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1 Osteology, fossil record and palaeodiversity of the European lizards

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21 **Abstract.** The capability of palaeontologists to identify fossil remains of a particular
22 group of vertebrates strongly depends on the knowledge they have of its comparative
23 osteology and on the actual presence of diagnostic differences among the considered
24 taxa. This could have a relevant influence on the study of palaeodiversity, since a low
25 recognisability causes a loss of data when trying to reconstruct the history of taxa that
26 lived on Earth in the past. Currently, more than 6000 extant species of lizards and worm
27 lizards are known, and new ones continue to be discovered, mainly based on molecular
28 data. But are we able to recognise this high diversity using osteology? As far as
29 European taxa are concerned, the osteological recognisability of non-snake squamates is
30 very low: only 31% of the extant European taxa can be identified based on their skeletal
31 morphology. This is balanced partially by the fact that most recognisable taxa have been
32 actually recognised in the fossil record, suggesting that the lost data are mainly due to
33 the scarce knowledge of the comparative osteology of these reptiles and less influenced
34 by other biases, such as taphonomic or collection biases. In this context, specimen-level
35 phylogenetic analysis has proved to be a useful tool to identify diagnostic combinations
36 of osteological features, at least for lacertid species, as evidenced by a case study
37 focused on the genus *Lacerta*.

38 **Keywords:** Identification, Squamates, Reptiles, Palaeontology, Biodiversity

39 **Introduction**

40 Non-snake squamates (i.e., lizards and worm lizards) exist since at least the Middle
41 Jurassic (Rage, 2013), and are represented by more than 6000 extant species worldwide
42 (Uetz and Hošek, 2016) and a number of extinct taxa (for a summary of extinct species
43 see the now dated review of Estes, 1983, but also Böhme and Ilg, 2003). In order to
44 identify the current diversity of these reptiles, herpetologists can rely on various
45 different tools, in particular external morphology, behaviour, molecular and
46 distributional data. Lately, the rate of new lizard descriptions was rising considerably

47 (Pincheira-Donoso et al., 2013). But what about the palaeodiversity? How precisely can
48 we recognise the diversity of taxa that lived on Earth in the past? Except for a few
49 remarkable examples (e.g., specimens in amber that preserve also the integument like
50 *Succinilacerta succinea* (Boulenger, 1917) or those recently described by Daza et al.,
51 2016), vertebrate palaeontologists are mostly restricted to osteological features to
52 identify fossil remains and study palaeodiversity. This makes the task of
53 palaeoherpetologists much more complex and error-prone than that of
54 neoherpetologists, given that it strongly depends on the degree of knowledge of the
55 comparative osteology of the considered group and on the actual presence of diagnostic
56 differences among the taxa. We here try to quantify the current osteological
57 recognisability of the extant European non-snake squamates, in order to evaluate to
58 what degree it affects our ability to comprehend the past diversity of these reptiles in the
59 continent. The degree of recognisability is also evaluated at different hierarchical levels
60 and within different clades, in order to understand where the information is scarcer and
61 new studies are needed. Last but not least, we try to assess the utility of phylogenetic
62 analyses to identify diagnostic osteological features for lizards, and lacertids in
63 particular.

64 **Materials and methods**

65 We included 75 species of lizards and 3 worm lizards in our analysis. The included species correspond to
66 the European amphibians and reptiles reported by Sillero et al. (2014), plus the lizards and worm lizards
67 living on the Greek islands along the coast of Asiatic Turkey as reported by Speybroeck et al. (2016).
68 Recently introduced taxa have been excluded (as e.g., *Chamaeleo africanus*). The definition of Europe
69 largely follows Arnold and Ovenden (2002), but with the exclusion of Madeira and the Canary islands in
70 the west, because they do not belong to the continent in geological terms.

71 The evaluation of the recognisability of the different taxa is based on existing bibliography, as
72 well as on personal observations (see supplementary text S1 for a list of the studied specimens). Details
73 about the osteology of European lizards and worm lizards have been mentioned in more than 90 papers,

74 either dealing directly with comparative osteology (e.g., Evans, 2008) or simply reporting features in the
75 remarks of the identification of fossil material of extant taxa (e.g., Blain, 2009). For a complete list of
76 these works, see supplementary text S2. In order to avoid circular reasoning (as outlined by Bell et al.,
77 2010), geographical and/or chronological criteria are not considered useful for the identification of a
78 taxon, since the range of a species may strongly vary during time.

