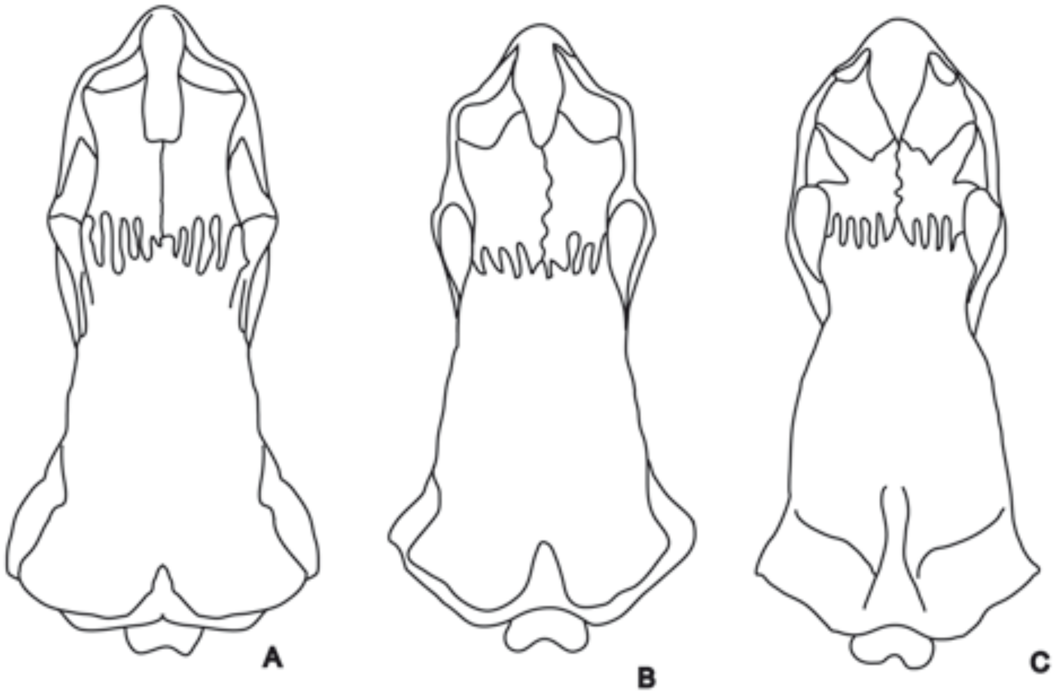

Figure S4

Video S1 (caption in printed version/video in PDF version)

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