79 The recognisable taxa are not always represented by species, but often by different kinds of
80 higher taxonomic ranks. Because of this, the recognisability is here analysed in two ways: 1) in terms of
81 Operational Taxonomic Units (OTUs), regardless whether they represent family, genus or species level;
82 and 2) at the level of species, genus, and family separately. The first analysis tells us how many
83 taxonomic bins can be recognised when having skeletons of all the 78 extant European lizards, in order to
84 depict the recognisable diversity based only on osteology. This diversity is then compared with the actual
85 one recognised by neoherpetologists using other tools, in which OTUs are represented by the 78 extant
86 species of European lizards and worm lizards. The second analysis quantifies how many species, genera,
87 and families of lizards can actually be diagnosed with osteological characters, and, assuming that
88 diagnostic characters are present, in which taxon we need more work to be done to increase this
89 recognisability. Finally, given the widespread individual variation in lizard skeletons, and thus the low
90 probability to find unambiguous, osteological autapomorphies for the species, we implemented a case
91 study to evaluate the utility of specimen-level phylogenetic analysis for the identification of diagnostic
92 combinations of osteological features of the European species of the genus *Lacerta* (as defined by Arnold
93 et al., 2007). We compiled a novel phylogenetic matrix based on osteology only, including 159
94 character statements taken from earlier works (see references in the supplementary text S2) and personal
95 observations of ET. These character statements were scored in 37 OTUs consisting of single specimens
96 (see supplementary text S1), which were identified before skeletonization, based on external morphology
97 by the collectors or curators of the respective collections. The matrix was compiled in the software
98 Mesquite v. 3.04 (Maddison and Maddison, 2015), and includes nine specimens of *Lacerta agilis*, nine
99 specimens of *Lacerta bilineata*, five specimens of *Lacerta schreiberi*, four specimens of *Lacerta*
100 *trilineata*, and four specimens of *Lacerta viridis*, which have all been scored based on first hand
101 observations. The outgroup consists of specimens of the European lacertids *Timon lepidus* (1), *Podarcis*
102 *muralis* (2), *Archaeolacerta bedriagae* (1), *Algyroides nigropunctatus* (1), and *Psammodromus algeris*
103 (1). The matrix was analysed with TNT v.1.1 (Goloboff et al., 2008). We used an extended implied
104 weighting approach (Goloboff, 2014) in order to reduce the influence of highly variable characters and

105 missing data. The tree search was performed using the New Technology Search, enabling all algorithms,
106 and stabilizing the consensus tree five times with a factor of 75. In order to find all most parsimonious
107 trees (MPTs), a second iteration of tree bisection and reconnection was performed.

108 **Results**

109 *Recognisability*

110 The recognisability of European lizards and worm lizards appears to be rather low (Tab.
111 1): the recognisable OTUs represent only 31% (24 out of 78 taxa) of the current
112 European lizard diversity. A large number of lacertids and scincids, as well as all
113 species of the genus *Anguis*, can only be identified at genus or even at family level
114 (species complex in the case of *Anguis*). It has to be noted that agamids and
115 chamaeleonids are poorly identifiable too, but since a single autochthonous species of
116 each family is currently present in the continent, this has no evident effect on the count
117 of the recognisability of extant taxa. Finally, the most recognisable group is Gekkota: all
118 four species, belonging to four different genera, are clearly distinguishable from one
119 another.

120 The second analysis shows that recognisability highly depends on the hierarchical
121 levels. Whereas all families of lizards are recognisable based on osteological features,
122 only 45% of the genera and 17% of the extant species are known to have diagnostic
123 features in their skeletons (Fig. 1). Also the degree of recognisability varies greatly
124 within the different families: nearly half (43%) of the scincid and lacertid species can
125 only be identified as belonging to Scincidae and Lacertidae, and the two European
126 species of agamids and chamaeleonids cannot be distinguished from other, non-
127 European members of their family based on osteology. On the other hand, osteological
128 characters of the anguids and blanids allow to recognise all European taxa at least at the
129 genus level (Fig. 2).

130 As for the European fossil record, a large number of the recognisable OTUs
131 have been identified (20 out of 24, 83%; 26% of the 78 extant species, meaning a loss of
132 data of 74%; Tab. 1). Among the 24 OTUs, in fact, only those corresponding to
133 *Euleptes europaea*, *Mediodactylus kotschyi*, *Lacerta schreiberi* and worm lizards of the
134 *Blanus strauchi* complex have never been recovered as fossils.

135 *Phylogenetic analysis*

136 The first run of the case study of *Lacerta* produced a single MPT of a length of
137 39.25405, and recovered the specimen of *T. lepidus* among the specimens of *Lacerta*.
138 Given that all the recent phylogenetic analyses including these two genera find them as
139 sister taxa (e.g., Carranza et al., 2004; Arnold et al., 2007; Kapli et al., 2011; Mendes et
140 al., 2016), our result indicates that either we did not find enough osteological characters
141 to unite *Lacerta* to the exclusion of *Timon*, or that the osteological variability is too high
142 to obtain a meaningful tree topology based on osteological characters only. In order to
143 test this, we performed a second analysis, including a constraint forcing the software to
144 find all the specimens of *Lacerta* as a monophyletic group. This second run resulted in
145 nine MPTs with a length of 39.80892. With the exclusion of a single specimen of *L.*
146 *viridis*, all the other specimens form monophyletic clades with their respective species
147 members in the strict consensus tree (Fig. 3).

148 **Discussion**

149 *The impact of recognisability on the study of fossil European non-snake squamates*

150 The knowledge we have of past ecosystems is incomplete, because of the different
151 biases that cause loss of information in the palaeontological record (among others,
152 Dunhill et al., 2012). Among them, taphonomic bias has a major effect, in particular
153 when it comes to small animals (Soligo and Andrews, 2005; Cooper et al., 2006). When
154 an excavation is not directly focused on the recovery of small vertebrate remains, a
155 collection bias may also occur, caused by the difficulty of discovering and collecting

156 small bones without proper methods and tools. This latter issue is particularly
157 significant when old works are considered, whereas an increased attention towards these
158 fossils became established in XX century. Finally, also a historical bias probably
159 influenced the fossil record of poorly studied vertebrates, such as lizards: studies on
160 their osteology were, in fact, rare until about the 1970s, with a significant increase from
161 the 1980s onwards (Fig. 4). This increase in the number of lizard osteology papers still
162 continues: nearly 25% of all the descriptions used for the current study were published
163 between 2010 and 2016. Obviously, this lack of osteological data until recently
164 hampered the identification of fossil taxa, even if the increasing number of description
165 is highly promising for the future. Also, current taxonomic trends based on molecular
166 analyses tend to raise subgenera and subspecies to genus and species level, respectively
167 (e.g., Arribas and Carranza, 2004; Arnold et al., 2007), and it remains to be seen if this
168 is also reflected in their osteology.

169 The mentioned biases result in a significant loss of data, especially in small,
170 fossil vertebrate taxa whose comparative osteology is poorly known, such as
171 amphibians or reptiles. Delfino (2004) estimated the loss to be of 58% when comparing
172 the Italian palaeoherpetological fossil record with the extant Italian herpetofauna.
173 Within lizards, only the 36% of the diversity of extant Italian species has been
174 recognised in the fossil record (Delfino, 2004), which amounts to a loss of data of 64%.

175 Results are even worse when fossils of all European lizards and worm lizards are
176 considered, with an increase in the lost information of 10% (74% versus the above-
177 mentioned 64% in Italy). The same holds true for the percentage of recognisability of
178 extant lizards, which is 44% for Italian species (Delfino, 2004) and only 31% for
179 European ones. The trend of decreasing recognisability when going from higher to
180 lower taxonomic levels (Fig. 1) clearly shows that detailed osteological studies are
181 strongly needed at genus and species level. As far as lacertids are concerned, this issue

182 is exacerbated by the fact that they are the most speciose family of lizards in Europe (56
183 species out of 78, 72%) and that, among them, the sole genus *Podarcis* includes 21
184 species, which can currently not be distinguished based on osteology. Moreover, the
185 recognisability of *Podarcis* itself can be also questioned, because of the poor knowledge
186 of the osteology of other small-sized European lacertids that can be potentially confused
187 with it. Nonetheless, as will be shown below, detailed osteological study combined with
188 novel methodological approaches like specimen-level phylogenetic analysis appears to
189 be well suited to identify diagnostic combinations of osteological traits for lacertid
190 species. This promising result indicates that at least for lacertids, if not for all lizards,
191 the main issue decreasing recognisability may not be the lack of osteological traits in
192 their skeletons, but the lack of our current osteological knowledge. As for anguids, this
193 may hold true for the genus *Anguis* too, whose species have been mostly erected based
194 on molecular data (Gvoždík et al., 2010, 2013), and for which no comparative
195 osteological study has yet been published. Finally, despite not distinctly affecting the
196 recognisability of extant European lizards, the fact that both European agamids and
197 chamaeleonids can only be recognised at the family level will likely cause a loss in our
198 knowledge of the past diversity of these two groups because of the absence of characters
199 useful for distinguishing them from extant taxa that are currently extralimital, or from
200 other species that have become extinct in the meantime.

201 The degree of lost data about the palaeodiversity of non-snake squamates in
202 Europe, at least when extant taxa are considered, is therefore very high, and most
203 probably even higher considering that our estimation is made under the implied premise
204 of an equal probability of fossilization for all taxa. However, as already stated by
205 Delfino (2004), this is probably not true: some taxa (such as *Iberolacerta* spp.) live in
206 environments that complicate fossilization, such as high-altitude forests or areas with
207 acid soils, and nearly no sedimentation. Therefore, these species have lower

208 probabilities of being preserved in the fossil record. Moreover, some osteological
209 features of certain species (e.g., the scarce robustness of the bones of small gekkotans
210 and scincids) could prevent their preservation. It is also true that fossils are often
211 represented by isolated skeletal elements or incomplete specimens, missing the
212 necessary bones or bone features to identify them. Therefore, even if a species is
213 theoretically recognisable based on its osteology, taphonomic bias often prevents
214 identification of the fossils. Nonetheless, both in the Italian and the European fossil
215 record, most recognisable OTUs have been recovered as fossils (Tab. 1). This further
216 corroborates that the loss of diversity is not significantly due to an absence of remains
217 (i.e., taphonomic and collection biases may be less influent), but mainly due to the lack
218 of detailed knowledge of potentially diagnostic, osteological features.

219 Given that, it appears evident that an improvement of our knowledge of the
220 comparative osteology of lizards and worm lizards (but also of other reptiles and
221 amphibians) is crucial in order to increase our understanding of the past diversity of
222 these animals (as already pointed out by Bell and Mead, 2014). In particular, agamids,
223 chamaeleonids, lacertids, scincids and *Anguis* need further investigations. The paucity
224 of scholars interested in the comparative osteology of lizards in past times has surely
225 prevented us to have a better capability to recognise fossil representatives of these
226 animals, also because few researchers could not cover the whole extent of lizard
227 diversity. New studies dealing with the osteology of extant species will surely benefit
228 palaeontologists working with Pleistocene and Holocene fossils, which appear to be
229 mostly attributable to modern taxa, but they will have an impact on the study of older
230 fossils as well, because they will allow researchers to better recognise extinct forms and
231 their relationships. Moreover, a better knowledge of the comparative osteology of extant
232 species could also be useful for neoherpetologists to better understand the relationships
233 between them, adding to other information such as external morphology and molecular

234 data, as shown by our phylogenetic analysis. Finally, only apomorphy-based
235 identifications of fossil and sub-fossil material will allow to overcome the circular
236 reasoning in palaeobiogeographical reconstructions, which led to the flawed recognition
237 of herpetofaunal stability throughout the Pleistocene and Holocene of North American
238 taxa (Bell et al. 2010). We should therefore be cautious with referrals of European
239 Quaternary remains to extant taxa.

240 *The case of Lacerta*

241 Although the high variability within *Lacerta* species was confirmed by our phylogenetic
242 analysis, the second run of the phylogenetic analysis with the constrained searches
243 shows that specimen-level phylogeny can be a useful tool to identify diagnostic
244 combinations of osteological features for lizard species. Given that the vast majority of
245 specimens formed monophyletic clades with the other specimens of the same species,
246 the set of character states uniting these monophyletic clades can be interpreted to be a
247 diagnostic combination of osteological features of the respective species. It is important
248 to stress that most single features of these diagnostic combinations can be variable
249 within a clade, or shared with specimens of other species, so that they can rarely be
250 considered unique autapomorphies of a particular species. However, the combination of
251 all these osteological features is unique, and can be added to differential, morphological
252 diagnoses of the species. The single specimen of *L. viridis*, which was found within the
253 clade formed by the specimens of *L. bilineata*, is very incomplete, and does not preserve
254 cranial material. It is possible that the erroneous placement of this specimen is due to
255 that lack of cranial material, which is generally considered to be more diagnostic at
256 species level than postcranial bones. Also, *L. bilineata* has only relatively recently been
257 separated as distinct species from *L. viridis* (Rykena, 1991; Amann et al., 1997;
258 Marzahn et al., 2016), and no morphological characters have been reported to date to
259 distinguish the two species. Our results therefore appear to corroborate the general

260 assumption that cranial material is more readily identifiable to the species level than
261 postcranial bones. Finally, it is important to note that only a constrained search managed
262 to find the specimens of a single species in monophyletic clades. This result indicates
263 that in the case of *Lacerta*, osteological characters alone do not seem to be enough to
264 recover a reliable tree topology at the species level. Although the referral of the
265 specimens to a single species was successful in nearly all cases (actually all the
266 specimens that included cranial elements), the position of the *Lacerta* species as found
267 in our strict consensus tree might thus not represent true phylogenetic relationships.
268 More methodological work will be needed to address this discrepancy, but this would
269 be out of the scope of the present study. In any case, the current analysis highlights the
270 utility of specimen-level phylogeny to identify diagnostic combinations of osteological
271 features for lacertid species. It also shows that lizard skeletons bear taxonomically
272 significant features, and that detailed osteological studies are promising for the
273 recognition of diagnostic traits and finally for identifying lizard remains in the fossil
274 record.

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Table 1) Recognisability of European lizards and worm lizards and their presence in the fossil record.

Extant species	Recognisable OTU	Fossil record
<i>Laudakia stellio</i>	Agamidae indet.	Yes
<i>Chamaeleo chamaeleon</i>	Chamaeleonidae indet.	Yes
<i>Euleptes europaea</i>	<i>E. europaea</i>	No
<i>Hemidactylus turcicus</i>	<i>H. turcicus</i>	Yes
<i>Mediodactylus kotschy</i>	<i>M. kotschy</i>	No
<i>Tarentola mauritanica</i>	<i>T. mauritanica</i>	Yes
<i>Acanthodactylus erythrurus</i>	<i>A. erythrurus</i>	Yes
<i>Algyroides fitzingeri</i>	Lacertidae indet.	Yes
<i>Algyroides marchi</i>		
<i>Algyroides moreoticus</i>		
<i>Algyroides nigropunctatus</i>		
<i>Anatololacerta anatolica</i>		
<i>Anatololacerta pelasgiana</i>		
<i>Archaeolacerta bedriagae</i>		
<i>Dalmatolacerta oxycephala</i>		

Darevskia armeniaca

Darevskia lindholmi

Darevskia praticola

Darevskia saxicola

Dinarolacerta

montenegrina

Dinarolacerta

mosorensis

Hellenolacerta graeca

Iberolacerta aranica

Iberolacerta aurelioii

Iberolacerta bonnali

Iberolacerta cyreni

Iberolacerta galani

Iberolacerta horvathi

Iberolacerta

martinezricai

Iberolacerta monticola

Zootoca vivipara

Eremias arguta Eremiadini indet. Yes

Ophisops elegans

Lacerta agilis *L. agilis* Yes

Lacerta bilineata *L. bilineata* Yes

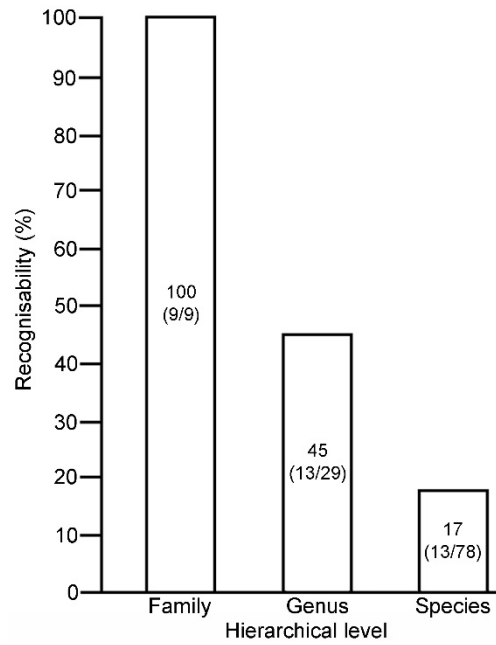
Lacerta viridis *L. viridis* Yes

Lacerta schreiberi *L. schreiberi* No

<i>Lacerta trilineata</i>	<i>L. trilineata</i>	Yes
<i>Podarcis bocagei</i>	<i>Podarcis</i> sp. (?)	Yes
<i>Podarcis carbonelli</i>		
<i>Podarcis cretensis</i>		
<i>Podarcis erhardii</i>		
<i>Podarcis filfolensis</i>		
<i>Podarcis gaigeae</i>		
<i>Podarcis hispanicus</i>		
<i>Podarcis levendis</i>		
<i>Podarcis lilfordi</i>		
<i>Podarcis liolepis</i>		
<i>Podarcis melisellensis</i>		
<i>Podarcis milensis</i>		
<i>Podarcis muralis</i>		
<i>Podarcis</i>		
<i>peloponnesiacus</i>		
<i>Podarcis pityusensis</i>		
<i>Podarcis raffonei</i>		
<i>Podarcis siculus</i>		
<i>Podarcis tauricus</i>		
<i>Podarcis tiliguerta</i>		
<i>Podarcis vaucheri</i>		
<i>Podarcis waglerianus</i>		
<i>Psammodromus algirus</i>	<i>Psammodromus</i> sp.	Yes

<i>Psammodromus</i>		
<i>hispanicus</i>		
<i>Timon lepidus</i>	<i>T. lepidus</i>	Yes
<i>Ablepharus kitaibelii</i>	Scincidae indet.	Yes
<i>Ophiomorus</i>		
<i>punctatissimus</i>		
<i>Trachylepis aurata</i>		
<i>Chalcides bedriagai</i>	<i>Chalcides</i> sp.	Yes
<i>Chalcides chalcides</i>		
<i>Chalcides striatus</i>		
<i>Chalcides ocellatus</i>	<i>C. ocellatus</i>	Yes
<i>Anguis cephalonica</i>	<i>Anguis</i> gr. <i>A.</i> <i>fragilis</i>	Yes
<i>Anguis colchica</i>		
<i>Anguis fragilis</i>		
<i>Anguis graeca</i>		
<i>Anguis veronensis</i>		
<i>Pseudopus apodus</i>	<i>P. apodus</i>	Yes
<i>Blanus cinereus</i>	<i>Blanus</i> sp. (Western Group)	Yes
<i>Blanus mariae</i>		
<i>Blanus strauchi</i>	<i>B. strauchi</i> complex	No
78	24 (31%)	20 (26%)

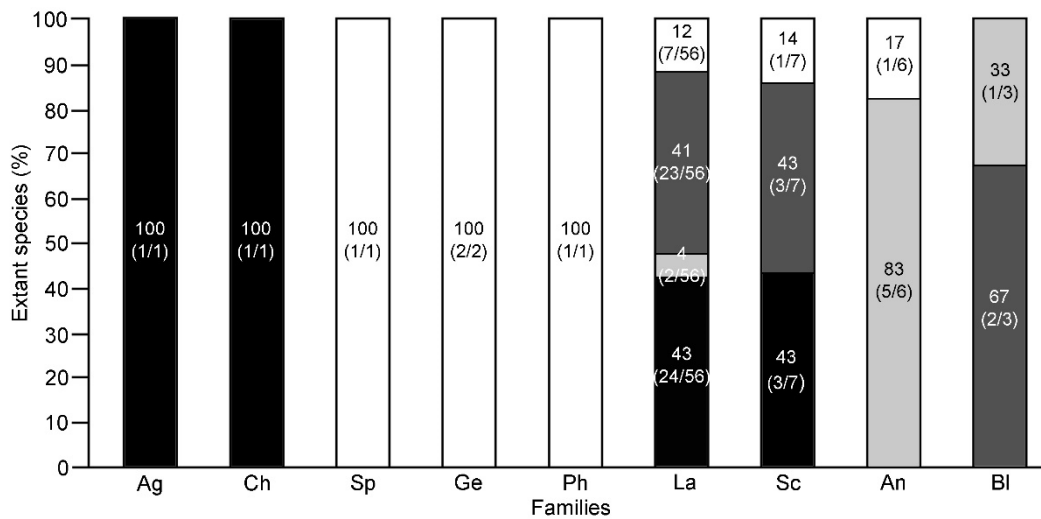
391 **Figure 1)** Recognisability of extant European lizards at family, genus and species
392 levels. Numbers inside the columns represent the exact percentage of recognisable taxa
393 and their number compared to the total number of family, genera and species
394 respectively (between parentheses).



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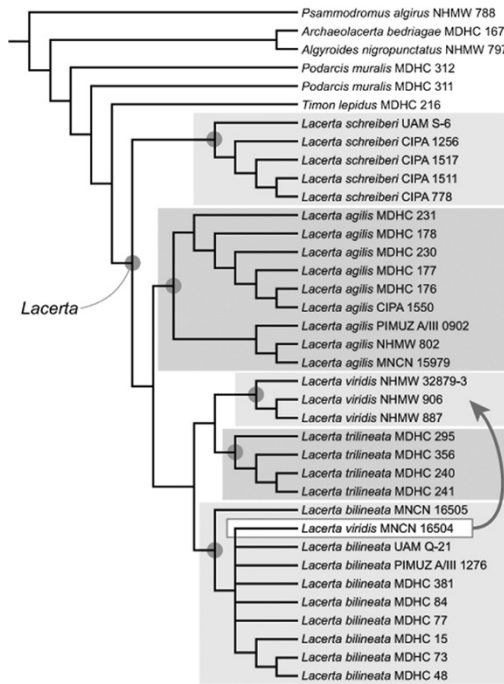
397 **Figure 2)** Hierarchical level of the recognisability in the different families of European
 398 lizards and worm lizards: percentage of extant species recognisable at family level is
 399 depicted in black, percentage at genus level in dark grey, percentage at species level in
 400 white, percentage at subfamily or species complex level in light grey. Numbers inside
 401 the columns represent the exact percentage of extant species recognisable at a specific
 402 level and their number compared to the total number of species included in the family
 403 (between parentheses). Abbreviations: Ag, Agamidae; Ch, Chamaeleonidae; Sp,
 404 Sphaerodactylidae; Ge, Gekkonidae; Ph, Phyllodactylidae; La, Lacertidae; Sc,
 405 Scincidae; An, Anguidae; Bl, Blanidae.



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408 **Figure 3)** Strict consensus tree of 9 MPTs resulting from a constrained search forcing
 409 all specimens of *Lacerta* into a monophyletic clade (as confirmed by phylogenetic
 410 studies based on molecular data). All but one specimen (*L. viridis* MNCN 16504,
 411 marked in white) were recovered in monophyletic clades together with the other
 412 members of their species (highlighted by the grey rectangles). The character states
 413 uniting these clades at their base (indicated by dark grey dots) can be interpreted as
 414 autapomorphic combination of osteological traits of the respective species, and used to
 415 identify fossil material. The questionable position of MNCN 16504 is probably due to
 416 the lack of cranial material (the specimen only preserves a partial vertebral column).

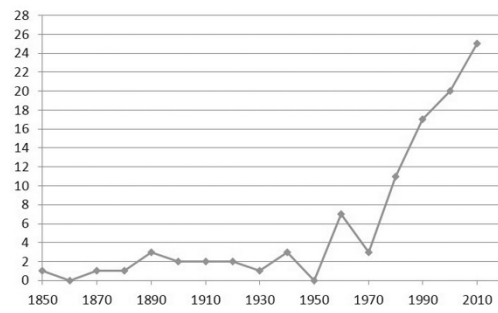


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419 **Figure 4)** Number of articles dealing with European lizard osteology per 10 years from
420 the 1850s to today.

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Osteology, fossil record and palaeodiversity of the European lizards

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Supplementary material

Supplementary text S1

List of studied specimens. The specimens marked with an asterisk were included in the phylogenetic analysis. Abbreviations: CIPA - Laboratório Arqueociências Lisboa, Portugal; HUI.OST - Osteological collection of the Hebrew University of Jerusalem, Israel; MCCI - Museo Civico di storia naturale di Carmagnola, Italy; MDHC - Massimo Delfino Herpetological Collection, Department of Earth Sciences, University of Torino, Italy; MNCN - Museo Nacional de Ciencias Naturales, Madrid, Spain; MNHN - Muséum national d'Histoire naturelle, Paris, France; NHMW - Naturhistorisches Museum Wien, Austria; PIMUZ - Paläontologisches Institut und Museum der Universität Zürich, Switzerland; UAM.R - Universidad Autónoma de Madrid (Reptiles), Spain; ZMS - Zoologische Staatssammlung München, Germany.

Laudakia stellio: MDHC 245; HUI.OST-Z-5, 423, 424.

Chamaeleo chamaeleon: MNHN 241, 1942-103, 2002-24, 1887-875; HUI.OST-Z-380, 425.

Euleptes europaea: MDHC 384, 388, 389.

Hemidactylus turcicus: MDHC 26, 238

Mediodactylus kotschy: MDHC 201, 285.

Tarentola mauritanica: MDHC 97, 98, 119, 194, 302.

Acanthodactylus erythrurus: UAM.R.AC VII; EBD 1266 (specimen from the collection of Salvador Bailon).

Algyroides fitzingeri: MDHC 351.

Algyroides moreoticus: MDHC 174.

Algyroides nigropunctatus: MDHC 171, 242, 243; NHMW 797*.

Archaeolacerta bedriagae: MDHC 167*; unnumbered specimen from the collection of Salvador Bailon.

Eremias arguta: MNHN 1944-168.

Iberolacerta bonnali: UAM.R.Lm28A.

Iberolacerta cyreni: UAM.R.Lm4.

Iberolacerta monticola: UAM.R.Lm77, Lm92.

Lacerta agilis: CIPA 1550*; MDHC 176*, 177*, 178*, 230*, 231*; MNCN 15979*; NHMW 802*; PIMUZ A/III 0902*.

Lacerta bilineata: MDHC 15*, 48*, 73*, 77*, 84*, 381*; MNCN 16505*; PIMUZ A/III 1276*; UAM.R.Q21*.

Lacerta schreiberi: CIPA 778*, 1256*, 1511*, 1517*; UAM.R.S-6*.

Lacerta trilineata: MDHC 240*, 241*, 295*, 356*.

Lacerta viridis: MNCN 16504*; NHMW 778*, 906*, 32879-3*.

Ophisops elegans: MDHC 281, 282; unnumbered specimen from the collection of Salvador Bailon.

Podarcis bocagei: UAM.R.PB48.

Podarcis filfolensis: MDHC 385.

Podarcis hispanicus: UAM.R.H30; two unnumbered specimens from the collection of Salvador Bailon.

Podarcis lilfordi: two unnumbered specimens from the collection of Salvador Bailon.

Podarcis melisellensis: MDHC 217, 218.

Podarcis muralis: MDHC 6, 65, 66, 72, 81, 89, 90, 222, 267, 311*, 312*, 313, 395, 413; MNHN 1992.192.

Podarcis siculus: MDHC 25, 91, 125, 229.

Podarcis tauricus: MDHC 244.

Podarcis tiliguerta: MDHC 153, 154.

Podarcis waglerianus: MDHC 390; MNHN 1992.189, 1992.190.

Psammodromus algirus: MNHN 1992.41; NHMW 788*; UAM.R.Ps9.

Timon lepidus: MDHC 216*; MNHN 1988.6629, 1991.4010, 1991.4242; unnumbered specimen stored in the Institut Català de Paleontologia Miquel Crusafont.

Zootoca vivipara: MDHC 179; UAM.R.Lv24.

Ablepharus kitaibelii: MDHC 239.

Chalcides bedriagai: unnumbered specimen from the collection of Salvador Bailon.

Chalcides chalcides: MDHC 94, 329, 398, 408.

Chalcides ocellatus: MDHC 193, 250; MNHN 1992.193; specimen number 28 from the collection of Salvador Bailon.

Chalcides striatus: MDHC 404; MNCN 16508; unnumbered specimen from the collection of Salvador Bailon.

Trachylepis aurata: MDHC 280; MNHN 1887-863.

Anguis gr. A. fragilis: MDHC 45, 49, 67, 102, 213, 221, 236, 237, 310, 367, 402.

Pseudopus apodus: MDHC 214, 215; MNHN 1918.95, 1992.199; PIMUZ A/III0975.

Blanus cinereus: MDHC 156; ZSM 175-1993-1, 175-1993-2, 227-1975, 548-2003, 652-0-1, 652-0-2, 653-0-1, 653-0-2.

Blanus mariae: ZSM 27-1988-1, 27-1988-2.

Blanus strauchi: MCCI R-1635, 1668; MDHC 93, 286, 287, 288.

Supplementary text S2

List of the published works dealing with the osteology of extant European lizards and worm lizards. The references marked with an asterisk provided useful information for the creation of the phylogenetic matrix.

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- *Barbadillo, L.J., Sanz, J.L. (1983): Análisis osteométrico de las regiones sacra y presacra de la columna vertebral en los Lagartos Ibéricos *Lacerta viridis* Laurenti, *Lacerta lepida* Daudin y *Lacerta schreiberi* Bedriaga. Amphibia-Reptilia **4**: 215-239.
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